

MORPHOLOGY, TAXONOMY, PHYLOGENY AND STRATIGRAPHIC RANGES OF SOUTH AFRICAN MIDDLE PERMIAN PAREIASAURS

by

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Dissertation

Submitted in fulfilment of the requirements for the degree

Doctor of Philosophy

in

Palaeontology

in the Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa

Co-supervisors:

Professor Bruce Rubidge

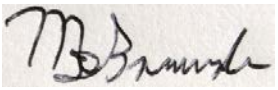
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March 2020

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg, South Africa. It has not been submitted before for any degree or examination in any other University.



On this 17th day of March 2020 in Johannesburg.

The financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the NRF.

ABSTRACT

The morphology, taxonomy, phylogeny and stratigraphic ranges of the basal pareiasaurs of the middle Permian of South Africa are revised.

The first detailed cranial description of *Nochelesaurus alexanderi* is produced, recognising the more distinctive cranial ornamentation, new dental features (non-symmetrical marginal cusp arrangements on both upper and lower jaw teeth, up to ten marginal cusps on lower jaw teeth, incipient horizontal cingulum and medially placed cusps). Updated cranial diagnoses are produced for *Embrithosaurus schwarzi*, the only taxon with wide maxillary teeth lacking an elongated, central, three cusped trident at the apex of the crown and possessing the largest cheek flange amongst the group of middle Permian pareiasaurs. *Bradysaurus baini* has one cranial autopomorphy in the large dorsomedially oriented posterior process of the distal paroccipital process of the opisthotic. A large maxillary boss and the ventromedially oriented upper jaw teeth are confirmed as important distinguishing characters.

The first detailed postcranial descriptions are produced for *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi* and an updated description for *Bradysaurus baini.* The three pelvic autopomorphies of *Embrithosaurus* are confirmed: anterior iliac blades flat and vertical/dorsoventral (not everted or upturned); iliac blades not parallel but diverge anteriorly, oriented 45-60^0 off the sagittal plane, and the very thick pelvic symphysis. *Bradysaurus baini* has one postcranial autapomorphy: osteoderms convex, without a central boss and with very smooth ornamentation.

Bradysaurus seeleyi is synonymised with *Bradysaurus baini*, reslting in three valid middle Permian pareiasaur taxa: *Bradysaurus baini, Embrithosaurus schwarzi* and *Nochelesaurus alexanderi.* A rigorous cladistic analysis of middle Permian pareiasaurs recovers the three basal South African forms as a monophyletic group for the first time, named the Bradysauria, supported by six

synapomorphies, indicating a first pulse of pareiasaurian evolution restricted to the South African Karoo. *Nochelesaurus* and *Bradysaurus* are sister taxa and *Embrithosaurus* is the most basal member of the group.

The Bradysauria are stratigraphically restricted to the Abrahamskraal Formation of the Beaufort Group. *Bradysaurus baini* is first to appear, in the Koornplaats Member, followed by *Nochelesaurus* in the Swaerskraal Member and by *Embrithosaurus* in the Moordenaars Member. All three taxa terminate at a similar stratigraphic level in the Karelskraal Member at the top of the Abrahamskraal Formation. The fact that *Embrithosaurus* is phylogenetically the most basal genus, suggests a long ghost linage for the genus.

ACKNOWLEDGEMENTS

In 2012, I spent my Saturday mornings attending a volunteer osteology course given by Doctor Christine Steininger at the University of the Witwatersrand. Thanks to her influence, I enjoyed the course so much that I decided to pursue studies in Palaeontology in 2013.

My PhD supervisors, Professor Bruce Rubidge, Professor Fernando Abdala and Doctor Julien Benoit must be acknowledged for the countless meetings, discussions and project reviews held over 2017-2019 and their time spent on guidance, feedback, suggestions and comments, which went far beyond what should be expected.

Fellow pareiasaurian workers and authors Michael Soon Yoong Lee, Michael Benton, Nour-Eddine Jalil, Juan Carlos Cisneros, Andrey Sennikov, Elena Boyarinova and Linda Tsuji are sincerely thanked for their friendly and accommodating discussions and interactions.

This project has involved travel to institutions and museums on three continents. For access to the material I thank: Billy de Klerk and Rose Prevec (AM); Carl Mehling and Mark Norell (AMNH); Ellen de Kock, Johann Neveling, and Nonhlanhla Mchunu (CGP); Bernhard Zipfel and Sifelani Jirah (ESI); Bill Simpson and Kenneth Angielczyk (FMNH); Sandra Chapman, Michael Day and Paul Barrett (NHMUK); Valeriy V Bulanov, Valeriy K Golubev and Andrey Sennikov (PIN); Zaituna Skosan, Roger Smith and Claire Browning (SAM); Heidi Fourie (TM); Tom White (UMZC); and Rochelle Vlok (VW).

The research trips to New York (AMNH) and Chicago (FMNH) would not have been possible were it not for accommodation provided by Dylan Kammerer (brother of Christian Kammerer) in Brooklyn, New York and Kenneth Angielczyk and his family in Chicago. I will not forget Viktor Radermacher's company in New York. My parents Naomi and John Van den Brandt (SAM-Cape Town), my sister Tanya Van den Brandt, my brother –in-law Peter van't Hoogerhuys (NHMUK-

London) and their canine Tandi, kindly hosted me during multiple research trips to their cities and I am deeply indebted to Zaituna Skosan for daily local transport in Cape Town over several weeks.

This project was only made possible by the financial support provided by a Centre of Excellence in Palaeosciences (CoE-Pal) PhD “Top up” Bursary (2017, 2018, 2019), the National Research Foundation (NRF) Special-Block Bursary at the University of the Witwatersrand (2017, 2018, 2019), the Paleontological Scientific Trust (PAST) postgraduate degree support bursary (2017), the African Origins Programme (AOP-NRF) under Bruce Rubidge (2017, 2018), and the University of the Witwatersrand’s Postgraduate Merit Awards (2017, 2018, 2019). The research trip to the American Museum of Natural History in New York was made possible through a PAST conference/research trip grant (2018) and a Knowledge, Interchange, Collaboraiton (NRF-KIC) grant under under Bruce Rubidge. The research trip to the Paleontological Institute of the Russian Academy of Sciences (PIN) in Moscow, was made possible through the support of the Bi-national Cooperation project between South Africa (NRF to Fernando Abdala) and Russia (Russian Foundation for Basic Research to Andrey Sennikov). The support of the DST-NRF Centre of Excellence in Palaeosciences (CoE-Pal) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the CoE.

The Evolutionary Studies Institute at the University of the Witwatersrand is a special place to spend time and creates meaningful relationships between palaeontological friends, students and colleagues and I must thank Ashley Kruger, Natasha Barbolini, Cameron Penn-Clarke, Viktor Radermacher, Fredrick Tolchard, David Groenewald, Kevin Rey, and Alienor Duhamel for their friendship. Dr Mike Day is thanked for the use of his stratigraphic range data for the deposits from farm localities of the South Western Karoo. David Groenewald is thanked for help with the software Global Mapper version 15.

Additional preparation of the holotypes of *Embrithosaurus schwarzi* (SAM-PK-8034) and *Nochelesaurus alexanderi* (SAM-PK-6239) was performed by Gilbert Mokgethoa and Charlton Dube (ESI).

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1. CHAPTER ONE: INTRODUCTION AND LITERATURE REVIEW

1.1 Background: Parareptiles

Pareiasaurs were a group of relatively abundant armoured, predominantly medium- to large-sized herbivorous parareptiles with a world-wide distribution, that flourished exclusively in the middle to late Permian (Boonstra 1969, Lee 1993, 1994, 1997a, 1997b). All members of the group possess leaf-shaped (labio-lingually flattened) teeth specialised for herbivory, with five or more small cusps on the edges of the crowns (Lee 1993, 1994, 1997a, 1997b). The group is also characterised by dermal armour consisting of osteoderms; cranial ornamentation typically comprising bosses, pits and rugose ridges on the skull, an expanded quadratojugal bone that produces a unique "cheek" flange on the side of the skull; and a prominent boss on the ventral surface of the angular bone of the lower jaw (Owen 1876, Seeley 1888, 1892).

Pareiasaurs are classified within the monophyletic clade of Parareptilia, a group of basal amniotes which bear no living representatives (Tsuji and Muller 2009). Members of Parareptilia are united through the presence of six autapomorphies, and include diverse groups such as the "nycteroleters", pareiasaurs, procolophonids, bolosaurids and lanthanosuchids (Tsuji and Muller 2009). Several of these parareptilian groups have recently been the subject of renewed taxonomic revisions, which have included re-descriptions of existing taxa or descriptions of new taxa and have also included updated phylogenetic analysis, e.g. procolophonids (Cisneros 2008), pareiasaurs (Lee 1994, 1997a, 1997b, Jalil and Janvier 2005), and "nycteroleters" (Muller and Tsuji 2007). This work allowed Tsuji and Muller (2009) to compile the most recent updated phylogeny of the parareptiles, wherein they confirmed the pareiasaurs as sister taxon to the "nycteroleters" (Fig. 1.1). Pareiasaurs are contained within the Ankyramorpha, with its members primarily united by an "anchor-shaped" interclavicle (Tsuji and Muller 2009, Fig. 1.1).

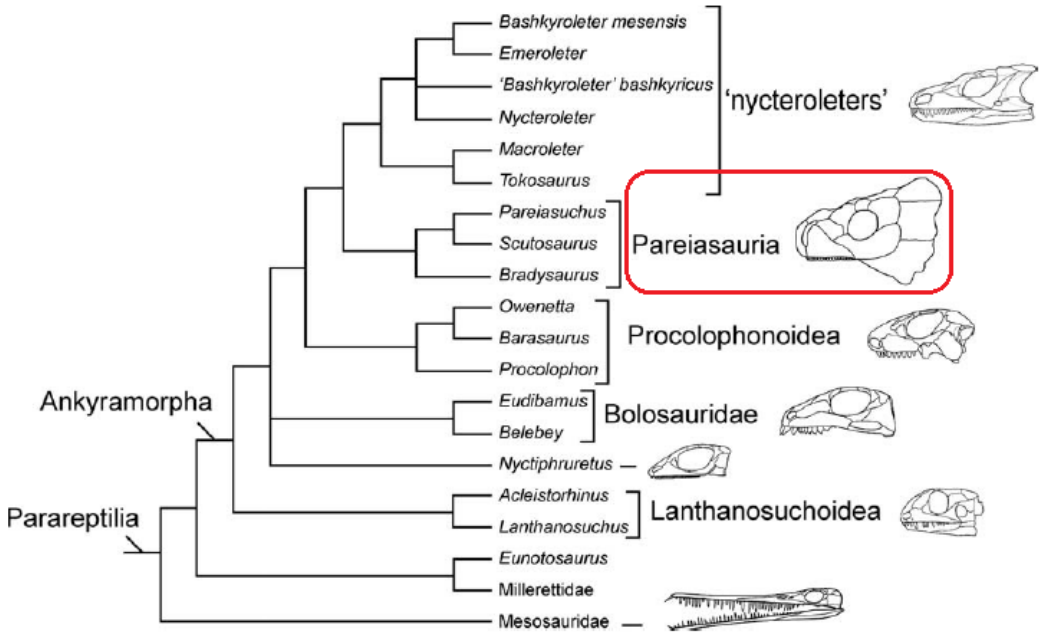


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1.2 Background: Pareiasaurs

The first pareiasaur described was *Parasaurus geinitzi* (von Meyer 1857), but was not recognised as pareiasaurian for nearly 100 years until 1956 when von Huene (1956) assigned the taxon to the Pareiasauria. Using two holotype specimens and new referred material, Tsuji and Muller (2008) and Tsuji (2010) recently completed a detailed re-description of *Parasaurus geinitzi* and confirmed the species as a valid member of the Pareiasauria.

Owen (1876) named the group ”pareiasaur” (meaning cheek-lizard), after the “depth and breadth of the zygomatic arch” (Owen 1876:7), a reference to the ventrolaterally expanded quadratojugal bone on the side of the skull that creates the characteristic pareiasaurian “cheek flange”. In the same publication, Owen (1876) described the first species assigned to the Pareiasauria, *Pareiasaurus serridens*, for a specimen popularly called the “Blinkwater Monster”, found near Blinkwater, in the Eastern Cape Province of South Africa. Thereafter, the overwhelming majority of pareiasaur material described came primarily from

South Africa and secondly from Russia in the late 1800's and early 1900's (e.g. Seeley 1888, 1892, Broom 1912, 1913, 1914, 1924, Haughton 1913, Broom and Haughton 1913, Watson 1914a, 1914b, Boonstra 1932a, Amalitzky 1922, Hartmann-Weinberg 1933, 1937) with Scotland yielding one specimen from this time (Newton 1893). More recently, several new species have been described from Zambia (Lee *et al.* 1997), Tanzania (Maisch and Matzke, 2019), Niger (Sidor *et al.* 2003, Tsuji *et al.* 2013, Turner *et al.* 2015), Morocco (Jalil and Janvier 2005), Brazil (Araujo 1985, Cisneros *et al.* 2005), China (Young 1979, Li *et al.* 2008, Xu *et al.* 2015, Benton 2016, Liu and Bever 2018) and Russia (Bulanov and Yashina 2005).

In the *Tapinocephalus* Assemblage Zone (AZ) of the Beaufort Group of the South African Karoo Supergroup pareiasaurs are relatively abundant, comprising approximately 25% of all vertebrate fauna (Boonstra 1969, Smith and Keyser 1995a, Nicolas 2007, Van der Walt 2011, Smith *et al.* 2012, Day 2013). All phylogenetic analyses performed on the Pareiasauria have shown that the pareiasaurs from the *Tapinocephalus* AZ of South Africa are the most basal genera strongly implying a Gondwanan origin for the entire group (Fig. 1.2) (Lee 1994, 1997a, 1997b, Jalil and Janvier 2005, Tsuji 2010, Tsuji *et al.* 2013, Turner *et al.* 2015, Benton 2016, Liu and Bever 2018).

The South African pareiasaurs include representatives of three different morphotypes, distributed in two distinct stratigraphic ranges:

1) In the middle Permian *Tapinocephalus* AZ (Boonstra 1932a, Lee 1997a, Smith and Keyser 1995a) only large basal pareiasaurs from three genera have been found and show restricted dermal armour comprising a narrow band of isolated osteoderms above the vertebral column: *Bradysaurus*, *Nochelesaurus*, and *Embrithosaurus* (Watson 1914b, Boonstra 1934b, 1935, Lee 1994, 1997a, Scheyer and Sander 2009, Canoville and Chinsamy 2017). These taxa become extinct at the top of the Abrahamskraal Formation of the Beaufort Group (Day

2013, Nicolas 2007) which Day (2013, and Day *et al.* 2015) has correlated with the end-Guadalupian extinction event.

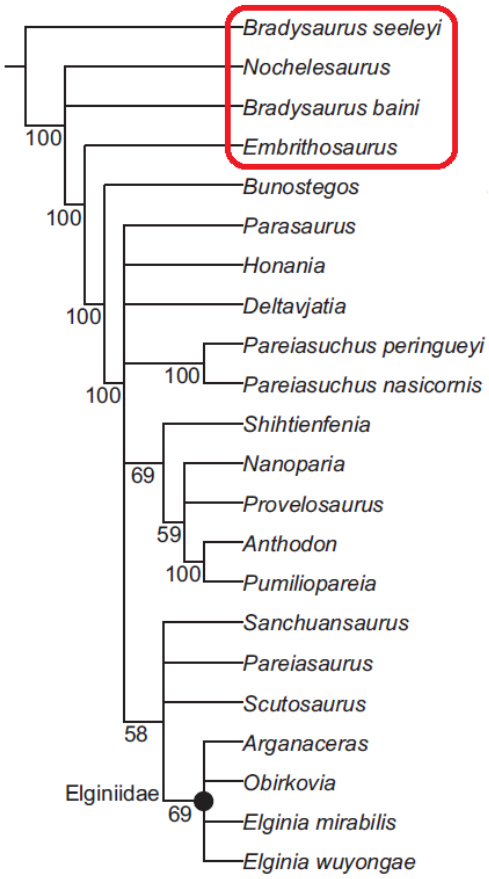


Figure 1.2: Most recent phylogenetic relationships of pareiasaurians. Majority rule consensus tree of 2695 most parsimonious trees (taken from Liu and Bever 2018:9: Fig. 5A) and modified by outlining the four species from the *Tapinocephalus* AZ in a red box. The numbers indicate the frequency of clades in the fundamental trees. The most basal pareiasaurs are known only from the middle Permian *Tapinocephalus* Assemblage Zone of South Africa and are represented by four species (red box): *Bradysaurus seeleyi*, *Nochelesaurus alexanderi*, *B. baini* and *Embrithosaurus schwarzi.*

2) In the late Permian *Tropidostoma, Cistecephalus* and *Daptocephalus* Assemblage Zones (Smith and Keyser 1995c, 1995d, Kitching 1995) are more derived medium- to large-sized pareiasaurs which have isolated osteoderms covering the entire body (*Pareiasaurus* and *Pareiasuchus*), and derived dwarf pareiasaurs with united osteoderms forming a carapace over the entire body (*Nanopareia*, *Anthodon* and *Pumiliopareia*) (Watson 1914b, Boonstra 1934b, Findlay 1970, Lee 1997a, Scheyer and Sander 2009, Canoville and Chinsamy

2017). These taxa become extinct at the Permo-Triassic boundary (Lee 1997a, Nicolas 2007).

The basal pareiasaurs appear abruptly in the fossil record in the middle Permian of South Africa, with species exhibiting all the characteristic pareiasaurian traits at their first occurrence (Seeley 1888, 1892, Watson 1914b, Haughton and Boonstra 1929a, Boonstra 1934a). The group must therefore have a long history beginning in the early Permian or even the late Carboniferous (Boonstra 1932a) but little evidence of clear ancestor candidate fossils have been found. The clade achieved a high level of diversity and a world-wide distribution by the late Permian, before their ultimate demise at the Permo-Triassic boundary. The basal South African forms are therefore crucial to understanding the origin and subsequent diversification of the group.

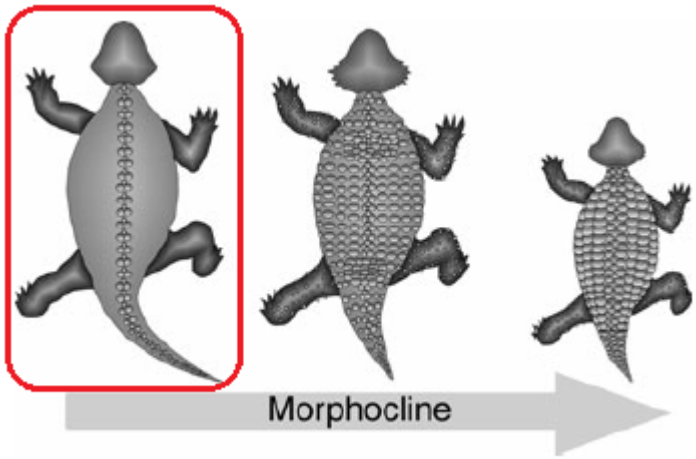


Figure 1.3: Three pareiasaurian shape models (morphotypes) illustrating the pareiasaur morphocline from left to right: 1) larger, sparsely armoured forms, to 2) medium to large forms with more coverage, to 3) smaller, very heavily armoured dwarf pareiasaurs. The dermal coverage of the tail is speculative in the dwarf pareiasaur (figure taken from Scheyer and Sander (2009), not to scale, and modified here by outlining the large, sparsely armoured morphocline of the *Tapinocephalus* AZ pareiasaurs in a red box).

1.3 Brief taxonomic history of *Tapinocephalus* AZ pareiasaurs

Van den Brandt (2016) produced a detailed review of the taxonomic history of the South African middle Permian pareiasaurs and thus only a brief summary is presented here.

The discovery of large numbers of pareiasaurian specimens in the late 1800's and early 1900's in South Africa led to the naming of several new taxa by early workers (Owen 1876, Seeley 1888, Seeley 1892, Broom 1912, 1913, 1914, 1924, Haughton 1913, Broom and Haughton 1913). In the late 1800's South African fossils were sent to London, where they were curated and described. These initial descriptions were often based on fragmentary material, such as NHMUK R1714/43525, the holotype of *Pareiasaurus bombidens* Owen 1876. Most later workers ignored or rejected this taxon, considering the specimen as indeterminate (Watson 1914b, Haughton and Boonstra 1929a, Boonstra 1934a, Lee 1994, 1997a, Van den Brandt 2016). Some of the first described specimens were lost (e.g. Owen 1876, NHMUK R4063/R1710/R1710a, holotype skull of *Pareiasaurus serridens*) or mistakenly referred to other taxa (e.g. Owen 1856, 1862, NHMUK R4063/R1710/R1710a referred to *Dicynodon tigriceps*). Additionally, these early descriptions were often very brief and included short, ambiguous diagnoses, causing much initial taxonomic confusion and disagreement amongst workers.

Well aware of the taxonomic disorder and confusion existing at the time, Watson (1914b) re-classified the Pareiasauria in a brief, but very important paper. He carefully re-examined museum catalogues, reassigned incorrectly referred specimens, and re-evaluated holotypes held at the Natural History Museum, London. Watson (1914b), who focused mostly on postcrania, was the first to distinguish the South African pareiasaurs into the large, basal, sparsely armoured representatives from the *Tapinocephalus* AZ (*Bradysaurus* and *Embrithosaurus*), and the small- and medium-sized, more derived, extensively armoured members of the later *Cistecephalus* AZ (*Pareiasaurus*, *Propappus*, and *Anthodon*). Watson (1914b) recognised two genera in the *Tapinocephalus* AZ; *Bradysaurus* and *Embrithosaurus* and applied the name *Pareiasaurus* to one species from the overlying *Cisticephalus* AZ.

Table 1.1 (A) Descriptive Papers								
Owen 1876	**Seeley 1888**	**Seeley 1892**	**Broom 1903**	**Broom 1912**	**Broom 1913**	**Broom 1914**	**Broom 1924**	
Pareiasaurus serridens (Owen 1876) NHMUK R4063/R1710			*Pareiasaurus serridens* (Owen 1876) SAM-PK-8034					→
Pareiasaurus bombidens (Owen 1876) NHMUK R1714/43525								→
	Pareiasaurus bombidens (Seeley 1888) NHMUK 49426							→
		Pareiasaurus baini (Seeley 1892) NHMUK R1971						→
				Propappus rogersi (Broom 1912) SAM-PK-8953 postcrania				→
					Pareiasaurus acutirostris (Broom 1913) AM 3748			→
						Pareiasaurus whaitsi (Broom 1914) AMNH 5567		→
							Pareiasaurus strubeni (Broom 1924)	→

Table 1.1 (A): Descriptive papers. Each row represents an important historic holotype or referred specimen, and the eight columns show the identification and species assigned by each original descriptive author. Arrows in the right column align with the relevant rows in Table 1.1 (B), which shows the identifications of each specimen in subsequent taxonomic papers.

	Table 1.1 (B) Taxonomic revisions of middle Permian South African pareiasaurs and the changes proposed in this study								
	Watson 1914	**Haughton & Boonstra 1929**	**Boonstra 1934**	**Broom 1935**	**Boonstra 1969**	**Kuhn 1969**	**Lee 1995, 1997a**	**Van den Brandt 2016**	**This Study**
→	*Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034	*Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034	*Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034	*Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034	*Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034	*Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034	*Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034	*Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034	*Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034
→	NHMUK R1714/43525 indeterminant	NHMUK R1714/43525 indeterminant	NHMUK R1714/43525 indeterminant	*Bradysaurus bombidens* (Owen 1876) NHMUK R1714/43525		*Bradysaurus bombidens* (Owen 1876) NHMUK R1714/43525	NHMUK R1714/43525 indeterminant	NHMUK R1714/43525 indeterminant	NHMUK R1714/43525 indeterminant
→		*Bradysaurus seeleyi* (Haughton & Boonstra 1929) NHMUK 49426	*Bradysaurus seeleyi* (Haughton & Boonstra 1929) NHMUK 49426	*Bradysaurus bombidens (Owen 1876) NHMUK 49426*	*Bradysaurus seeleyi* (Haughton & Boonstra 1929) NHMUK 49426	*Bradysaurus seeleyi* (Haughton & Boonstra 1929) NHMUK 49426	*Bradysaurus seeleyi* (Haughton & Boonstra 1929) NHMUK 49426	*Bradysaurus seeleyi* (Haughton & Boonstra 1929) NHMUK 49426	*Bradysaurus baini* (Seeley 1892) NHMUK 49426
→	*Bradysaurus baini* (Seeley 1892) NHMUK R1971	*Bradysaurus baini* (Seeley 1892) NHMUK R1971	*Bradysaurus baini* (Seeley 1892) NHMUK R1971	*Bradysaurus baini* (Seeley 1892) NHMUK R1971	*Bradysaurus baini* (Seeley 1892) NHMUK R1971	*Bradysaurus baini* (Seeley 1892) NHMUK R1971	*Bradysaurus baini* (Seeley 1892) NHMUK R1971	*Bradysaurus baini* (Seeley 1892) NHMUK R1971	*Bradysaurus baini* (Seeley 1892) NHMUK R1971
→		*Brachypareia rogersi* (Broom 1912) SAM-PK-5012 Neotype skull	*Brachypareia rogersi* (Broom 1912) SAM-PK-5012 Neotype skull		indeterminant juveniles	*Bradysaurus rogersi* (Broom 1912) SAM-PK-5012 Neotype skull	*Bradysaurus seeleyi* SAM-PK-5012 skull, SAM-PK-8953 postcrania Pareiasaurus serridens	*Bradysaurus seeleyi* SAM-PK-5012 skull	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-5012
→		*Koalemasaurus acutirostris* (Broom 1913) AM 3748	*Koalemasaurus acutirostris* (Broom 1913) AM 3748	*Bradysaurus acutirostris* (Broom 1913) AM 3748		*Bradysaurus acutirostris* (Broom 1913) AM 3748	AM 3748 indeterminant		*Bradysaurus baini* (Seeley 1892) AM 3748
→		*Bradysuchus whaitsi* (Broom 1914) AMNH 5567	*Bradysuchus whaitsi* (Broom 1914) AMNH 5567	*Bradysaurus whaitsi* (Broom 1914) AMNH 5567	*Bradysaurus* AMNH 5567	*Bradysaurus whaitsi* (Broom 1914) AMNH 5567	*Bradysaurus* AMNH 5567		*Embrithosaurus schwarzi* (Watson 1914) AMNH FARB 5567
→		*Nochelesaurus strubeni* (Broom 1924)	*Nochelesaurus strubeni* (Broom 1924)	*Bradysaurus strubeni* (Broom 1924)	*Bradysaurus strubeni* (Broom 1924)	*Embrithosaurus strubeni* (Broom 1924)	indeterminant		indeterminant
		Bradysaurus vanderbyli (Haughton & Boonstra 1929) SAM-PK-3718	*Bradysaurus vanderbyli* (Haughton & Boonstra 1929) SAM-PK-3718			*Bradysaurus vanderbyli* (Haughton & Boonstra 1929) SAM-PK-3718	*Bradysaurus seeleyi* (Haughton & Boonstra 1929) SAM-PK-3718	*Bradysaurus seeleyi* (Haughton & Boonstra 1929) SAM-PK-3718	*Bradysaurus baini* (Seeley 1892) SAM-PK-3718
		Platyoropha broomi (Haughton & Boonstra 1929) SAM-PK-5002	*Bradysaurus baini* (Seeley 1892) SAM-PK-5002		*Bradysaurus baini* (Seeley 1892) SAM-PK-5002	*Bradysaurus broomi* (Haughton & Boonstra 1929) SAM-PK-5002	*Bradysaurus baini* (Haughton & Boonstra 1929) SAM-PK-5002	*Bradysaurus baini* (Haughton & Boonstra 1929) SAM-PK-5002	*Bradysaurus baini* (Seeley 1892) SAM-PK-5002
		Nochelesaurus alexanderi (Haughton & Boonstra 1929) SAM-PK-6239	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6239			*Embrithosaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6239	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6239	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6239	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6239
		Dolichopareia angusta (Haughton & Boonstra 1929) SAM-PK-6238	*Dolichopareia angusta* (Haughton & Boonstra 1929) SAM-PK-6238		*Bradysaurus angusta* (Haughton & Boonstra 1929) SAM-PK-6238	*Embrithosaurus angusta* (Haughton & Boonstra 1929) SAM-PK-6238	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6238	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6238	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6238
		Brachypareia watsoni (Haughton & Boonstra 1929) SAM-PK-6240	*Brachypareia watsoni* (Haughton & Boonstra 1929) SAM-PK-6240		indeterminant juvenile	*Bradysaurus watsoni* (Haughton & Boonstra 1929) SAM-PK-6240	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6240	*Nochelesaurus alexanderi* (Haughton & Boonstra 1929) SAM-PK-6240	*Nochelesaurus alexanderi (Haughton & Boonstra 1929)* SAM-PK-6240

Table 1.1 (B): Taxonomic revisions of middle Permian South African pareiasaurs and the changes proposed in this study. Each row represents a different important holotype specimen, and shows the identification assigned by each author. Arrows in the left column align with the relevant rows in Table 1.1 (A).

Broom (1916) disagreed with Watson's (1914b) new generic names for pareiasaurs from the *Tapinocephalus* AZ and continued to name new species of *Pareiasaurus* based on new specimens recovered from this biozone. Between 1912 and 1924, Broom named and described four new species from the *Tapinocephalus* AZ (*Propappus rogersi* Broom 1912, *Pareiasaurus acutirostris* Broom 1913, *Pareiasaurus whaitsi* Broom 1914 and *Pareiasaurus strubeni* Broom 1924).

The next major revision was by Haughton and Boonstra between 1929 and 1934 in their eleven-part "pareiasaurian studies" series of papers, which included two taxonomic reassessment papers based on cranial characteristics.

In their first, brief, taxonomic paper, Haughton and Boonstra (1929a) noted very brief diagnostic features. They focused primarily on dentition, separating the pareiasaurs into three primary divisions by the number of cusps on their teeth. Secondarily, considering the ratio of the width between the orbits relative to the width between the tabulars (posterior corners of the skull). They further subdivided the taxa into three secondary subdivisions. This created, by their own admission, a somewhat compromised classification scheme. For the *Tapinocephalus* Assemblage Zone they retained the two genera recognised by Watson (*Bradysaurus* and *Embrithosaurus*), added two further species of *Bradysaurus* (*B. seeleyi* and *B. vanderbyli*), named four new species based on new material (*Dolichopareia angusta, Platyoropha broomi, Nochelesaurus alexanderi* and *Brachypareia watsoni*) and reassigned the four taxa named by Broom between 1912 and 1924: *Propappus rogersi* to *Brachypareia rogersi, Pareiasaurus whaitsi* to *Bradysuchus whaitsi, Pareiasaurus strubeni* to *Nochelesaurus strubeni,* and *Pareiasaurus acutirostris* to *Koalemasaurus acutirostris*). Thus Haughton and Boonstra (1929a) recognised eight genera and twelve species from the *Tapinocephalus* Assemblage Zone.

Boonstra (1934a) considered *Platyoropha broomi* a junior synonym for *Bradysaurus baini* and so retained seven genera and eleven species recognised

by Haughton and Boonstra (1929a). In this comprehensive and lengthy paper, Boonstra (1934a) produced a detailed cranial description for a generalised pareiasaurian skull, including comprehensive accounts of all individual cranial elements. He added significantly more detailed diagnostic cranial features to each species, and comprehensively, although roughly, illustrated all individual species in all major cranial views. However, he did not include separate cranial descriptions for individual species and his updated species level diagnoses included many shared features across many taxa (Lee 1994, 1997a, Van den Brandt 2016).

These two landmark contributions of Haughton and Boonstra (1929a), and Boonstra (1934a) resulted in a plethora of new pareiasaurian taxa with few unambiguous diagnostic or clearly identifiable features to separate taxa.

Broom (1935) produced a short summary classification in which he briefly discussed the history of the important pareiasaurian specimens discovered and described. By now he had come to accept the two genera named by Watson (1914b) for specimens from the *Tapinocephalus* AZ. He reduced the number of taxa recognised by Haughton and Boonstra (1929a), and Boonstra (1934a) by recognising only five species of *Bradysaurus* (*B. baini, B. acutirostris, B. whaitsi, B. strubeni* and *B. bombidens*) and *Embrithosaurus schwarzi.*

Boonstra (1969) briefly reviewed the Pareiasauridae from the *Tapinocephalus* AZ. Similar to Broom (1935), Boonstra lumped all species with fewer than nine cusps on their teeth into *Bradysaurus* (recognising four species: *B. baini, B. seeleyi, B. strubeni* and *B. angusta*) and also recognised *Embrithosaurus schwarzi* with nine cusps on its teeth. He removed several species that he had mistakenly considered valid in his earlier assessment (Boonstra 1934a) as they were either based on immature specimens (*Brachypareia*) or pathological features (*Bradysuchus*).

Kuhn (1969) likewise considered all basal South African taxa as either *Bradysaurus* (for those with fewer than nine cusps per tooth) or *Embrithosaurus*

(for those with nine cusps per tooth). He considered as valid the full set of twelve species originally diagnosed by Haughton and Boonstra (1929a) and resurrected *B. bombidens* which had been rejected by all previous workers except for Broom (1935), resulting in thirteen recognised species. Thus he recognised nine species of *Bradysaurus* (*B. baini, B. bombidens, B. vanderbyli, B. seeleyi, B. whaitsi, B. acutirostris, B. watsoni, B. rogersi,* and *B. broomi*) and four species of *Embrithosaurus* (*E. schwarzi, E. strubeni, E. alexanderi*, and *E. angusta*).

In a PhD designed to resolve the historic taxonomic confusion and reduce the inflated number of species in the Pareiasauridae, Lee (1994, 1997a) performed an alpha taxonomic reassessment of all pareiasaur species around the world. Through a detailed study of all holotypes, he reduced the number of valid species from 49 to 17 with extraordinary aplomb. In the *Tapinocephalus* AZ, Lee considered only four of the original twelve species recognised by Haughton and Boonstra (1929a) to be valid, namely: *Bradysaurus seeleyi, B. baini*, *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi.* Amended diagnoses for each valid taxon were produced by Lee and he also designed, defined and presented the first phylogenetic analysis for the Pareiasauridae (Lee 1994, 1997a, 1997b).

Most recently, Van den Brandt (2016), in his detailed descriptive study of the crania of *Embrithosaurus schwarzi,* conducted a taxonomic reassessment of the *Tapinocephalus* AZ pareiasaurs. He studied the holotype crania of nine of the original twelve species recognised by Haughton and Boonstra (1929a) and confirmed the validity of the four members of the group put forward by Lee (1994, 1997a). Van den Brandt (2016) updated the cranial diagnoses of each valid taxon, and concluded that *Bradysaurus seeleyi* is the least secure member of the group due to its lack of cranial autapomorphies. Van den Brandt's (2016) taxonomic review was limited by the fact that he studied only crania and did not produce an updated phylogenetic analysis.

1.4 Recent pareiasaurian anatomical work

Since Lee's important alpha-taxonomic reassessment (Lee 1994, 1997a) the group has received renewed attention as researchers have worked within the simplified taxonomic structure that he established. Lee provided updated detailed cranial re-descriptions for *Scutosaurus karpinskii* (Lee 1994) and *Pareiasuchus nasicornis* (Lee *et al.* 1997). Modern detailed re-descriptions and diagnoses have also recently been produced for *Parasaurus geinitzi***,** cranial and postcranial (Tsuji and Muller 2008, Tsuji 2010), *Deltavjatia vjakensis*, cranial and postcranial (Tsuji 2010, Tsuji 2013) and *Embrithosaurus schwarzi* cranial only (Van den Brandt 2016, Van den Brandt *et al.* 2019).

In recent years, several new species have been discovered and described in detail: *Bunostegos akokanensis***,** cranially (Sidor *et al.* 2003, Tsuji *et al.* 2013, Turner *et al.* 2015); *Obirkovia gladiator*, cranially and postcranially (Bulanov and Yashina 2005); *Arganaceras vacanti,* cranially (Jalil and Janvier 2005); and most recently *Elginia wuyongae*, cranially and postcranially (Liu and Bever 2018). Jalil and Janvier (2005) also described the postcrania of two new but unnamed forms.

Xu *et al.* (2015) re-established *Honania complicidentata* (previously removed by Lee 1994, 1997a) based on a re-examination of existing material and the discovery of new material and produced a detailed cranial and postcranial description. Benton (2016) synonymized three Chinese genera (*Shihtienfenia*, *Shansisaurus* and *Huanghesaurus*) into *Shihtienfenia permica* based on re-examination of the holotypes and referred material and produced an updated detailed cranial and postcranial description for this taxon. Finally, Maisch and Matzke (2019) tentatively re-established *Pareiasaurus* (?) *haughtoni* (previously removed by Lee (1994, 1997a) based on a re-examination of existing material, after very distinctive osteodermal armour.

The result is that of the current recognised pareiasaurian species (Figure 1.2), less than half of all taxa described, have recently updated descriptions.

1.5 Stratigraphic ranges of *Tapinocephalus* AZ pareiasaurs

Pareiasaurs form a large and important component of the middle and late Permian tetrapod fossil record of South Africa where the most diverse record of pareiasaur species occurs. Eleven of the currently recognised 23 species are found in South Africa: four in the middle Permian *Tapinocephalus* AZ and seven in the younger Late Permian zones (*Tropidostoma, Cistecephalus* and *Daptocephalus* AZ's). Because of the historic taxonomic confusion, the biostratigraphic distribution of pareiasaurian species in the Beaufort Group of South Africa has historically been poorly understood.

Using the Karoo vertebrate fossil database from the Karoo of South Africa, successive studies at the Evolutionary Studies Institute (ESI) at the University of the Witwatersrand (Rubidge 2005, Nicolas 2007, van der Walt *et al.* 2011, Day 2013, Day *et al.* 2015) have, over the past three decades, refined the stratigraphic ranges of most of the major tetrapod groups.

Extensive middle Permian stratigraphic range studies have provided evidence for an extinction event at the end of the Guadalupian period, which Day (2013, Day *et al.* 2015) has correlated with the end-Guadalupian extinction recognised in the marine realm from China. On land, the end-Guadalupian extinction event, corresponds with a marked faunal changeover of the pareiasaurs, as the large basal forms give way to more derived, medium- to small-sized forms and the dinocephalian therapsids become extinct (Nicolas 2007, van der Walt *et al.* 2011, Day 2013, Day *et al.* 2015).

Only since Lee's (1994, 1997a) alpha-taxonomic reassessment of the pareiasaurs, has it been possible to refine their stratigraphic distribution in the Karoo as stratigraphic range studies rely on a clear, updated taxonomy, with reliable and unambiguous diagnoses, allowing for accurate and positive identification of the fossils collected from each stratigraphic interval.

Stratigraphic ranges for middle and late Permian South African pareiasaurs have been produced by Smith and Keyser (1995a), Tsuji (2010), Day (2013, Day *et al.* 2015) and Van den Brandt (2016). The recently produced charts by Day (2013, Day *et al.* 2015) and Van den Brandt (2016) are the most detailed charts for the middle Permian pareiasaurs of South Africa, compiled for species considered valid by Lee (1994, 1997a). Since pareiasaurs comprise a large proportion of middle Permian biomass, about 25% of the Guadalupian terrestrial tetrapod fauna (Van der Walt 2011, Smith *et al.* 2012), comprehension of their stratigraphic occurrence is essential to understanding the nature and progression of the end-Guadalupian extinction event on land.

Van den Brandt (2016) positively re-identified 39 out of 108 skulls, across all four valid species, and produced updated stratigraphic ranges for all taxa (Figure 1.5). This study was limited to crania only and did not attempt to re-identify postcranial specimens.

1.6 *Tapinocephalus* AZ pareiasaurs: challenges

Pareiasaurs from the *Tapinocephalus* AZ present particularly challenging problems for workers. They are very large, heavy, and it is time-consuming to access and examine them. Parts of a single specimen are often spread amongst numerous boxes and shelves.

Pareiasaurian external cranial sutures are typically obscured by highly ossified and heavily fused skulls and cranial ornamentation consisting of thick bosses and raised rugose ridges. It is not possible to observe external cranial sutures in the majority of specimens. Where accessible, a few workers have successfully used internal cranial surfaces, where sutures are easier to identify than externally, (e.g. Watson 1914a, Van den Brandt 2016).

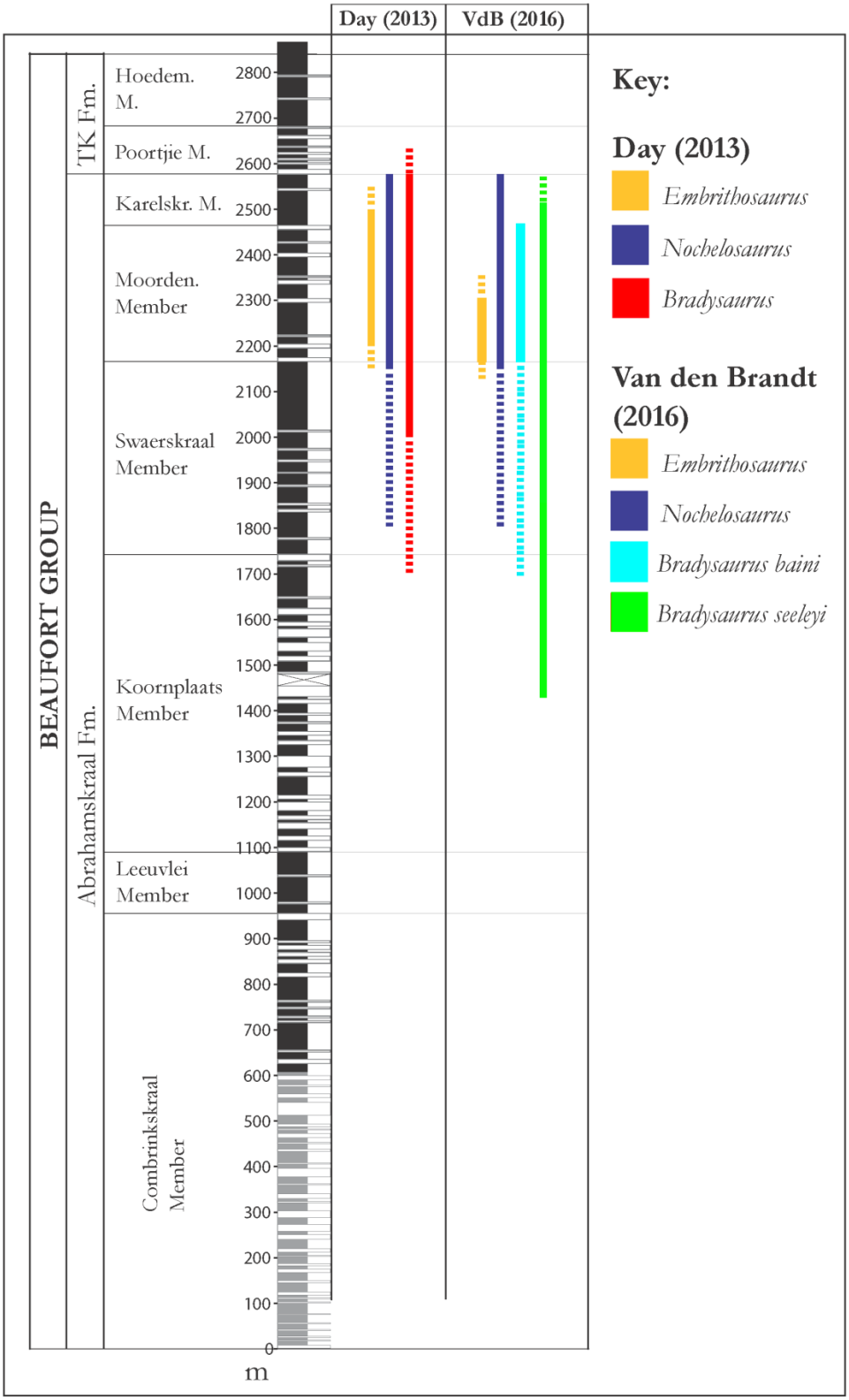


Figure 1.4: Composite stratigraphic ranges of pareiasaur species in the middle Permian Beaufort Group. Numerals denote meters above the base of the Abrahamskraal Formation. Solid lines indicate well constrained stratigraphic provenances, dotted lines indicate poorly constrained stratigraphic provenances with a wide range.

To further hinder research, the matrix of the *Tapinocephalus* AZ is extremely hard (Broom 1924, Broom 1924, Lee 1994, 1997a, Tsuji 2010) which severely hampers preparation. The majority of specimens were found in the late 1800's and early 1900's, when only crude preparation techniques involving hammers and chisels were employed, often damaging the specimens. Distortion and compression of specimens further complicates analysis making the identification of undistorted morphology challenging. The result of all of these noted afflictions is that most workers have been very reluctant to study this group.

Early workers in this field specifically commented on the large numbers of anatomically very similar, yet all slightly different specimens, sharing numerous overlapping features, often falling somewhere on a continuum or range, making it subjective to decide which anatomical features create the boundaries or diagnostic separation between species (Boonstra 1934a, Haughton and Boonstra 1930a). This lead to descriptions of an inflated number of species, based on only very subtle morphological differences between specimens or the use of characters that are not unique to a single species (Haughton and Boonstra 1929a, Boonstra 1934a).

After South Africa, the second most prolific region for pareiasaur remains is Russia where different pareiasaurian faunas from similar stratigraphic intervals are morphologically very distinct, or may attain different sizes, and are therefore readily identifiable, e.g. the large *Scutosaurus karpinskii* and the medium-sized *Deltavjatia rossicus* are both late Permian (Amalitsky 1922, Hartmann-Weinberg 1937, Shishkin *et al.* 2018). Other Russian pareiasaurs are morphologically distinct, e.g. the small *Obirikovia gladiator* (Bulanov and Yashina 2005) or from separate geographic areas, e.g. *Deltavjatia rossicus* from the Vjatka River, Kotel'nich, Kirov Province (Tsuji 2010, 2013). Accordingly the taxonomy of the Russian pareiasaurs is well established, apart from the placement of *Proelginia permiana,* which Lee (1997a) synonymised with *Scutosaurus*, a contentious decision (A. Sennikov pers comm). In contrast, the middle Permian South African

pareiasaurs are all large and anatomically similar, all found in the upper *Tapinocephalus* AZ, and all from the same geographic region, making it difficult to establish a taxonomic framework of clearly separated species.

1.7 *Tapinocephalus* AZ pareiasaurs: level of anatomical knowledge

Currently, anatomical knowledge of the four valid pareiasaurian species from the middle Permian of South Africa is limited. Historic taxonomic assessment papers provide brief, mostly cranial diagnoses often using only the holotype and a few referred specimens (Haughton and Boonstra 1929a, Boonstra 1934a, and Kuhn 1969) and more recently including postcrania (Lee 1994, 1997a).

The four currently valid species of pareiasaurs from the *Tapinocephalus* AZ were included in the series of 'Pareiasaurian Studies' papers produced by Haughton and Boonstra between 1929-1934, where each paper focused on a particular anatomical region (i.e. manus, Boonstra 1929a; pes, Boonstra 1929b; hind limbs, Haughton & Boonstra 1930b; fore limbs, Boonstra 1932b; dermal armour, Boonstra 1934b; and vertebrae and ribs, Boonstra 1934c). However, these historic postcranial papers contain an inflated number of pareiasaurian species that are no longer valid (Lee 1994, 1997a).

The level of anatomical knowledge of the middle Permian South African pareiasaurs may be summarized as follows:

- For *Bradysaurus seeleyi* and *Bradysaurus baini*, cranial and postcranial descriptions using the holotype and a few referred specimens were produced by Seeley (1888, 1892) more than 100 years ago and are in need of being updated. Lee (1994, 1997a) produced updated accurate cranial illustrations for *Bradysaurus baini*.
- For *Embrithosaurus schwarzi*, Broom (1903) produced a very brief cranial and postcranial description using only the holotype. An updated cranial re-description and cranial diagnoses of the holotype was produced by

Van den Brandt (2016) and Van den Brandt *et al.* (2019), but an updated postcranial description was not undertaken.

- For *Nochelesaurus alexanderi*, the species was named and briefly described by Haughton and Boonstra (1929a) based on the holotype and a few referred specimens and detailed cranial and postcranial descriptions have never been produced.

1.8 Problem statement: aims and design of this thesis

Amongst the members of the pareiasaurs from the *Tapinocephlaus* AZ, *Embrithosaurus schwarzi* is the only taxon for which a modern detailed cranial description has recently been produced (Van den Brandt 2016, Van den Brandt *et al.* 2019). All other taxa in the group are currently lacking in modern detailed descriptions of their crania and postcrania and only brief diagnostic cranial and postcranial features have been defined as part of taxonomic reassessment papers (Watson 1914b, Haughton and Boonstra 1929a, Boonstra 1934a, Kuhn 1969, Lee 1994, 1997a, Van den Brandt 2016). Despite updated cranial and postcranial diagnoses provided by Lee (1994, 1997a), the currently accepted four taxa are still poorly known and individual specimens are a challenge to positively identify using the literature of Lee (1994, 1997a).

Most recently, Van den Brandt (2016) included several new diagnostic cranial features in his taxonomic review of the basal pareiasaurs, but also noted numerous overlapping cranial features between the four taxa and a lack of clear cranial autapomorphies to confidently separate the four taxa. Both Van den Brandt (2016) and Lee (pers comm.) have postulated that the densely sampled and time-extensive *Tapinocephalus* AZ has preserved pareiasaur specimens from a continuously evolving or splitting lineage where species boundaries are difficult to establish as anatomical features “grade” into each other. This explains the lack of clear cranial autapomorphies between these species.

In addition to cranial features, Lee (1994, 1997a) noted a number of postcranial characters useful for diagnoses. Lee concluded that the postcranial features of pareiasaurs are diagnostically as useful as cranial features, and that postcranial studies had historically been undervalued.

This thesis will address two important research aims:

- Determine the number of valid species of pareiasaurs from the middle Permian *Tapinocephalus* Assemblage Zone of the Beaufort Group through performing a detailed taxonomic reassessment, based on new detailed cranial and postcranial descriptions of taxa and updated species level diagnoses.
- Contribute towards understanding middle Permian tetrapod biodiversity and the terrestrial occurrence of the end-Guadalupian extinction event, through determining the stratigraphic ranges of all valid pareiasaurian species.

The chapters of this thesis have been designed to address these aims as follows.

The cranium and postcranium of *Nochelesaurus alexanderi* are described in chapters 3 and 5 respectively, based on the holotype and important referred specimens, as no detailed descriptions exist. Additional preparation using modern techniques were applied to these specimens, improving the accuracy of the descriptions. Chapter 4 provides the first detailed description of the postcranium of *Embrithosaurus schwarzi,* using the holotype and important referred specimens. Only a very brief postcranial description currently exists for this species (Broom 1903). Extensive additional preparation of the holotype facilitated the updated description. Chapter 6 provides the first updated postcranial description of *Bradysaurus baini*, since the lengthy original description by Seeley (1892), using the holotype and important referred specimens.

The comparative cranial and postcranial anatomy of these three taxa is discussed in chapter 7, along with a taxonomic discussion. The new cranial and postcranial descriptions enabled a taxonomic review of valid middle Permian pareiasaur species from South Africa (chapter 8), including new species level diagnoses. An updated phylogenetic analysis for these basal pareiasaurs from the *Tapinocephalus* AZ is produced in chapter 9.

A comprehensive re-identification of middle Permian South African pareiasaurs in museum collections was undertaken and enabled the production of updated stratigraphic ranges and geographic positions for all valid South African middle Permian pareiasaur species (chapter 10). Finally, chapter 11 provides the conclusion of this project.

2. CHAPTER TWO: MATERIAL AND METHODS

2.1 Material

2.1.1 *Embrithosaurus schwarzi*

The holotype of *Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034 comprises a distorted skull with occluded lower jaw, vertebrae 1-27 with articulated isolated osteoderms and two articulated digits, two articulated caudal vertebrae (47th? and 48th? vertebrae), partial left scapulocoracoid and cleithrum, partial left clavicle, partial right clavicle and interclavicle, right humerus, both radii, both ulnae, both femora, both tibia, right fibula, partial left fibula, complete pelvis, two phalanges of the forelimb and two phalanges of the hindlimb. The holotype material also includes several dozen small unprepared fragments of vertebrae, ribs and phalanges, labelled as “doubtful association”. This fragmentary material reveals little useful anatomical information and has been excluded from the postcranial description.

2.1.2 Horizon and locality

According to Broom (1903) the holotype of *Embrithosaurus schwarzi* was collected by Mr A.W. Rogers and Mr E.H.L. Schwarz in 1902 on the farm Hoogeveld Lot A (Hoogeveld 270), in the Gouph region, near Knoflock’s Fontein, Van der Byl’s Kraal, Prince Albert district of the Western Cape Province of South Africa (Broom 1903). Day (2013) and Day *et al.* (2015) consider this locality to be high in the *Tapinocephalus* Assemblage Zone, in the stratigraphic interval of 2150-2250 m above the base of Abrahamskraal Formation, which is in the lower part of the Moordenaars Member.

2.1.3 *Nochelesaurus alexanderi*

The holotype of *Nochelesaurus alexanderi* (Haughton and Boonstra 1929) SAM-PK-6239 comprises the dorsal and right side of the skull and fragments of the right lower jaw, braincase and palate. Postcranial material comprises a partial

right scapulocoracoid , cleithrum and clavicle, partial interclavicle, somewhat damaged left humerus, seven articulated osteoderms, complete right femur and tibia, fibula fragment, astragalocalcaneum and about a dozen unnumbered unidentified fragments.

2.1.4 Horizon and locality

Specimen SAM-PK-6239 was collected in 1923 from the farm Boesmanskop (Bushmans Kop 302), Beaufort West district of the Western Cape Province of South Africa and named after Dr. Alexander du Toit, a noted South African geologist (Haughton and Boonstra 1929a). Kitching (1977) assigns the farm of Boesmanskop, to the Low Horizon of the *Tapinocephalus* Assemblage Zone, Abrahamskraal Formation, Beaufort Group. More recently Day (2013) and Day *et al.* (2015) considered that this locality is high in the *Tapinocephalus* Assemblage Zone, restricted to the uppermost Karelskraal Member of the Abrahamskraal Formation, and represents the highest stratigraphic occurrence of *Nochelesaurus*.

2.1.5 *Bradysaurus baini*

The holotype of *Bradysaurus baini* (Watson 1914) NHMUK R1971 comprises a complete skull and separate lower jaw. Postcranial material is very complete, including a complete shoulder girdle and pelvis, complete vertebral column, missing only the tip of the caudals. All major limb elements on the right side are completely preserved, including the humerus, radius, ulna, femur, tibia, fibula, manus and pes. On the left, the humerus, radius, ulna, femur, tibia, and fibula are partial. Both astragalocalcania are preserved. Most of the ribs are not preserved.

2.1.6 Horizon and locality

NHMUK R1971 was collected on 12 August 1889 by Seeley, T. Bain, J.S. Marais and S Marais from the farm De Bad in the Beaufort West district of the Western

Cape Province of South Africa (Seeley 1892). Kitching (1977) assigns the farm of Die Bad 286, Beaufort West, to the Low Horizon of the *Tapinocephalus* Assemblage Zone, Abrahamskraal Formation, Beaufort Group. More recently, Day (2013) and Day *et al.* (2015) considered this locality to be high in the *Tapinocephalus* Assemblage Zone, and assigned to the lower to mid Moordenaars Member of the Abrahamskraal Formation.

2.2 Methods

2.2.1 *Embrithosaurus schwarzi* preservation and preparation

The skull and postcranium of the holotype of *Embrithosaurus schwarzi* had previously been mechanically prepared under the direction of Broom in 1902/1903 at the Iziko South African Museum in Cape Town. Van den Brandt (2016, Van den Brandt *et al.* 2019) performed additional preparation of the crania and dentition and reconstructed nine cranial fragments into three large portions

For the current project, additional postcranial preparation, using compressed air driven air scribes with a tungsten carbide tip, was undertaken by Pepson Mukanela of the ESI at the University of the Witwatersrand, Johannesburg, in 2017. Historic mechanical preparation has damaged the surface of most postcranial elements with long scratches and chisel gauge marks into the bone's external cortical surface. Weathering has also damaged many exposed regions of the external bony surface. All these various forms of damage make it difficult to identify and describe fine surface details and often only dominant and obvious features and general overall shapes are discernible on most postcranial elements. It is also challenging to distinguish bone from matrix.

2.2.2 *Nochelesaurus alexanderi* cranial preparation

The skull and postcranium of the holotype of *Nochelesaurus alexanderi* had previously been mechanically prepared using hammer and chisel between 1923

and 1929. For the current project additional preparation, using compressed air driven air scribes with a tungsten carbide tip, was undertaken by Pepson Mukanela of the ESI at the University of the Witwatersrand, Johannesburg, in 2017, to expose the palatal flanges of the premaxilla and maxilla, the sphenethmoid bone on the inner skull surface, the lateral walls of the braincase, the ventral surface of the pterygoid fragment, the lower jaw and selected upper and lower dentition.

Referred *Nochelesaurus alexanderi* specimen SAM-PK-6238 had been over prepared, damaging and eroding into the external surface. Specimen SAM-PK-6239A is well prepared and preserved, with some erosion of the external surface. Specimen CGP JA 109 is also well prepared and exposed.

2.2.3 *Nochelesaurus alexanderi* postcranial preservation and preparation

Additional postcranial preparation was performed on the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239) using compressed air driven air scribes with a tungsten carbide tip, by Pepson Mukanela, Gilbert Mokgethoa and Charlton Dube of the ESI at the University of the Witwatersrand, Johannesburg, in 2018. Similar to the postcranial elements of the holotype of *Embrithosaurus schwarzi*, long scratches and chisel marks are present on SAM-PK-6239 as a result of historic preparation using hammers and chisels, making it difficult to identify fine surface features. Several postcranial elements have been historically fragmented and reconstructed using dark grey plaster as a binder, such as the left humerus and right femur, each consisting of three or four large fragments glued together. As is the case with the holotype of *Embrithosaurus schwarzi*, it is challenging to distinguish bone from matrix due to the metasedimentary nature of the preservation of the postcranial elements.

2.2.4 *Nochelesaurus alexanderi* cranial sutures

The external cranial surface of the holotype skull is reasonably well exposed due to better than average mechanical preparation from the 1920's, with only minor deposits of matrix still present within long, thin, furrowed depressions between raised rugose ridges. Unusual for a pareisaur skull from the *Tapinocephalus* AZ, and despite SAM-PK-6239 being a large specimen and therefore presumable an adult individual, the external cranial sutures are easily identifiable as dark grey matrix filled interdigitating crisscross lines that are readily apparent against the much lighter white-grey appearance of the bone. On the medial surface of the skull sutures are also readily apparent and served to confirm the external sutural contacts. Watson (1914a) and Van den Brandt (2016, Van den Brandt *et al.* 2019) used identifiable internal cranial sutures to assist in determining sutural contacts in their pareiasaurian cranial descriptions, noting the validity of this method as most sutures pass directly perpendicularly through the bone between the internal and external surfaces.

External and internal cranial sutures are readily identifiable on referred specimens SAM-PK-6238 and SAM-PK-6239A.

Microscopes, magnification glasses and temporary wetting of the holotype and referred specimens with water or alcohol helped to expose and confirm sutural contacts.

2.2.5 *Bradysaurus baini* preservation and preparation

The postcranium of the holotype of *Bradysaurus baini* was mechanically prepared at the Natural History Museum in London in 1891 (Seeley 1892). Seeley (1892) states that the right side of the animal is better preserved and in natural articulation, compared to the exposed, weathered and somewhat scattered left side. For the current project, the specimen was completely dismounted from display and disassembled for direct study. The original preparation by Mr. R. Hall (Seeley 1892) of the then British Museum is admirable in the historic context,

considering the tools available at the time and no additional postcranial preparation was needed for this study. The external bony surfaces are in excellent condition, generally better preserved than the postcranial elements of the holotypes of *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi*. Most major elements on the right side are completely preserved, but on the left side large portions of most major elements are reconstructed in dark grey plaster, clearly mirrored and modelled from the more intact elements of the right side.

2.2.6 Referred material

Refer to Appendix A for a list of referred specimens of *Embrithosaurus schwarzi*, *Bradysaurus baini* and *Nochelesaurus alexanderi*.

2.2.7 Comparative material

In addition to the holotypes and referred specimens of *Embrithosaurus schwarzi*, *Bradysaurus baini* and *Nochelesaurus alexanderi* (Appendix A), comparative cranial and postcranial material of other pareiasaur species directly studied include the following specimens: (taxonomic identifications are as per Lee 1994, 1997a).

PIN 2212/2, holotype skull and lower jaw of *Deltavjatia rossicus*; PIN 2212/1, PIN 2212/6, and PIN 2212/8, skulls with lower jaws of *Deltavjatia rossicus*; PIN 4546/18, holotype quadratojugal of *Obirkovia gladiator*; PIN 2005/1883, and 2005/1880 skulls lacking lower jaws of *Scutosaurus karpinski*; PIN 2005 1536 skull with lower jaw of *Scutosaurus karpinski;* PIN 2005/1532 articulated holotype skull and skeleton of *Scutosaurus karpinski*; PIN 2005/1533, PIN 2005/1534, PIN 2005/1535, PIN 2005/1536, PIN 2005/1537, and PIN 2005/1578, articulated skulls and skeletons of *Scutosaurus karpinski;* NHMUK PV R 4027 casts of ulnae of *Scutosaurus karpinski;* BP/1/3653, complete skull and lower jaw of *Pareiasuchus nasicornis*; BPI/I/548 skull and skeleton of an almost complete vertebral column with hundreds of weathered osteoderms, and parts of the shoulder and pelvic girdles of a *Anthodon serrarius.*

2.2.8 Literature consulted

The following recent detailed pareiasaurian cranial descriptions in the literature were consulted: *Scutosaurus karpinski* (Lee 1994); *Pareiasuchus nasicornis* (Lee *et al.* 1997); *Bunostegos akokanensis* (Tsuji *et al.* 2013); *Deltavjatia rossicus* (Tsuji 2013); *Honania complicidentata* (Xu *et al.* 2015); *Obirkovia gladiator* (Bulanov and Yashina 2005); *Provelosaurus americanus* (Cisneros *et al.* 2005); *Shihtienfenia permica* and *Sanchuansaurus pygmaeus* (Benton 2016); and *Elginia wuyongae* (Liu and Bever 2018).

The following detailed pareiasaurian postcranial descriptions were consulted for comparison: *Embrithosaurus schwarzi* (Broom 1903); *Bradysaurus seeleyi* (Seeley 1888); *Bradysaurus baini* (Seeley 1892); *Bunostegos akokanensis* (Turner *et al.* 2015); *Deltavjatia rossicus* (Tsuji 2010, 2013); *Parasaurus geinitzi* (Tsuji & Muller 2008, Tsuji 2010); *Honania complicidentata* (Xu *et al.* 2015); *Shihtienfenia permica* (Benton 2016); and "Pareiasauria gen. et sp. indet. 1"and "Pareiasauria gen. et sp. indet. 2" (Jalil and Janvier 2005). Six postcranial descriptive papers from the eleven-part 'Pareisaurian Studies' series produced by Haughton and Boonstra between 1929 and 1934 were also consulted: part 3, manus (Boonstra 1929a); part 4, pes (Boonstra1929b); part 6, hindlimb (Haughton & Boonstra 1930b); part 8, forelimb, (Boonstra 1932c); part 10, dermal armour (Boonstra 1932b); and part 11, vertebrae and ribs (Boonstra 1934c).

2.3 Abbreviations

2.3.1 Institutional abbreviations

AM, Albany Museum, Grahamstown; **AMNH,** American Museum of Natural History, New York; **BPI**, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg (formerly the Bernard Price Institute for Palaeontological Research); **CGP,** Council for Geosciences, Pretoria; **NHMUK,** Natural History Museum of London, United Kingdom; **NMQR,** National Museum, Bloemfontein; **PIN**, Paleontological Institute, Moscow, Russia; **SAM,** Iziko South

African Museum, Cape Town; **TM,** Ditsong National Museum of Natural History (formerly Transvaal Museum, Northern Flagship Institution), Pretoria; **UMZC,** University Museum of Zoology, Cambridge, United Kingdom; **VW,** Victoria West Regional Museum, Victoria West.

2.3.2 Anatomical abbreviations

2.3.2.1 Cranial

aam, area articularis mandibularis; **ab**, angular boss; **af**, adductor fossa; **Ang**, angular; **Art**, articular; **Bo**, basioccipital; **bt**, tubera basispheniodales (basal tubera); **btp,** basipterygoid process; **cd**, crista dentalis; **cs**, crista supraoccipitalis; **Cor**, coronoid; **cp**, cultriform process; **D**, dentary; **dnp**, descending nasal process; **Ect**, ectopterygoid; **Ept**, epipterygoid; **Exo**, exoccipital; **F,** frontal; **fdm**, foramen dentofaciale majus; **fic**, foramen intermandibularis caudalis; **fim,** foramen intermandibularis medius; **fm**, foramen magnum; **fo**, fenestra ovalis; **for,** foramen orbitonasale; **fpp**, foramen palatinum posterius (suborbital vacuity); **imc**, intra-mandibular cavity; **itv**, interpterygoid vacuity; **J,** jugal; **jf**, jugular foramen; **Lac**, lacrimal; **mb**, maxillary boss; **mf**, maxillary foramen; **Mx**, maxilla; **N**, nasal; **oc**, occipital condyle; **Op**, opisthotic; **P**, parietal; **Pal**, palatine; **Pbs**, parabasisphenoid**; pf,** pineal foramen; **Pm**, premaxilla; **Po**, postorbital; **Pof**, postfrontal; **Pp**, postparietal; **ppf,** prepalatal foramen; **Pra**, prearticular; **Prf**, prefrontal; **Pro**, prootic; **Pt**, pterygoid; **pw,** pterygoid wing; **Q**, quadrate; **qf**, quadrate foramen; **Qj**, quadratojugal; **rap**, retroarticular process**; So,** supraoccipital; **Sph**, sphenethmoid; **Spl**, splenial; **Sq,** squamosal; **St**, supratemporal; **Sur,** surangular; **V**, vomer.

2.3.2.2 Postcranial

acor, anterior coracoid; **acr**, acromion process; **ce**, centrum; **cla**, clavicle; **cle**, cleithrum; **cof**, coracoid foramen; **dcp**, deltopectoral crest; **dp**, diapophysis; **ect,** ectepicondyle**; ect for**, ectepicondylar foramen; **enf,** groove for entepicondylar foramen**; ent**, entepicondyle**; ent for,** entepicondylar foramen; **gl**, glenoid; **ib**,

ischial buttress; **icf** , intercondylar fossa; **icla**, interclavicle; **ics,** intercondylar sulcus; **it**, internal trochanter; **itf**, intertrochanteric fossa**; lat.sig.p**, lateral sigmoidal process; **med.sig.p**, medial sigmoidal process; **mt**, major trochanter; **na**, neural arch; **nc**, neaural canal; **nsp**, neural spine; **ole**, olecranon process; **pb**, pubic buttress; **pcor**, posterior coracoid; **pf**, popliteal fossa; **pof**, pubic/obturator foramen; **poz**, postzygapophysis; **pp**, parapophysis; **prox.lat.c**, proximal lateral crest; **prox.med.c**, proximal medial crest; **prz**, prezygapophysis; **rad fac**, radial condyle; **sb**, supra-acetabular buttress; **sca,** scapula blade; **sgb**, supraglenoid buttress; s**ig.n**, sigmoid notch; **ssf**, subscapular fossa; **tp**, transverse process; **uln fac**, ulnar facet.

2.4 Key to interpretive drawings

2.4.1 Cranial

Sutures in solid lines have been positively identified; those in dotted lines are extrapolated from internal surfaces and the sides of bones. Light grey indicates sides of bones, bone breaks or plaster, dark grey indicates foramen or fenestra, black indicates deep cavities such as the orbits. Numbers indicate: marginal cheek bosses; teeth positions counting back from the front; or tooth cusps. Cranial bosses are in bold.

2.4.2 Postcranial

Dotted lines represent missing sections. Light grey indicates sides of bones, bone breaks or matrix, dark grey indicates foramen or fenestra, black indicates deep cavities.Note: The postcranial descriptive chapters (chapters 4, 5, 6) employ the method used by Benton (2016) of noting the relevant phylogenetic character states, as each element is described.

3. CHAPTER THREE: CRANIAL DESCRIPTION OF *NOCHELESAURUS ALEXANDERI*

3.1 Introduction

Haughton and Boonstra (1929a) erected the genus *Nochelesaurus* recognising two species; *N. strubeni* and *N. alexanderi*, and provided only brief cranial diagnoses. Boonstra (1934a) expanded the cranial diagnoses with basic cranial illustrations for the holotype skulls in all major views, and produced photographs of the holotype skull of *N. alexanderi* in dorsal and lateral view. Subsequent authors have reproduced Boonstra's original (1934a) rough cranial illustrations of *N. alexanderi* (e.g. Kuhn 1969, Van den Brandt 2016) and have provided only minor modifications and improvements to the descriptions and diagnoses of this species (e.g. Lee 1994, 1997a, Van den Brandt 2016).

To clearly diagnose and distinguish *N. alexanderi* from the other co-occurring pareiasaurid species of the *Tapinocephalus* Assemblage Zone, a new and updated detailed cranial description is required, including updated diagnoses and cranial illustrations.

3.2 Directional terms and directional vocabulary

Directional terms and directional hierarchy used in this description: the terms wide, broad and narrow refer to the mediolateral or transverse directions; long, short, forwards or backwards the anteroposterior or longitudinal plane; and high, tall, top, above, low, bottom or below, the dorsoventral directions. Dentition: Anterior or mesial, posterior or distal, lingual and labial. Directional vectors are described in the anteroposterior direction first, followed by the dorsoventral and mediolateral directions when necessary.

3.3 Material

3.3.1 Holotype

Refer to chapter two, material and methods.

3.3.2 Referred material

Refer to Appendix A for a list of referred specimens of *Nochelesaurus alexanderi*.

3.3.3 Comparative material

Refer to chapter two, material and methods.

3.3.4 Literature consulted

Refer to chapter two, material and methods.

3.3.5 Preservation and preparation

Refer to chapter two, material and methods.

3.3.6 Holotype horizon and locality

Refer to chapter two, material and methods.

3.4 Systematic Palaeontology

REPTILIA Laurenti, 1768

PARAREPTILIA Olsen, 1947

PAREIASAURIA Seeley, 1888

PAREIASAURIDAE Cope, 1896

NOCHELESAURUS Haughton and Boonstra, 1929

Nochelesaurus alexanderi Haughton and Boonstra, 1929

3.5 Cranial description

3.5.1 Skull roof

General Comments

Unless otherwise noted, the description of the skull roof is based on the holotype (SAM-PK-6239). Reference to referred specimens (SAM-PK-6238, SAM-PK-6239A, CGP JA 109) are made where appropriate.

The holotype skull preserves the dorsal skull table and the right lateral facial and cheek regions of the skull. The left cheek is not preserved, and only a small piece of the left facial region is present with a partial lacrimal. White plaster has been used internally to reinforce the right side of the skull and completely covers the internal surface of the right frontal, parietal, prefrontal, postfrontal, and postorbital and partially the internal surface of the right nasal, lacrimal, maxilla, jugal, quadratojugal, squamosal, and the single median postparietal.

The skull roof of SAM-PK-6238 is partially preserved in three large fragments: the anterior half or snout of the skull, a large right cheek fragment, and a small part of the dorsal skull table. The left cheek is not preserved. Specimen SAM-PK-6239A consists of a large fragment of the right cheek, containing the right quadratojugal, jugal, squamosal, supratemporal and postorbital. Specimen CGP JA 109 consists of a partial skull, composed of two large fragments held together with white plaster. The snout, palate and lower jaw on the left is not preserved. Most of the palate and braincase is poorly preserved or not preserved.

The holotype skull, SAM-PK-6239A and CGP JA 109 are heavily ornamented with distinct protruding bosses, with long, thin, raised rugose ridges and depressions or furrows between them with small circular to oval pits in these furrows. Most bones have either one dominant, large boss or a complex of smaller bosses, near the centre of the bone, apart from for the premaxilla, maxilla and the squamosal. The straight, rugose ridges do not occur randomly but form a pattern, always

spreading radially out from a large central boss or a central complex of smaller bosses. Internally the bones of the skull are smooth, featureless and unornamented unless otherwise noted. Historic over preparation of the external surface of SAM-PK-6238 has resulted in levelling of most cranial ornamentation, which are “smoothed over” and as a result appear less distinct than they should be.

As in all South African basal pareiasaurs, a well-defined longitudinal ridge extends from the snout to the back of the skull and creates a sharp junction that separates the skull roof into two distinct regions: a) horizontally oriented central skull table, roughly rectangular, flat but slightly convex in anterior view; and b) ventrolaterally oriented facial and cheek regions on the side of the skull. The facial region is located in the anterior half of the skull, and is curved. The cheek region is located in the posterior half of the skull and is flat. The longitudinal ridge separating the dorsal skull table from the lateral face and cheek regions, comprises a series of cranial bosses anteriorly (the central nasal boss and the dorsal-most lacrimal boss), and along the dorsal margin of the orbital rim (the two lateral prefrontal bosses, the two central postfrontal bosses and the two orbital bosses of the postorbital). Posteriorly, behind the orbit, four thickened and continuous ridges on the postorbital, squamosal and supratemporal create an overhanging projection. The posterior border of each cheek has five large protruding bosses; four on the quadratojugal and one on the squamosal.

The holotype skull is severely dorsoventrally crushed, so that the dorsal skull table and the lateral face and cheek regions are almost on the same plane. In occipital view the right cheek appears much wider than it would if undistorted. On the postorbital and squamosal the longitudinal ridge separating the dorsal skull table from the lateral cheeks is less distinct as it has been compressed and dorsoventrally flattened. The snout is low and much wider than high due to the dorsoventral crushing. In life the snout would have been only very slightly wider than high or about as wide as high. The external skull table has been displaced

backwards, resulting in anterior stretching and displacement of the palatal flange of the premaxilla and maxilla, the ventral floor of the external naris and the occluded partial right quadrate. In lateral view, the right orbit appears posterodorsally elongated and oval (and not circular) and the lateral margins of the external naris are posterodorsally elongated (instead of vertically oriented) as a result of the dorsoventral crushing and backwards displacement of the skull table.

SAM-PK-6238 is severely mediolaterally compressed resulting in the snout appearing much higher than wide and the pineal foramen being anteroposterioly elongated instead of circular. The undistorted lower jaw is much wider than the mediolaterally compressed snout. The skull roof is also posteriorly displaced such that the right orbit appears posterodorsally elongated and not circular and the naris appears posteriorly stretched. The snout is twisted to the right.

CGP JA 109 is severely dorsonventrally crushed and posteriorly displaced, such that the right orbit is almost completely posterodorsally flattened and clearly unnaturally narrow.

Premaxilla (Figs. 3.1, 3.2, 3.3, 3.4)

In anterior view the T-shaped and smooth premaxilla is located at the anterior tip of the snout and wedged between the maxillae and the nasals. Medially, the premaxilla sutures with its partner along the midline and posterolaterally, on the floor of the external naris, it forms a long, anterodorsally directed suture with the maxilla.

At the point where the premaxilla forms the medial half of the ventral border of the external naris it is noticeably anteroposteriorly elongated and a longitudinal groove is present on the anteromedial ventral floor of the external naris.

Along the midline, the vertically ascending premaxillary process forms the anteromedial border of the external naris and the ventral half of the internarial bar.

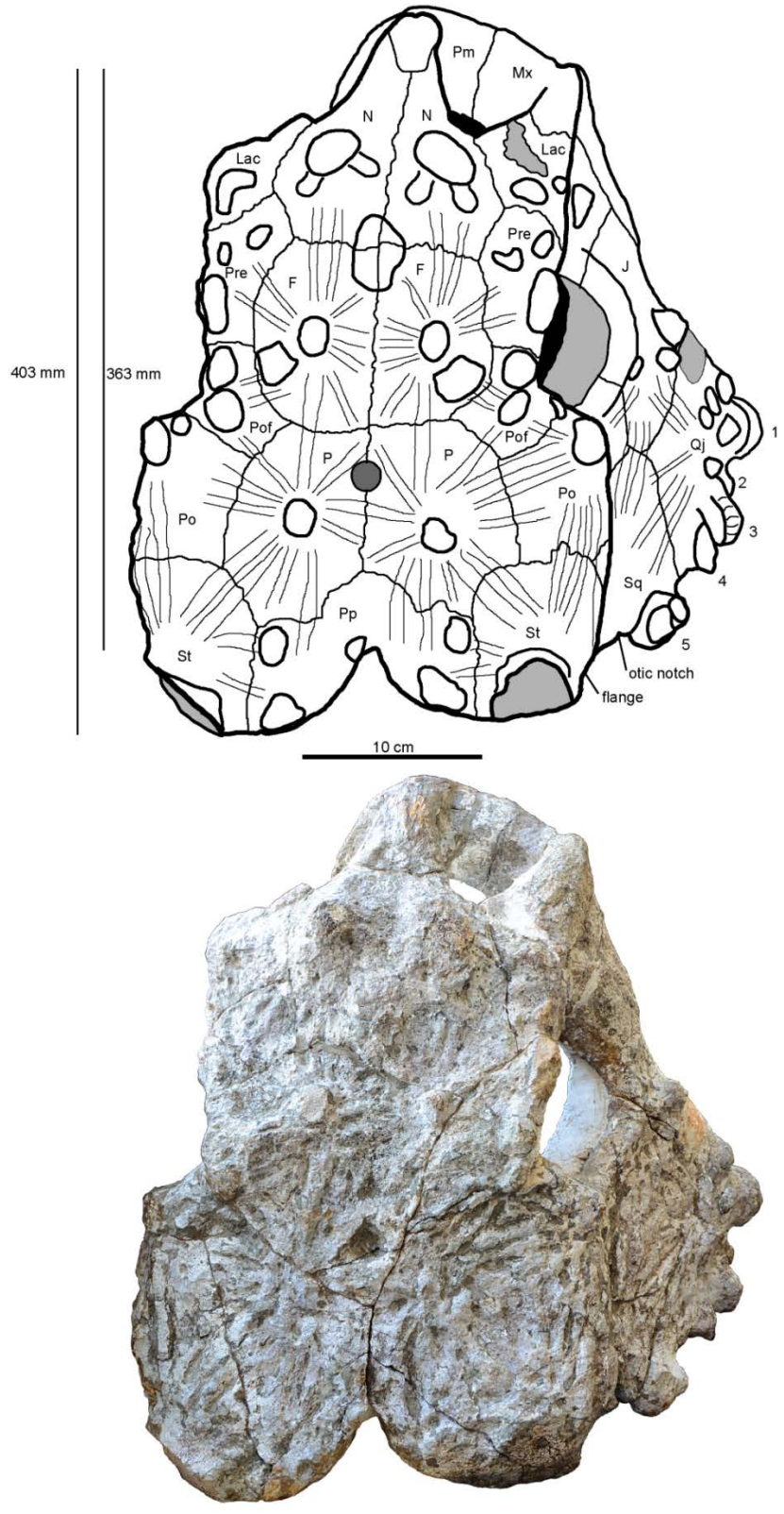


Figure 3.1: Photograph and interpretive drawing of the skull of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in dorsal view. Skull Length of 403 mm: posterior edge of the dorsal premaxilla to the posterior edge of the midline occipital flange; or 363 mm: posterior edge of the dorsal premaxilla to the posterior edge of the left-most corner of the occipital flange.

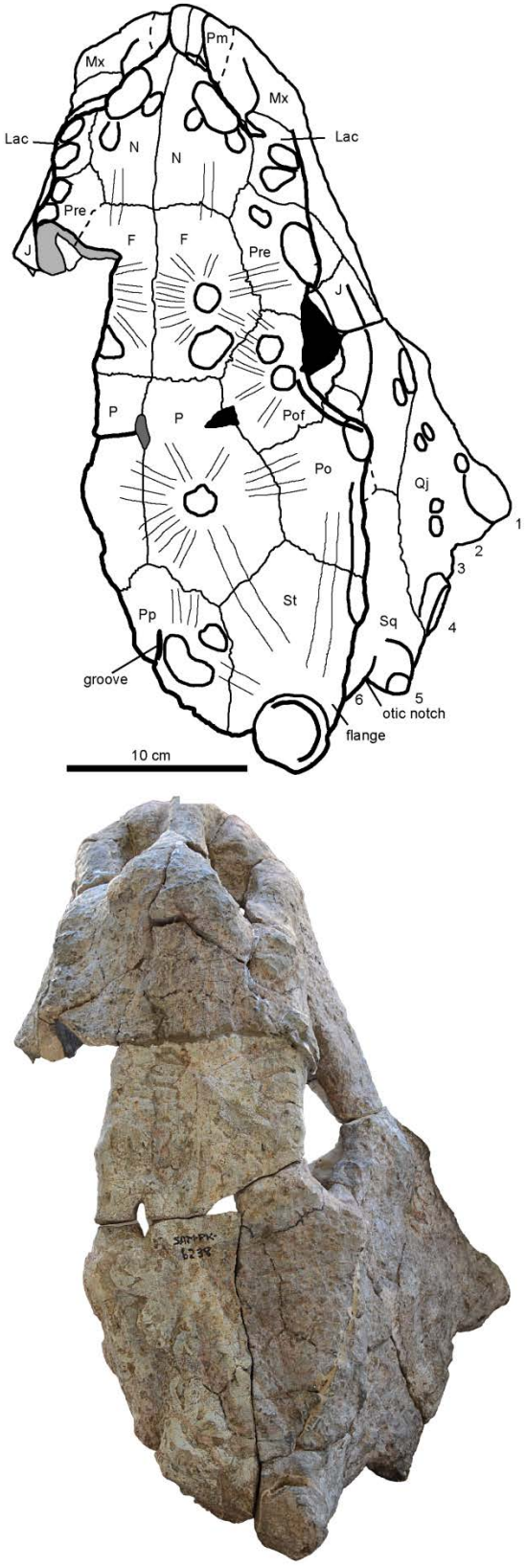


Figure 3.2: Photograph and interpretive drawing of the skull of SAM-PK-6238 (*Nochelesaurus alexanderi*), in dorsal view.

The premaxillary portion (i.e. lower half) of the internarial bar of the holotype and SAM-PK-6238 are vertically oriented, but slope slightly posterodorsally as a result of the backwards displacement of both skulls. In all other undistorted basal South African pareiasaur specimens, it slopes vertically and slightly anterodorsally. The premaxilla is clasped laterally by the descending processes of the nasal, and dorsomedially it overlaps the nasal. Externally, the premaxilla is unornamented and smooth.

The premaxilla of the holotype, SAM-PK-6238 and CGP JA 109 is narrow and forms a thin, vertical wall, which is only slightly wider (<5 mm) than the three teeth they each carry (see Dentition) The straight to slightly curved roots of the premaxillary teeth are more than twice as long as the length of the exposed crown and can only be accommodated vertically in the premaxilla. Erupted tooth crowns point straight downwards in the holotype, SAM-PK-6238 and CGP JA 109, with no medial infliction. The maxilla of *Nochelesaurus* shows the same morphology and resultant orientation of the teeth, as the premaxilla (see Maxilla). In comparison, the holotype of *Embrithosaurus* shows similar premaxillary and maxillary morphology to *Nochelesaurus* and shares the condition of downwards pointing upper jaw teeth. In contrast the premaxilla and maxilla of *Bradysaurus baini* is curved just above the tooth row and has a 20 mm wide horizontally flat area which accommodates curved and horizontally oriented long tooth roots, producing the diagnostic posteriorly oriented upper jaw teeth of this species.

Internally, at a level several centimetres above the tooth row, the premaxilla has a thin, horizontally oriented, flange that forms part of the palate and extends posteriorly behind the internarial bar. This palatal flange of the premaxilla has a short transverse sutural contact with the vomer and forms the anteromedial border of the internal naris (choana) and the anterior and lateral walls of the large, elongated prepalatal foramen. The prepalatal foramen is oval and its posterior border is formed by the vomer (Fig. 3.7).

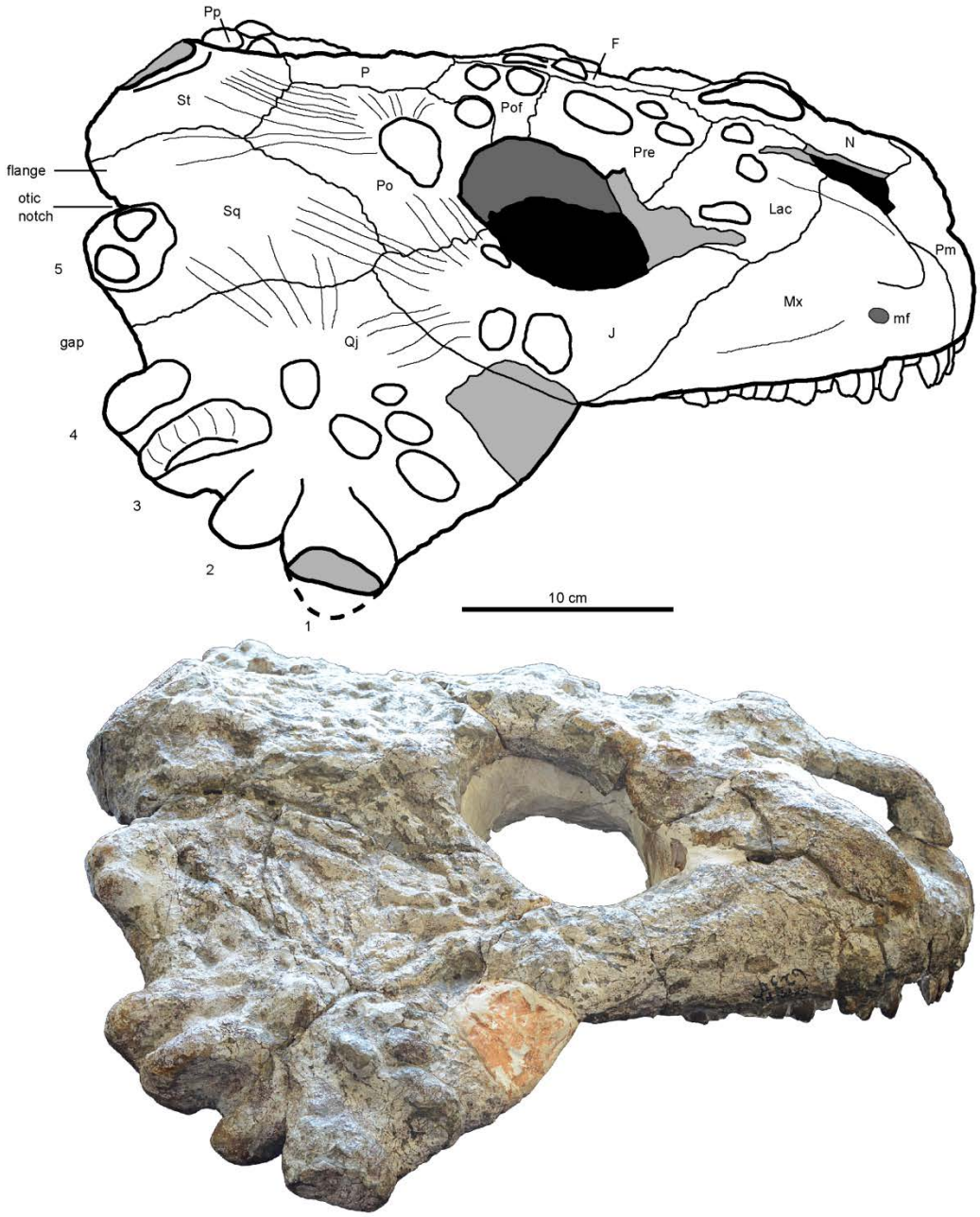


Figure 3.3: Photograph and interpretive drawing of the skull of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in right lateral view.

Maxilla (Figs. 3.1, 3.2, 3.3, 3.4)

In lateral view the triangular maxilla is highest anteriorly and tapers posteriorly and forms most of the anterolateral side of the face. Externally the maxilla is a large, vertical, curved plate and internally it has a small, horizontal flange that forms part of the palate. The bone has a long anterior sutural contact with the

premaxilla, long posterodorsally oblique sutures with the lacrimal and jugal, and a short posteroventral contact with the quadratojugal. The maxilla does not contribute to the orbital margin. Anteriorly the maxilla forms the lateral half of the floor of the external naris, and a small part of its ventolateral border. The posterior portion of the maxilla extends along the ventral margin of the skull to midway along the orbit, to contact the quadratojugal. In lateral view this contact is obscured by the ventral-most portion of the jugal, as in *Bunostegos akokanensis* (Tsuji *et al.* 2013) and *Deltavjatia* (Tsuji 2013) and is visible in ventral view only in both the holotype and SAM-PK-6238.

A parareptilian synapomorphy is the presence of a large, prominent anterolateral maxillary foramen below the ventrolateral corner of the external naris, above the 3rd or 4th maxillary tooth (Laurin and Reisz 1995). This foramen is very large and prominent in the holotype and SAM-PK-6238 (Figs. 3.3, 3.4) and CGP JA 109 and probably accommodated a branch of the trigeminal nerve as suggested by Tsuji *et al.* (2013) for *Bunostegos*. In SAM-PK-6238 this foramen is followed posteriorly by two smaller nutritive foramen.

In dorsal view, the anterolateral margin of the maxilla is strongly convex. Near the ventrolateral corner of the external naris of the holotype, a protruding piece of the right maxilla has been dislodged by dorsoventral crushing of the skull creating the misleading appearance of a maxillary boss. No maxillary boss is present on the maxilla of the holotype, SAM-PK-6238 or CGP JA 109. All these specimens have a distinct, low, posterodorsally oriented, maxillary-lacrimal ridge (20-25 mm wide) with a sharp lateral edge that follows the contour of the lateral border of the external naris, above the large anterolateral maxillary foramen. *Bradysaurus baini* has a much more swollen and bulging maxillary-lacrimal ridge (40 mm wide) absorbing the maxillary and lacrimal bosses, making them indistinct. *Embrithosaurus* has a small, distinct and pointed maxillary boss and a moderately swollen maxillary-lacrimal ridge, formed by the bosses of the maxilla and lacrimal.

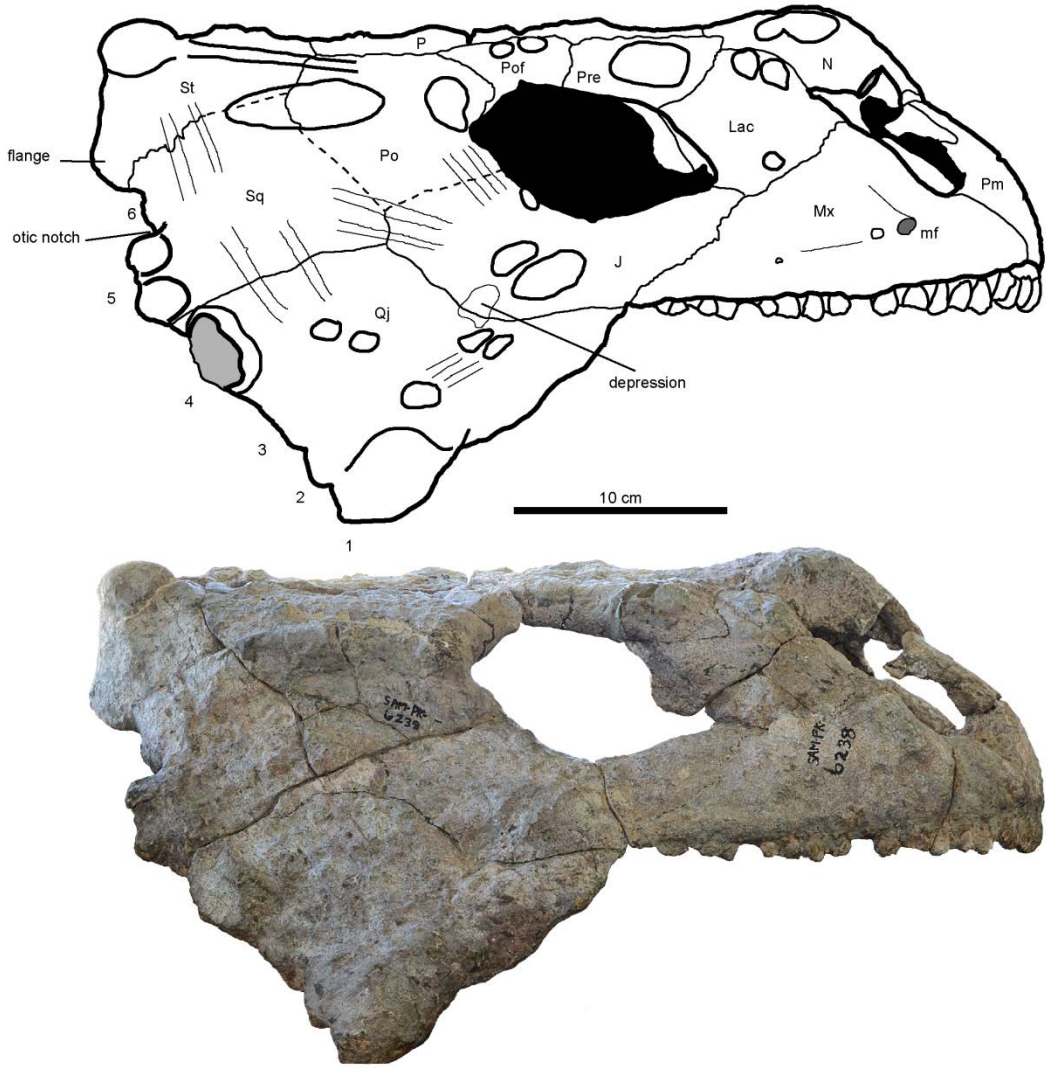


Figure 3.4: Photograph and interpretive drawing of the skull of SAM-PK-6238 (*Nochelesaurus alexanderi*), in right lateral view.

The external surface of the maxilla of *Nochelesaurus* is generally smooth and unornamented but has few short slightly raised rugose ridges and small oval to circular pits below the orbit and near the posterior limits of the bone. As in all basal South African pareiasaurs, a long, shallow, horizontal groove runs parallel with the tooth row on the external surface of the maxilla.

The ventral surface of the maxilla of the holotype bears 15-16 teeth (see Dentition). As with the premaxilla, the maxilla of the holotype, specimen SAM-PK-6238 and specimen CGP JA 109 forms a narrow thin wall, only slightly wider

(<5 mm) than the teeth. The erupted teeth of the maxilla point directly downwards as is the case for the premaxillary teeth.

On the internal surface of the holotype and SAM-PK-6238 a thin, horizontal, maxillary palatal flange projects medially at the same high level above the maxillary tooth row as the palatal flange of the premaxilla, forming the anterolateral margin of the internal naris, and contacting the premaxilla anteromedially (Fig. 3.7). The posterior portion of the maxillary palatal flange is not preserved on the holotype but is in SAM-PK-6238 where sutural contacts occur with the palatines posteromedially and ectopterygoids posteriorly (Fig. 3.8). Each tooth of the holotype has a large and distinct, shallow circular pit, 20-30 mm above the base of each tooth, at the start of each tooth root. These pits are also present on the premaxilla.

Septomaxilla

No septomaxilla is preserved on any specimen of *Nochelesaurus*.

Jugal (Figs. 3.1, 3.2, 3.3, 3.4, 3.5, 3.6)

The elongated jugal forms the posteroventral, ventral and anteroventral margins of the orbit on the sides of the face and the anteroventral portion of the lateral cheek. It has a short anterodorsal sutural contact with the lacrimal, a long oblique anteroventral suture with the maxilla, a long curved posteroventral suture with the quadratojugal, a very short posterodorsal contact with the squamosal and a short dorsal suture with the postorbital.

The posterior half of the jugal, behind the orbit, is relatively thin and plate-like. Anteriorly, the jugal is much thicker, rounded and curves anteromedially. In the orbital margin of the holotype, the jugal forms the anteroventral part of the antorbital buttress (orbital margin) as a wide, flat, medial horizontal flange. The vertical antorbital flange of the jugal, reported for *Scutosaurus* (Lee 1994), is not present in any specimen of *Nochelesaurus*.

Two bosses arranged in an obliquely oriented line occupy the lateral surface of the jugal, near the centre of the bone, and low, immediately above the curved suture with the quadratojugal. The anteroventrally located boss is the largest and most distinct. Straight, rugose ridges radiate from these two bosses in three directions: vertically oriented ridges continue dorsally onto the postorbital, posterodorsally oriented ridges persist onto the squamosal, and horizontally oriented ridges extend posteriorly onto the quadratojugal. Higher on the jugal, a separate, smaller and less distinct boss is present on the lateral surface, on the posteroventral orbital margin, just below the jugal-postorbital suture. *Embrithosaurus and Bradysaurus baini* show very similar arrangements of the bosses and radiating ridges of the jugal.

Quadratojugal (Figs. 3.1, 3.2, 3.3, 3.4, 3.5, 3.6)

The quadratojugal is a large, flat, thin, roughly square plate of bone located on the posteroventral corner of the lateral cheek on the side of the skull. It forms the ventral border and most of the posterior border of the cheek. This expanded bone creates the ventrolateral “cheek flange” behind and below the orbit and extends well below the level of the tooth row. Dorsally, the quadratojugal has a long, straight, longitudinal sutural contact with the squamosal and anterodorsally a long curved suture with the jugal.

A complex of bosses on the lateral surface of the quadratojugal are arranged in a posterodorsally oriented curved arc. Three to four distinct pointed bosses are present on the holotype, SAM-PK-6239A and CGP JA 109. Each boss is oval. A similar morphology and arrangement of bosses is present in the holotype of *Embrithosaurus*, but in specimens of *Bradysaurus baini* there are no high, distinct bosses, instead several long rugose ridges are present which are indistinct and low, and closely fused together. Anterior to the curved arc of bosses of *Nochelesaurus*, are several horizontally oriented rugose ridges (also present in *Embrithosaurus* and *Bradysaurus baini*) which extend anterodorsally towards the central lateral boss complex of the jugal.

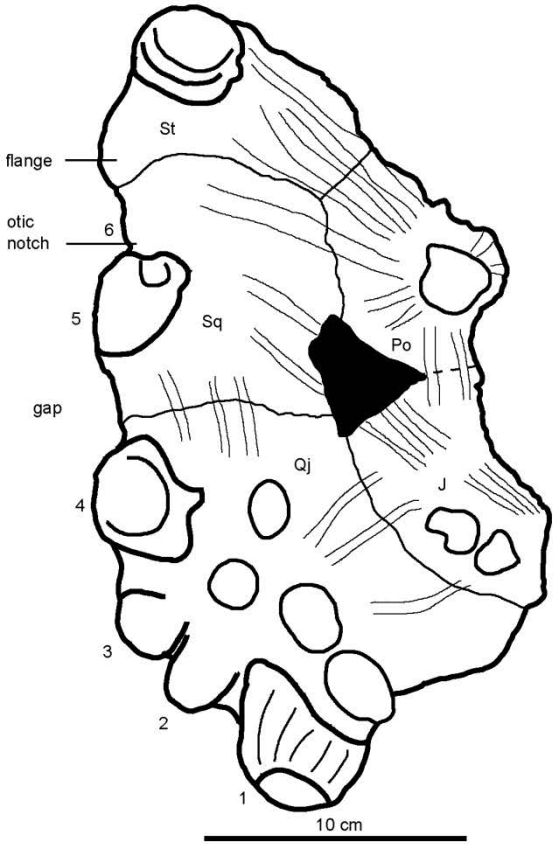




Figure 3.5: Photograph and interpretive drawing of specimen SAM-PK-6239A (*Nochelesaurus alexanderi*), in right lateral view.

It must be noted that the lateral bosses on the quadratojugal of the holotype of *Nochelesaurus*, SAM-PK-6239A and CGP JA 109 are the most distinct of all the basal South African taxa, as they are high and project well clear of the flat quadratojugal external lateral surface. This is not the case in specimen SAM-PK-6238 (Fig. 3.4) as a result of weathering and overpreparation. Below the lateral bosses, the ventral portion of the quadratojugal of *Nochelesaurus* is only slightly swollen in transverse width. In contrast, in *Bradysaurus baini*, the lower half of the quadratojugal is greatly swollen and transversely wider as it is thickened by the several indistinct, partially fused, posterodorsally oriented rugose ridges mentioned above.

Vertically oriented long and thin rugose ridges on the posterodorsal portion of the lateral surface of the quadatojugal, extend dorsally onto the squamosal, in all basal South African pareiasaurian taxa.

The quadratojugal houses four bosses on the posterior margin of the cheek. At the posteroventral corner is the largest boss which is very long (almost twice as long as wide), posteriorly elongated, and slightly posterolaterally oriented in occipital view. Proximally, it has a slightly narrow neck and distally it widens and forms a round rim of raised bone that circumscribes the boss. The neck is particularly narrow and the rim extremely thick on the right side of specimen CGP JA 109 (Fig. 3.6). The distal tip is sheared off in the holotype, but the other specimens have a pointed tip. Rugose ridges extend distally, tapering to the tip of the boss. In contrast, the equivalent boss of *Embrithosaurus* and *Bradysaurus baini* is shorter, only slightly longer than wide, more bulbous, without a narrow neck, has no raised rim, ends with a blunt distal tip, and has less distinct rugose ridges.

Above the corner boss, *Nochelesaurus* shows variability in both the morphology and the placement of the bosses on the posterior edge of the quadratojugal. Above the corner boss the holotype has a single, small, round to pointed boss (not bulbous), with deep cavities above and below it, followed dorsally by a large

boss that itself comprises two smaller bosses fused together (with each of its component bosses having a long anterior projection on the lateral surface of the quadratojugal) The quadratojugals of referred *Nochelesaurus* specimens SAM-PK-6238, SAM-PK-6239A and CGP JA 109 show a different configuration. Above the corner boss are two small, distinct, round to pointed bosses, with deep cavities between each other and the bosses above and below the pair. Dorsally a larger, distinct, pointed boss follows. Regardless which of the two configuration patterns are present, the smaller boss(s) above the corner boss, are always posteriorly directed and the large, dorsal boss posterolaterally.

The holotype of *Embrithosaurus* has the first configuration, but the bosses are more bulbous, lower, flatter, and indistinct with shallower cavities between the bosses. Different specimens of *Bradysaurus baini* exhibit both arrangement patterns, and sometimes even on the same individual, comparing the left to the right cheek (SAM-PK-5624).

A distinguishing feature of *Nochelesaurus* (not observed in any other basal South African pareiasaur species) is found on the holotype, SAM-PK-6239A and CGP JA-109 (but not in SAM-PK-6238): on the posterior edge of the cheek, the dorsal quadratojugal boss and the large squamosal boss are separated by a large indentation or gap (30-40 mm high), through which the horizontal quadratojugal-squamosal suture runs.

The posterior portion of the quadratojugal is thickest in mediolateral extent dorsally and thins ventrally, as in all other basal South African pareiasaurs. However, the posterior portion of the quadratojugal of all *Nochelesaurus* specimens is relatively narrow considering the large size of the skull when compared to similarly sized large specimens of *Bradysaurus baini*, where the posterior portions of the quadratojugal are much wider in mediolateral extent. The posterior and posteromedial edges of the quadratojugal show several irregular rugose ridges, furrows and circular to oval pits.

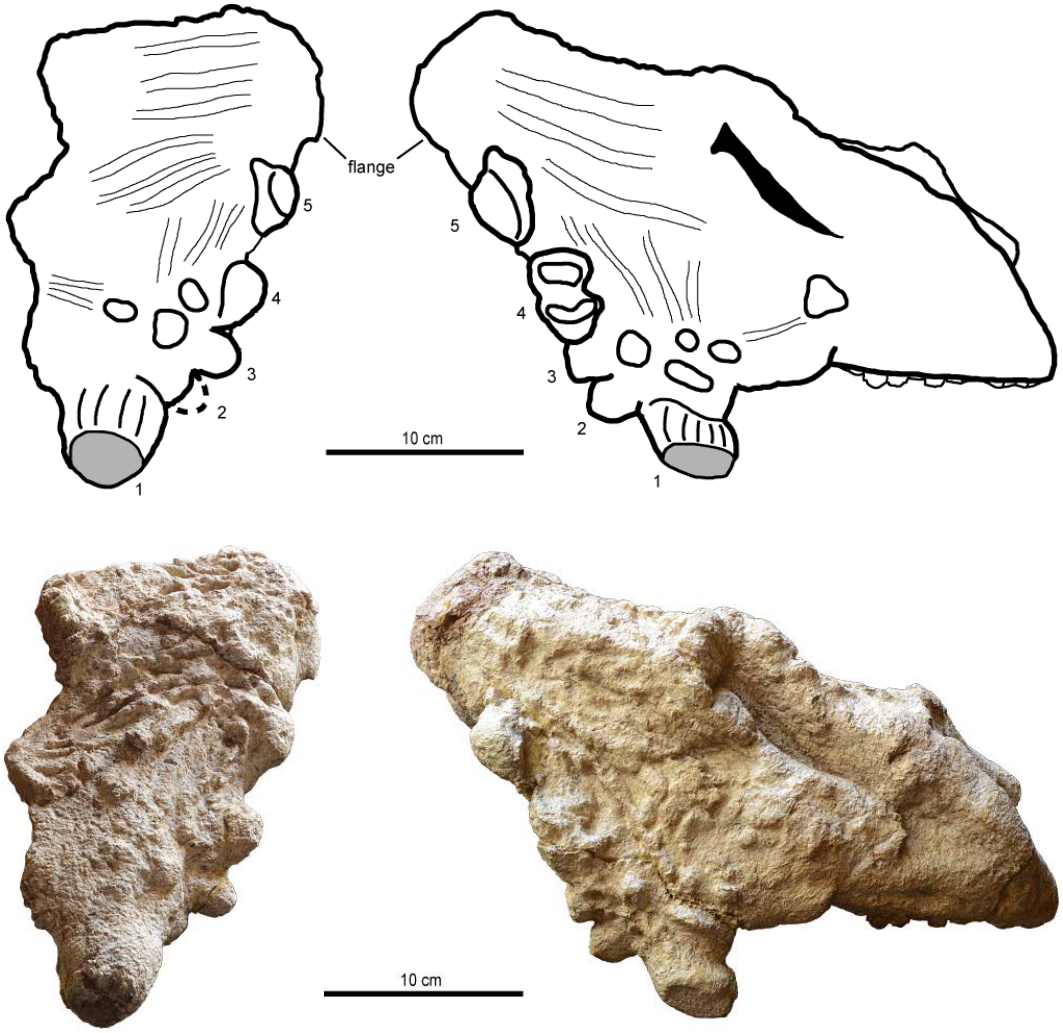


Figure 3.6: Photographs and interpretive drawings of specimen CGP JA 109 (*Nochelesaurus alexanderi*), in (A) left lateral and (B) right lateral view.

The ventral border of the cheek of the holotype is oriented anterodorsally and forms an angle of 33^{0} with the horizontal tooth row, forming a relatively large cheek flange compared to the other South African basal pareiasaurs, similar in size to the holotype of *Embrithosaurus* (29^{0}), but larger than many specimens of *Bradysaurus baini*. Common to all basal South African pareiasaurs, there are no bosses present on the ventral edge of the cheek except for a low, long, convex bulge that extends over entire ventral surface.

Internally, the quadratojugal sends out a thick vertical flange, which extends medially. At the level of the quadrate foramen, the quadratojugal has a horizontal suture with the squamosal dorsally, which continues this vertical

flange. Below the quadrate foramen, the quadratojugal flange has a long vertical suture with the vertical ramus of the quadrate flange.

Squamosal (Figs. 3.1, 3.2, 3.3, 3.4, 3.5, 3.6)

The squamosal is a flat plate-like bone that forms most of the posterodorsal portion of the cheek and a narrow section of the dorsal skull table. Dorsally, the squamosal has a longitudinal sutural contact with the supratemporal, anterodorsally an oblique suture with the postorbital, anteroventrally a very short suture with the jugal and ventrally a long longitudinal suture with the quadratojugal.

The longitudinally oriented sharp junction between the dorsal skull table and the lateral side of the skull passes through the dorsal most part of the squamosal, just below the squamosal-supratemporal suture.

The lateral surface of the squamosal is greatly ornamented, but unlike some more derived pareiasaurs (e.g. *Scutosaurus,* Lee 1994, *Pareiasuchus nasicornis,* Lee *et al.* 1997, *Deltavjatia,* Tsuji 2013) has no central boss or complex of bosses near the centre of the bone. Thick, long, parallel and posterodorsally oriented rugose ridges with furrows are present anteriorly and thinner and less distinct vertically oriented rugose ridges with furrows are seen in the central and posterior portion of the bone. Numerous small pits and depressions are also present. *Embrithosaurus* and *Bradysaurus baini* also lack a central boss on the lateral surface of the squamosal, and have a similar arrangement of rugose ridges. Lee (1994, 1997a) however illustrated the skull of *Bradysaurus baini* (using the holotype NHMUK R1971 and a specimen SAM-PK-5002) as possessing a central boss complex on the lateral surface of the squamosal. It appears that he may have misinterpreted the rugose anterior tab-like extension of the dorsal part of the squamosal's posterior cheek edge boss (see below), as a separate boss complex.

On the posterior edge of the squamosal, are numerous circular pits and indistinct rugose ridges and one very large and distinct boss. In cross section this boss is irregularly shaped but roughly oval, single to double lobed, and vertically elongated. Oriented and projecting posterolaterally, the dorsal portion of this boss has a thickened tab-like process that extends anteriorly 20-30 mm onto the lateral external surface of the squamosal. This is similar to the arrangement and morphology of squamosal bosses of all other basal South African pareiasaurian taxa. *Nochelesaurus* differs from other taxa in the significantly greater height of the posterolaterally projecting boss than in all other basal pareiasaur taxa from South Africa. In addition, the holotype and specimen SAM-PK-6238 also show separate dorsal and a ventral posterolateral projections on this boss (single or double lobed), which are not present in any other basal South African pareiasaurian taxa.

On the posterior edge of the dorsal portion of the squamosal of the holotype, above the large boss, is an embayment cause by damage and a section of missing bone. In *Scutosaurus*, Lee (1994) attributes a shallow, broad embayment on the dorsal portion of the posterior edge of the squamosal, to a weakly-developed otic notch, but reported no otic notch in *Pareiasuchus nasicornis* (Lee *et al.* 1997). Boonstra (1934a:12) notes the presence of a small, remnant, otic notch on the posterior edge of the squamosal of typical pareiasaurian skulls, just below the posterior shelf of the supratemporal. Tsuji (2013), in describing *Deltavjatia rossicus* reported a small notch facing internally on the posterior edge of the squamosal. This notch is not obvious in the holotype of *Nochelesaurus* (due to damage and missing bone) but is obvious in referred specimen SAM-PK-6238 where a deep horizontal otic notch is present, outlined by a raised rim, which extends medially and anteriorly some distance along the internal surface of the squamosal. Above the the otic notch, SAM-PK-6238 (Fig. 3.4, boss 6), SAM-PK-6239A (Fig. 3.5, boss 6) and CGP JA 109 (Fig. 3.6) have a second, small boss on the posterior edge of the squamosal (absent in the holotype, probably due to poor preservation). (This second, higher, smaller boss on the posterior edge of

the squamosal is rarely observed, but is present in a few other cranial specimens, across all basal South African pareiasaurian species, e.g. on *Bradysaurus baini* specimen SAM-PK-5002).

The extreme dorsal corner of the posterior edge of the squamosal forms the lateral-most portion of the occipital flange of the skull and is vertically oriented with a curved lateral side, a flat medial side and a sharp posterior edge. In *Nochelesaurus*, the posterodorsal portion of the squamosal is narrower in mediolateral extent than in *Embrithosaurus* and *Bradysaurus baini*.

Internally, medial to the posteroventral edge of the occipital flange, the squamosal has a sutural contact with the ventral portion of the distal end of the paroccipital process of the opisthotic. Below the contact with the paroccipital process, the squamosal forms a thick, vertical flange which medially has a long, vertical suture with the quadrate ramus and ventrally a short horizontal suture with the quadratojugal.

Lacrimal (Figs. 3.1, 3.2, 3.3, 3.4, 3.6)

The lacrimal is roughly rectangular in lateral view and located on the posterodorsal side of the face extending from the orbit to the external naris. It sutures with the nasal dorsally, prefrontal posterodorsally, jugal posteroventrally and maxilla anteroventrally. Sutural contacts with the nasal, prefrontal and jugal are short and generally straight, but the lacrimal-maxilla contact is long and sigmoidal. The lacrimal forms a large portion of the dorsolateral border of the external naris and a small part of the anterior margin of the orbit.

In the holotype, the right lacrimal is mostly complete, except for two small wedge-shaped pieces that are not preserved and have been reconstructed with plaster (Fig. 3.3). This plaster obscures the lacrimal's contribution to the antorbital buttress (orbital margin) of the holotype, but the right orbital marginal wall of the lacrimal of SAM-PK-6238 shows a long suture with the descending

flange of the medial prefrontal (Fig. 3.4) (as in *Embrithosaurus*) and shows the lacrimal forming the anterolateral part of the antorbital buttress.

Distinct cranial ornamentation covers the lacrimals of the holotype and SAM-PK-6238. Located 20 mm anterior of the anteroventral corner of the orbit is a small, pointed, boss. A little above the centre of the lacrimal is a central boss which is less distinct and wider, posterodorsally oriented and is a continuation of the posterodorsally oriented maxillary ridge that surrounds the lateral border of the external naris. At the maxilla-lacrimal suture is a gap in the ridge which is much longer in SAM-PK-6238 and CGP JA 109 than in the holotype. A third boss is located high on the lacrimal, where the nasal and prefrontal meet, and is small, elongated and transversely oriented. On the left lacrimal of the holotype, this dorsal boss has an additional longitudinally elongated component (not present in SAM-PK-6238) forming a right angled L-shaped boss. *Bradysaurus baini* and *Embrithosaurus* have a similar number and arrangement of lacrimal bosses compared to *Nochelesaurus*, but they are much less distinct in *Bradysaurus baini*

Prefrontal (Figs. 3.1, 3.2, 3.3, 3.4, 3.6)

The prefrontal is roughly rectangular in dorsal view and located almost entirely on the dorsal skull table where it forms the anterodorsal margin of the orbit. Anteroventrally, a small portion of the bone contributes to the lateral facial region of the skull. The bone is about twice as long as wide, is nearly horizontally flat, and is gently curved along the orbital margin. Medially, the prefrontal contacts the nasal and the frontal. Anteriorly, the prefrontal has a transverse suture with the lacrimal and posteriorly a transverse suture with the postfrontal.

The descending, tapering vertical flange of the prefrontal is present in the left and right orbital rims of SAM-PK-6238 (Fig. 3.4). It is not preserved on the holotype of *Nochelesaurus* and is present in the holotype of *Embrithosaurus*.

One large oval elongated boss, about twice as long as wide, is present above most of the anterodorsal orbital margin in the holotype and SAM-PK6238,

creating a thickened anterodorsal orbital margin. A similar large, elongated orbital boss is also present in *Bradysaurus baini,* whereas this boss is smaller and rounder in the holotype of *Embrithosaurus*.

Anteriorly, the prefrontal of the holotype and SAM-PK-6238 have two short rugose ridges: one positioned in the anteromedial corner of the bone that extends towards the posterolateral nasal tab-like process, and the other anterolaterally on the prefrontal, well above the orbital marginal rim, that extends towards the most dorsal lacrimal boss. The placement and size of these two tubercles is similar in *Bradysaurus baini* and *Embrithosaurus*, except that the anterolateral tubercle is much larger in the holotype of *Embrithosaurus*, where it forms a large, prominent, protruding boss.

Nasal (Figs. 3.1, 3.2, 3.3, 3.4, 3.6)

The nasal is roughly triangular in dorsal view, located anteromedially on the skull roof, and tapers anteriorly. Dorsoventral compression has flattened the nasal of the holotype but its natural shape would be slightly externally convex. The nasal has a long, straight, longitudinal midline suture with its contralateral element, a straight transverse suture with the frontal posteriorly, and short, slightly curved sutures with the prefrontal posterolaterally, and the lacrimal anterolaterally.

A long, thin, anteriorly tapering descending processes of the nasal forms the dorsomedial border of the external naris and the dorsal half of the internarial bar. Dorsoventral compression of holotype has oriented the dorsal half of the internarial bar horizontally, but SAM-PK-6238 preserves the more natural vertical and slight posterodorsal orientation.

A large anteromedially elongated boss is present at the centre of the nasal and is similar in size, shape and orientation in all basal South African pareiasaurian taxa. All basal taxa possess two small, elongated, oval rugose ridges (which I term nasal tab-like processes or nasal boss tabs) radiating from each main central nasal boss: a distinct posterolateral tab and a less distinct posteromedial tab.

Only *Bradysaurus baini* and *Embrithosaurus* carry a third very distinct anterolaterally oriented tab-like process, above the external naris. However, one specimen of *Nochelesaurus* (CGP JA 109) does have an anterolateral nasal tab-like process on the right. Additionally, in all these basal pareiasaurid species, several minor, thin and low rugose ridges radiate from the main nasal boss.

Internally, the nasal of the holotype and SAM-PK-6238 has a thin, longitudinally oriented ridge emanating posteriorly from the dorsal border of the external naris. Posteriorly, this ridge tapers and reaches a distinct and deep notch. This internal nasal ridge and notch is also present in the holotype of *Embrithosaurus*.

At the posteromedial corner of the nasal, at the junction of the nasal-frontal sutures, the holotype skull has a midline boss which is contributed to equally by all four bones. This nasal-frontal median boss is low, wide and irregular in cross section and unique to the holotype skull of *Nochelesaurus alexanderi* (SAM-PK-6239). Referred *Nochelesaurus* specimen SAM-PK-6238 was originally noted by Haughton and Boonstra (1929a) as possessing a similar median boss, but as pointed out by Lee (1994, 1997a) the small indistinct boss of this specimen is a taphonomic artefact caused by the mediolateral compression of the skull and the resultant buckling of the paired nasal bones on the midline.

Frontal (Figs. 3.1, 3.2, 3.3, 3.4, 3.6)

The frontal is rectangular in dorsal view and forms a large portion of the anteromedial dorsal skull table. It is almost twice as long as wide and is horizontally flat with a straight, midline, longitudinal suture with its contralateral element. Anteriorly the frontal has a straight, transverse suture with the nasal, anterolaterally a short, curved suture with the prefrontal, posterolaterally a short, curved suture with the postfrontal and posteriorly a short, straight suture with the parietal. The frontal does not participate in the orbital rim.

At the centre of the frontals of the holotype and SAM-PK-6238 (worn off in CGP JA 109) is a small high boss. Regular rugose ridges radiate out from the boss and

reach anterolaterally onto the posterior half of the prefrontal. On the holotype, this boss on the right frontal is complete but the left boss has been sheared off just above the base. On SAM-PK-6238 only the right frontal is completely preserved and the boss is weathered, but still identifiable. All other *Tapinocephalus* AZ pareiasaurid species show the same radial pattern of rugose emanations from the centre of the frontal, but from a very small tubercle in *Embrithosaurus* or from an indistinct, low swelling in most specimens of *Bradysaurus baini*. These two usually taxa do not show the larger, very distinct, high and clearly separated frontal central boss observed in *Nochelesaurus,* but few specimens do.

At the posterolateral corner of the frontal is a large and low, relatively indistinct and posterolaterally elongated boss. The size, shape and orientation of this low frontal boss is similar in all basal South African pareiasaurian taxa, with variation only in the level of clear separation between this boss and the bosses of the adjacent posterolateral postfrontal. In the holotype of *Nochelesaurus* and referred specimen CGP JA 109, this frontal boss is separated from the bosses of the postfrontal by a narrow trough that runs along the longitudinal frontal-postfrontal contact. In *Embrithosaurus* and *Bradysaurus baini* (left side of holotype) no definitive separation can be seen between this frontal boss and the two orbital marginal bosses of the postfrontal, all of which coalesce into a single large continuous boss. The more distinct separation of these bosses observed in *Nochelesaurus* is probably the result of better preservation of these skulls and not a true diagnostic feature.

Internally the surface of the frontal of the holotype of *Nochelesaurus* is smooth except for a short, longitudinal, low ridge near the centre of the bone, which is also present in the referred *Nochelesaurus* specimen SAM-PK-6238, and the holotype of *Embrithosaurus.* Posteromedially, along this ridge, in the holotype of *Nochelesaurus*, the cylindrically-shaped sphenethmoid sutures perpendicularly with the flat ventral surface of the frontal.

Postfrontal (Figs. 3.1, 3.2, 3.3, 3.4, 3.6)

The postfrontal is roughly square to slightly rectangular in dorsal view and forms a small part of the dorsal margin of the orbit. It shares a short transverse suture with the prefrontal anteriorly, a long curved suture with the frontal medially, and short straight sutures with the parietal posteromedially and the postorbital posterolaterally.

Wedged between the prefrontal and the postorbital, the sutures of the postfrontal do not pass directly perpendicularly through the bone, instead they constrict ventrally, so that in dorsal view (Figs. 3.1, 3.2) the shape and surface area of the bone is much larger than in ventral view (Fig. 3.7). In lateral view the ventral contraction of the bone can be seen (Figs. 3.3, 3.4) as it tapers ventrally to make only a very small contribution to the dorsal margin of the orbit. Referred specimen SAM-PK-6238 contracts ventrally less than the holotype and so makes a larger contribution to the orbit. Both the holotype and specimen SAM-PK-6238 show that dorsally, the postfrontal is roughly square to slightly elongated longitudinally, with the posterior portion of the bone directed medially. Internal sutures are not easily identified on the holotype and are not accessible in specimen SAM-PK-6238.

Two distinct bosses are present on the dorsal surface of the postfrontal of the holotype: one in the anterolateral corner of the bone, a little above the dorsal orbital margin; and the other in the centre of the bone, placed posteromedial to the first boss and further away from the dorsal orbital margin. These bosses are longitudinally arranged, round, and somewhat indistinct. In SAM-PK-6238 the bosses of the postfrontal are even less distinct as a result of surface erosion of the bone, but two low bosses appear to be present. The condition in CGP JA 109 is not clear.

Straight oblique rugose ridges that emanate radially from the central boss of the parietal, cover the posterior half of the postfrontal.

Postorbital (Figs. 3.1, 3.2, 3.3, 3.4, 3.5, 3.6)

The postorbital forms the dorsal half of the posterior margin of the orbit. It consists of two flat plates: a horizontally oriented plate on the dorsal skull table and a vertically oriented plate on the lateral cheek on the side of the skull. The bone is roughly pentagonal in lateral view and sutures with the postfrontal anteriorly, parietal medially, supratemporal posterodorsally, squamosal posteroventrally, and jugal ventrally.

A prominent, large, pear-shaped boss is present at the posterodorsal corner of the orbit of all specimens of *Nochelesaurus*. One or more small tubercles extend anteriorly from this boss along the orbital margin. The large boss and tubercles create a general thickening of the posterodorsol orbital margin of the skull. All basal South African pareiasaurian taxa show a very similar swollen posterodorsal orbital margin on the postorbital, created by one large boss at the posterodorsal orbital corner.

Four prominent straight ridges emanate posteriorly from the pear-shaped postorbital boss of the holotype, SAM-PK-6238 and SAM-PK-6239A. One ridge extends from the posterior edge of the boss, along the lateral side of the cheek of the skull, and continues on the squamosal. Three further ridges extend from the posterodorsal edge of the boss, and continue posteriorly and slightly medially onto the supratemporal. These merge with thick, projecting rugose lines, emanating anteriorly and slightly laterally from the very large central boss of the supratemporal. These four ridges together form the junction between the skull table and cheeks, and are similar in morphology in *Embrithosaurus*. In contrast in *Bradysaurus baini* the area consists of only a single swollen, thick cheek ledge and individual ridges are not identifiable.

Parietal (Figs. 3.1, 3.2, 3.3, 3.4)

The parietal forms a large portion of the posteromedial dorsal skull table. The bone is roughly square in dorsal view, horizontally flat, slightly convex in anterior view, and sutures with its partner along the midline.

The parietal has a straight transverse suture with the frontal anteriorly, short, straight suture with the postfrontal anterolaterally, longitudinal and slightly curved suture with the postorbital laterally, short sharply curved suture with the supratemporal posterolaterally and a straight oblique suture with the postparietal posteriorly.

One indistinct and low boss is present at the centre of the parietal, little more than a thickened general rugose swelling. However, from this indistinct central boss, extremely distinct rugose ridges extend outwards in a radial pattern, reaching some distance onto all the neighbouring elements. Small to large circular pits are present between them. The ridges that reach posterolaterally are the thickest and most distinct and merge with anteromedially extending ridges from the large main supratemporal boss. This indistinct central boss of the parietal with very distinct radial ridges is present in all basal South African pareiasaurian taxa.

A very large, circular pineal foramen is present on the midline suture. It is surrounded by a slightly raised rim of rugose bone, comprising ridges that emanate from the central boss of the parietal. The pineal foramen is situated very close to the frontal-parietal suture, within the anterior third of the parietal, similar to the situation in all basal South African pareiasaurian taxa. The shape may vary and appears anteroposteriorly elongated in some specimens, such as referred *Nochelesaurus* specimen SAM-PK-6238 and the holotype of *Embrithosaurus*. These elongated shapes are due to mediolateral compression.

Internally, on the ventral surface of the skull, the parietal anteriorly sutures with the posterior part of the cylindrically-shaped sphenethmoid bone which protrudes ventrally from the flat ventral surface of the parietal of the holotype.

Posteriorly, the parietal contacts the ventral process of the postparietal, observed in the holotype and SAM-PK-6238.

Postparietal (Figs. 3.1, 3.2, 3.3, 3.4)

The postparietal is rectangular and forms the median portion of the posterior part of the dorsal skull table. It is a single unpaired element, mediolaterally expanded, and approximately twice as wide as long. Straight oblique sutural contacts occur with the parietals anteriorly and straight longitudinal contacts with the supratemporals laterally. The postparietal is almost completely flat and in occipital view is slightly depressed and U-shaped.

On the posteromedial edge of the postparietal of the holotype, at the midline of the skull, a small wedge of bone is missing, creating the misleading appearance of a significant median anterior notch on the skull roof. At the anterior edge of this notch, a small, distinct boss is present which is unique to the holotype of *Nochelesaurus*.

Thick longitudinally oriented rugose ridges (posterior extensions from each central boss of the parietals) cover the anteromedial surface of the postparietal of the holotype and SAM-PK-6238.

In the anterolateral corner of the wide postparietal of the holotype specimen, SAM-PK-6238 and CGP JA 109 is a low, indistinct swelling, which is a thickening of the rugose lines emanating anterolaterally from each large supratempral central boss. In contrast, the narrow postparietal of *Bradysauris baini* and *Embrithosaurus* excludes this swelling, which occurs instead on the adjacent supratemporal bone.

A pair of long, thin and shallow longitudinally oriented depressions are present either side of the midline on the dorsal surface of the postparietal of all *Nochelesaurus* specimens. In *Bradysaurus baini* and *Embrithosaurus*, these depressions are on the postparietal-supratemporal suture.

Each posterolateral corner of the postparietal bears a large boss, which is irregularly shaped due to short, thick, tab-like processes emanating in a roughly radial pattern. On the holotype, the right boss is sheared off near its base. These posterolateral corner bosses of the postparietal are not present on the narrow postparietal of *Bradysauris baini* and *Embrithosaurus*, where they occur instead on the supratemporal.

The posterior border of the postparietal curves downwards to form a sharp, thin ventral edge which overhangs the occiput slightly. The overhanging occipital flange continues laterally on the supratemporal and squamosal and is common to all the basal South African pareiasaurs.

In the holotype and SAM-PK-6238 the internal surfaces of the cranial bones are well exposed. Internally, the posterior edge of the postparietal forms a thickened bar of bone (30 mm wide, 10 mm high) with a sharp edge at its anterior boundary. This bar persists laterally onto each supratemporal and follows the contours of and runs parallel to the posterior edge of the skull.

The descending process of the postparietal of the holotype has only a small preserved section on the left. This midline ventrally directed pillar on the postparietal is located at the anterior edge of the thickened bar of the postparietal. Referred specimen SAM-PK-6238 preserves the descending process of the postparietal as a thick pillar, diamond-shaped in cross section with anterior and posteriorly tapering edges. In *Embrithosaurus* and *Bradysaurus baini*, this process is triangular in cross section, with posteriorly tapering edges. The triangular shapes of these two taxa are probably the result of distortion as the descending process of the postparietal is diamond-shaped in all other pareiasaurian taxa where it is known. A 20 mm long, low, but sharp longitudinal ridge is present behind the descending process of the postparietal, on the midline, which extends posteriorly to the posterior border of the skull. This feature is also present in *Embrithosaurus*.

Supratemporal (Figs. 3.1, 3.2, 3.3, 3.4, 3.5, 3.6)

The supratemporal (termed the “tabular” by Haughton and Boonstra (1929a) and Boonstra (1934a)) is a very thick and robust bone which forms the posterolateral corners of the dorsal skull table. It is roughly square in dorsal view. It sutures with the postparietal medially, the parietals anteromedially, the postorbitals anteriorly and the squamosal laterally.

The largest boss on the skull of *Nochelesaurus* is on the supratemporal, at the posterolateral corner of the skull. As is typically found in many *Tapinocephalus* AZ pareiasaur specimens, this boss is sheared off near its base and its natural height and morphology cannot be determined accurately in the holotype or specimen CGP JA 109. Nevertheless, the preserved cross section of the right boss on the holotype, shows it to have been extremely large, slightly wider than long, and 45 mm wide at the base. SAM-PK-6238 and SAM-PK-6239A preserve the right supratemporal boss as more circular in cross section and taller. This boss is not placed on the posterior edge of the skull, but is situated more anteriorly and dorsally, with the posterior edge of the base of the boss located about 40 mm above the posterior edge of the curved occipital flange. The supratemporal boss has a similar morphology in all basal South African pareiasaurian species, and therefore does not appear to be diagnostically useful, but it does appear to be higher, taller and more distinct in specimens of *Nochelesaurus* than in specimens of *Bradysaurus baini*.

Thick rugose ridges extend outwards from each large supratemporal boss: three anteriorly and slightly laterally oriented ridges with furrows transmit anteriorly onto the postorbital; two to three obliquely oriented thick ridges transmit anteromedially onto the parietal; and one or two transmit medially and slightly anteriorly onto the postparietal. This pattern is consistent amongst all basal South African pareiasaurs.

The internal cranial surfaces of the holotype and SAM-PK-6238 show the thickened bar of bone (30 mm wide,10 mm high) that follows the posterior edge of the skull. Medially, the width of the bar is the same on the postparietal but

widens laterally to form a strengthened ventrally directed flange. Dorsally, this flange sutures with the dorsal distal end of the paroccipital process of the opisthotic, and ventrally with the squamosal.

3.5.2 Palate

General Comments

The palate comprises the vomer, palatine, pterygoid, ectopterygoid, epipterygoid and quadrate bones, as well as the palatal sections of the premaxilla and maxilla. The pareiasaurian palate forms an internal, flat, horizontally oriented shelf of bone, located at a level that is well above the level of the maxillary teeth.

Most of the palate of the holotype of *Nochelesaurus* is not preserved, apart from a small pterygoid fragment and portions of the internal palatal flanges of the premaxilla and maxilla. A partial vomer is also preserved.

Most of the palate and braincase of SAM-PK-6238 are present in articulation. The ventral surface of the palate was partially prepared by Johann van den Berg at the Iziko South African Museum in Cape Town in July 2017 to reveal the palatal teeth, however, much matrix remains, obscuring suture identification. Specimen CGP JA 109 has only a unprepared partial palate preserved, on the right side. The following palatal description is based on SAM-PK-6238, unless otherwise stated.

Vomer (Figs. 3.7, 3.8)

The holotype of *Nochelesaurus* preserves only a small portion of the anterior part of the vomer and SAM-PK-6238 preserves most of the element. The vomer is a generally flat, plate-like bone forming the anterior-most part of the palatal flange behind the prepalatal foramen. Anteriorly it has a short and straight transverse suture with the premaxilla at the posterior border of the prepalatal foramen. The vomer sutures with its partner element along the midline. Posteriorly, the vomer has a transverse suture with the pterygoid, visible in dorsal view in specimen SAM-PK-6238, just behind the posterior border of the

internal naris. The small posterior contact of the vomer with the palatine is unclear in SAM-PK-6238 and has been restored (Fig. 3.8) according to the position typical of basal South African pareiasaurs.

The dorsal surface of the vomer of SAM-PK-6238 reveals a longitudinally oriented midline ridge (20 mm high) which is an anterior continuation of the dorsal midline ridge of the pterygoid. Either side of this midline ridge, the alar flange of the vomer (Damiani and Modesto 2001) is much thinner and flatter and forms the medial border of the internal naris (choana). The internal naris of SAM-PK-6238 is distorted and very narrow, as a result of the mediolateral compression of the skull.



Figure 3.7: Photograph of the skull of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in ventral view.

Anteroventrally the vomer of SAM-PK-6238 bears several relatively large denticles (3-4 mm diameter), roughly arranged in two parasagittal rows on either

side of the midline. These teeth are broken off just above their bases, and would probably have been 10-15 mm in length. The denticles do not occur laterally on the thin alar flange of the vomer, but are positioned medially within 20 mm of the midline, where the vomer forms a thickened, longitudinal bar. On the posterior portion of the ventral vomer, the denticles are smaller (1-2 mm diameter) than the large anterior denticles, are arranged into two rough rows either side of the midline, and extend posteriorly on to the pterygoid. Several smaller denticles (<1 mm diameter) are interspersed or scattered irregularly around the anterior and posterior parasagittal rows.

Palatine (Fig. 3.8)

The palatine is a small flat, flange-like, palatal bone located anterolaterally on the palate. It forms the posterolateral border of the internal naris and sutures with the palatal flange of the maxilla anterolaterally. Posterolaterally the palatine contacts the ectopterygoid and forms the anteromedial and medial border of the large suborbital vacuity or foramen palatinum posterius. The ectopterygoid forms the anterolateral, lateral and posterior border of this foramen.

The double row of obliquely directed denticles, carried primarily on the pterygoid (see Pterygoid), extend anterolaterally onto the posterior portion of the palatine.

Pterygoid (Fig. 3.8)

The pterygoid is a complex bone forming the posteromedial portion of the palate. It comprises anteriorly a wide, flat, horizontally oriented plate containing multiple rows of denticles. Posterolaterally and posteromedially, vertically oriented, wall-like processes connect the pterygoid to the side of the skull and to the braincase.

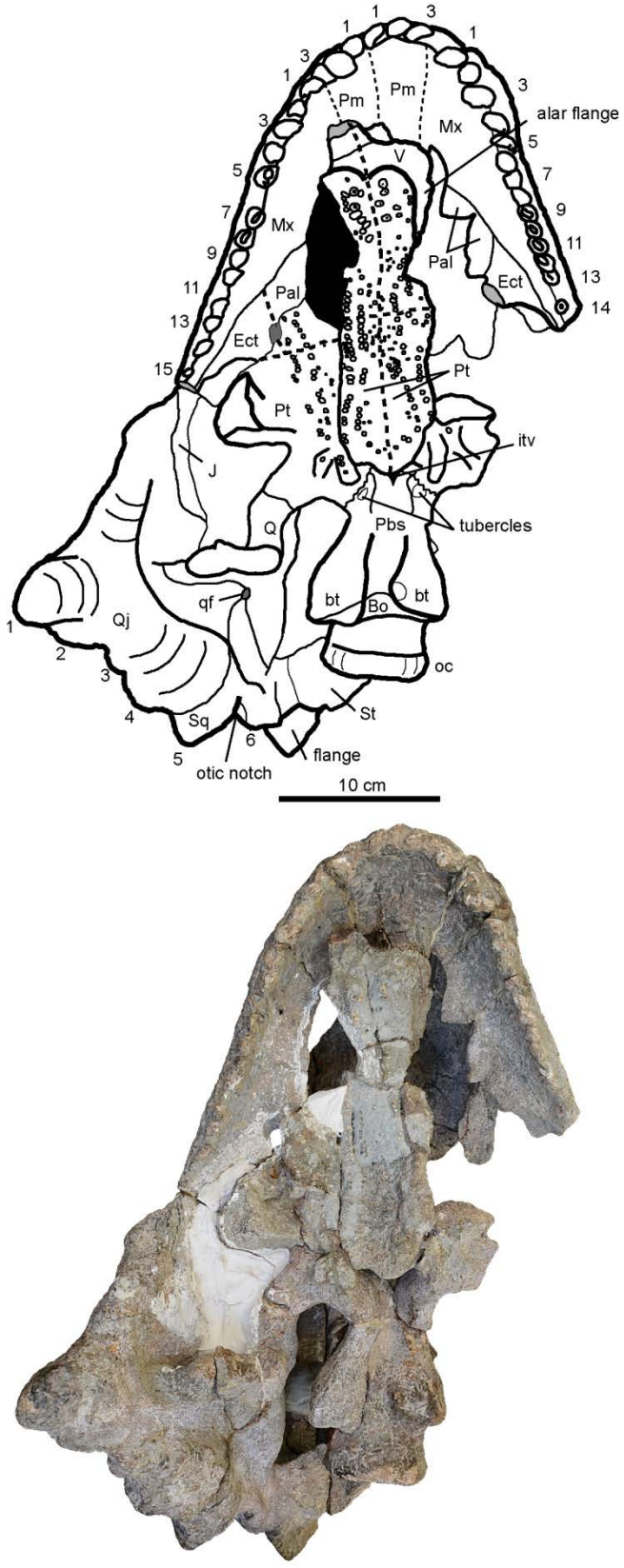


Figure 3.8: Photograph and interpretive drawing of the skull of SAM-PK-6238 (*Nochelesaurus alexanderi*), in ventral view.

Anteriorly the pterygoid sutures with the vomer. Either side of the midline two rows of denticles are present. There are 20-25 teeth (1-2mm diameter), longitudinally arranged in each row, which converge anteriorly towards the midline. Each double row of denticles are positioned either side of a shallow longitudinal midline depression. The depression contains several smaller randomly scatter denticles in its anterior portion. Posteriorly, the medial row of denticles curve medially to meet at the midline and follow the contour of the anterior border of the interpterygoid vacuity. An obliquely oriented double row of about 15 denticles, extends anterolaterally from near the posterior portion of the pterygoid, onto the palatine. The placement and orientation of the rows of denticles and the numbers and size of these denticles on the pterygoid are very similar in the holotypes of *Embrithosaurus* and *Bradysaurus baini*.

Anterolaterally, the pterygoid contacts the palatine and the ectopterygoid, but the sutures are unclear on SAM-PK-6238 and have been restored (Fig. 3.8) according to the positions typical of basal South African pareiasaurs.

Posteromedially the pterygoid forms the anterior and anterolateral borders of the interpterygoid vacuity, where it has an immobile and robust suture with the basipterygoid process of the parabasisphenoid. The interpterygoid vacuity is roughly rectangular in ventral view, transversely wide, with an anterior border that projects slightly posteriorly at the midline forming a shallow u-shaped border, as is the condition in the holotype skulls of *Embrithosaurus* and *Bradysaurus baini*. The lateral edges are shorter and taper towards the midline posteriorly. The shape of the interpterygoid vacuity, viewed ventrally, is very similar in the holotype of *Embrithosaurus.* In dorsal view the lateral border of the interpterygoid vacuity, formed by the pterygoid, is made of a thick vertical plate and there is a notable deep round notch (30mm diameter, 10mm deep) on the dorsal surface of the pterygoid, either side of the anterolateral corner of interpterygoid vacuity.

SAM-PK-6238 preserves a partial right transverse flange of the pterygoid. The lateral edge is curved and directed ventrally and projects 20-30 mm below the level of the rest of the palate. The posteroventral edge is flat, 30 mm high, and has a sharp ventrally projecting ridge. Although no denticles are present on SAM-PK-6238, specimen CGP JA 109 has a row of 10-15 large denticles on the posterior edges of both transverse processes as is the situation in *Embrithosaurus* and *Bradysaurus baini*. The transverse process extends laterally to almost reach the inner surface of the jugal, but this close proximity is a result of the mediolateral compression of the skull.

Posterolaterally, the pterygoid sutures with the quadrate along the quadrate ramus of the pterygoid, which is vertically oriented, wall-like, thicker ventrally than dorsally, and roughly triangular in cross section.

The dorsal surface of the pterygoid, as is evident from SAM-PK-6238 and the holotype fragment, has a anteroposteriorly oriented ridge that rises and widens posteriorly. This median ridge is also seen in *Embrithosaurus*. Lateral to the ridge is a longitudinal depression or trough.

The holotype of *Nochelesaurus* preserves only a small partial midline pterygoid fragment with two rows of denticles either side of the midline.

Ectopterygoid (Fig. 3.8)

The ectopterygoid, the smallest bone of the palate, is located anterolaterally. It is a flat, horizontally oriented flange, thicker laterally and thinner medially. It has a long suture with the maxilla anterolaterally and a short suture with the palatine anteromedially which passes through the large open foramen palatinum posterius. The posterior contact with the pterygoid, preserved on only the right of SAM-PK-6238, is difficult to identify with certainty.

Epipterygoid (Fig. 3.8)

The epipterygoid is not preserved in any specimen of *Nochelesaurus*, but is assumed to have been present as in other pareiasaurs, such as the holotype of *Embrithosaurus*, where it is present as a small flat bone that overlies the dorsal surface of the posterolateral portion of the pterygoid.

Quadrate (Fig. 3.8)

The quadrate is a vertically oriented, transversely directed plate-like bone which connects the palate to the inner skull roof. Medially it sutures with the pterygoid on the quadrate ramus and extends posterolaterally. Here the quadrate is thick, dorsoventrally low, and triangular in cross section (thicker ventrally, and tapering dorsally). The posteromedially facing surface of the medial portion of the quadrate of SAM-PK-6238 presents a long, oblique shelf which creates an anterior embayment, also observed in the holotype of *Embrithosaurus.* A distinct vertical ridge separates the medial and lateral portions of the quadrate, also present in all other co-occurring species. The lateral portion of the quadrate forms a tall, thin flange that connects perpendicularly to the inner surface of the cheeks. Laterally the quadrate sutures with the internal flanges of the squamosal dorsolaterally, with a long, vertical sutural contact, and the quadratojugal ventrolaterally, with a short, vertical suture.

Dorsoventral crushing of the holotype and mediolateral crushing of SAM-PK-6238 have displaced each right quadrate to lie closer and almost flush against the inner skull roof surface than would have been the situation in life.

A large oval quadrate foramen is present on the posterior facing lateral portion of the quadrate, at the intersection of the quadrate, squamosal and quadratojugal. Its medial borders are formed by the quadrate, the dorsolateral border by the squamosal, and the ventrolateral border by the quadratojugal.

The holotype of *Nochelesaurus* does not preserve the distal, ventral, articulation of the quadrate with the articular of the lower jaw. SAM-PK-6238 shows this

articulation as transversely expanded, anteroposteriorly narrow, and consisting of a small medial condyle and a larger and wider lateral condyle which are separated by a wide shallow groove.

3.5.3 Braincase and occiput

General Comments

The pareiasaurian braincase is formed by the parabasisphenoid, basioccipital, exoccipital, supraoccipital, prootic, opisthotic, sphenethmoid, and the stapes.

The holotype of *Nochelesaurus* preserves a large isolated fragment comprising most of the braincase. Posteriorly, the occipital condyle is not preserved, dorsally the supraoccipital is only partially preserved and the left the paroccipital process of the opisthotic is partially preserved. On the inside of the skull roof, the sphenethmoid is sutured to the ventral surface of the frontal and parietal, and a piece of the right quadrate is preserved sutured to the ventral surfaces of the squamosal and quadratojugal. The distal (lateral) portion of the left paroccipital process of the opisthotic is sutured to the inner surface of the supratemporal and squamosal.

SAM-PK-6238 preserves most of the braincase in articulation with the palate. In addition, two small fragments comprise the dorsal half of the cavum cranii. Most of the braincase of specimen CGP JA 109 is very poorly preserved and eroded and not useful for descriptive purposes, apart from the well preserved paroccipital processes of the opisthotics. The holotype and SAM-PK-6238 are used as the basis for this description.

In the large pareiasaurs from the *Tapinocephalus* AZ, the braincase is bulky and solid and the individual constituent elements are strongly fused into a single mass of bone. As a result, sutures between most of the constituent elements are difficult to determine. Despite the highly ossified nature of the braincase of the holotype, the external surface of the bone is variously damaged and eroded, which paradoxically has resulted in the sutures being more clearly identifiable as

eroded grooves in certain regions. Additional preparation to the lateral walls of the braincase of the holotype, undertaken for this project, revealed the sutures and dimensions of the fenestra ovalis, the jugular foramen and the cranial nerves of *Nochelesaurus* for the first time although the well prepared braincase of the referred specimen SAM-PK-6238 (*Dolichopareia angusta*) was briefly described by Haughton (1929).

Sphenethmoid (Pleurosphenoid)

The sphenethmoid is a paired, roughly rectangular structure on the inner midline surface of the skull roof. Called the pleurosphenoid by Lee (1994, Lee *et al.* 1997), this bone is termed the sphenethmoid or interorbital septum by most other pareiasaurian workers (e.g. Watson 1914b, Boonstra 1934a, Tsuji 2013, Tsuji *et al.* 2013, Van den Brandt 2016).

The sphenethmoid is a complex, curved plate of bone that surrounds the anterior part of the brain and is located anterior and dorsal to the cultriform process of the parabasisphenoid. This element is inaccessible and unprepared in the holotypes of *Bradysaurus baini*. Amongst the basal South African pareiasaurs, the sphenethmoid has been described in detail only for *Embrithosaurus* (Holotype SAM-PK-8034, Van den Brandt 2016; referred specimen NHMUK R7782, Watson 1914b). The sphenethmoid is not preserved in specimen SAM-PK-6238, but is present and well exposed ventrally and laterally in the holotype of *Nochelesaurus*, which permits a rare view of this element.

On either side of the midline, each sphenethmoid plate is anteroposteriorly elongated and thin. It is solidly fused to the ventral surface of the skull roof: anteriorly to the frontals and posteriorly to the parietals. From the ventral surface of the skull roof, either side of the midline, each sphenethmoid plate extends ventrally before curving medially to meet each other at the midline, creating a roughly cylindrical enclosed cavity. This cavity is longitudinally continuous with the braincase cavity (cavum cranii) of the parabasisphenoid, indicating a long braincase.

The midline contact is wide, open and partially filled with matrix, indicating that the bones were not solidly fused here. In contrast, the midline suture of *Embrithosaurus* is strongly fused, creating a ventrally projecting, sharp, raised ridge.

The cylindrical shape of the paired sphenethmoids narrows medially, producing a "dumbbell" shape. This constricted shape is further exacerbated as the anterolateral and posterolateral edges of the bone, where they anchor to the ventral skull roof surface, are swollen and each project laterally for 15mm compared to the narrowest point of the waist. This dumbbell shape and the laterally projecting anterolateral and posterolateral corners of the sphenethmoid of *Nochelesaurus* is very similar in *Embrithosaurus*. Anteriorly, on the midline, the sphenethmoid shows a large v-shaped posteriorly directed notch, as a result of damage to the bone. The better preserved holotype of *Embrithosaurus* has an anteriorly projecting triangular spike at the anterior midline point and no notch.

Posteriorly, the ventrally orientated plates of the sphenethmoid thin to 2-3 mm. Each plate also tapers in dorsoventral height and the mediolateral width between the plates tapers posterioly until they merge with the lateral edges of the descending flange of the postparietal. Between these thin plates, is a large matrix filled cavity, where the medial edges of the plates form the ventral borders of the pineal foramen.

Parabasisphenoid (basisphenoid and parasphenoid) (Figs. 3.8, 3.9, 3.10)

The basisphenoid and parasphenoid are fused into a single undifferentiated element in pareiasaurs called the parabasisphenoid. It is a medial, thick bone that forms the horizontal floor or the ventral portions of the braincase cavity. As in all pareiasaurs, the braincase cavity (cavum cranii) is a median anteroposteriorly elongated cylindrical cavity, formed by the parabasisphenoid ventrally, prootic anterolaterally, opisthotic posterolaterally and supraoccipital dorsally. The cavum cranii is nearly free of matrix in both the holotype and SAM-PK-6238.

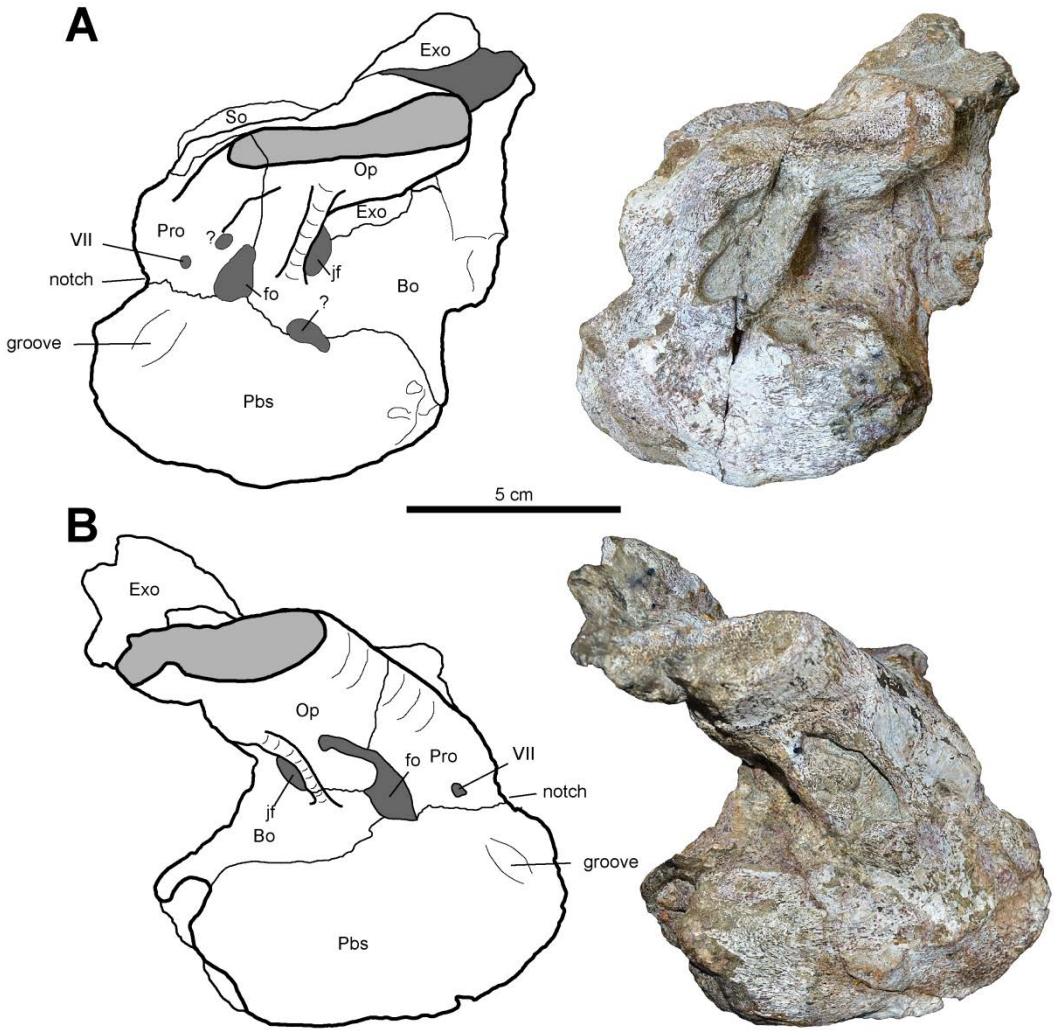


Figure 3.9: Photographs and interpretive drawings of the braincase of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in (A) left lateral view, and (B) right lateral view. Dorsal to the top of the page.

The parabasisphenoid sutures with the prootic anterodorsally and the basioccipital posterodorsally and posteriorly. The holotype does not preserve the anterolateral-most portions of the parabasisphenoid, but SAM-PK-6238 shows the anterior suture with the pterygoid on the basipterygoid process. Anteriorly, the parabasisphenoid of SAM-PK-6238 projects anterolaterally to form the vertically oriented, thin, plate-like basipterygoid processes. These processes are tear-shaped in cross section, wide and round ventrally and tapering dorsally where they form the posterior and posterolateral sides of the large interpterygoid vacuity.

The ventral surface of the parabasisphenoid of all specimens preserves the basal tubera. These are large anteroposterioly elongated, cylindrical structures that diverge and swell posteriorly either side of a deep midline depression. SAM-PK-6238 shows that the posterolateral edges of the basal tubera are positioned closer to the posterior edge of the occipital condyle (33 mm) than to the transversely narrowest part of the basipterygoid process (64 mm). This is the primitive pareisaurian condition shared with *Embrithosaurus, Bradysaurus baini* and *Bunostegos* (Tsuji *et al.* 2013).

Just posterior to the interpterygoid vacuity and the basipterygoid processes, the parabasisphenoid of the holotype and SAM-PK-6238 is transversely constricted and very narrow, (SAM-PK-6238: 52 mm wide, SAM-PK-6239: 35 mm wide). The posterolateral edges of the basal tubera are much wider (SAM-PK-6238: 88 mm wide, SAM-PK-6239: 85 mm wide). This produces a significant hourglass-shape when viewed ventrally.

Laterally, the sutures of the parabasisphenoid of the holotype are identifiable. Anteriorly there is a short horizontal suture with the prootic, which extends posteriorly to reach the anteroventral corner of the fenestra ovalis. The large fenestra ovalis is oval, posterodorsally oriented, and extends medially into the cavum cranii as is also evident in SAM-PK-6238. The anterior border of this fenestra is curved and the posterior border is vertically straight, on the left side of holotype and both sides of SAM-PK-6238. In addition, the right side of the holotype shows a strange, thin, long, posterodorsal extension of the fenestra (Fig. 3.9B), caused by deformation. The parabasisphenoid forms the ventral border of the fenestra ovalis, the prootic forms the anterior, anterodorsal and dorsal borders, the opisthotic the posterior border and the basioccipital the posteroventral border.

From the posteroventral corner of the fenestra ovalis a horizontal suture extends posteriorly to separate the parabasisphenoid from the basioccipital. The left side

of only the holotype, has a unidentified large, elongated fossa, positioned posteroventrally from the fenestra ovalis.

In dorsal view, the ventral floor of the cavum cranii is visible. Here the holotype shows a large foramen, just right of the midline, on the ventral surface of the horizontal floor of the cavum cranii. The midline cultriform process is not preserved in the holotype, nor SAM-PK-6238, as this part of the parabasisphenoid is missing in both specimens. It was likely short and wide as observed in the holotype of *Embrithosaurus*.

Interestingly, there is some rugosity on the bone on the ventral surface of each basipterygoid process on either side of the interpterygoid vacuity, just behind the suture with the pterygoid (Fig. 3.8). These tubercles are smaller and less distinct than the large and distinct tubercles present in specimens of *Scutosaurus* (e.g. PIN 2005/1883).

Basioccipital (Figs. 3.8, 3.9, 3.10)

The basioccipital is a medial bone located posteroventrally behind the cavum cranii and is strongly fused onto a single solid structure so as to be almost indistinguishable from the parabasisphenoid. The holotype preserves only the anterolateral and posteroventral portions of the basioccipital. Two deep and straight anteromedially oriented excavations, from either side of the midline, have removed the occipital condyle which is not preserved.

SAM-PK-6238 preserves the entire element where the basioccipital forms most of the large occipital condyle. The occipital condyle is round in occipital view, with a slightly flattened dorsal surface made by the exoccipitals. The condyle is 68 mm wide and 63 mm high. In ventral view the occipital condyle widens slightly posteriorly. In occipital view the condyle is concave, with a deep medial depression: 40 mm wide, 15 mm deep.

The basioccipital forms the posterior edges of the basal tubera which have pointed posterolateral ends. In ventral view, the posterior and posteroventral

surface of the basal tubera of the holotype show a number of irregular grooves and ridges and it is not clear whether these are a genuine feature or are due to damage. These areas are also rugose and irregular on the holotypes of *Bradysaurus baini* and *Embrithosaurus*. As also observed in the holotype of *Embrithosaurus*, an indistinct transverse ridge links the posterior edges of the basal tubera. In ventral view, SAM-PK-6238 shows a small tubercle on the posteromedial corner of the left tubera, which cannot be confirmed on the right due to damage, but is probably taphonomic.

Laterally, the horizontal sutural contacts of the basioccipital with the parabasisphenoid ventrally and the exoccipital dorsally are evident as the basioccipital is wedged between these two elements. Posterior to the fenestra ovalis, and more medially on the same horizontal level, the large jugular foramen is present. Between these fenestra the basioccipital shows a short horizontal suture with the dorsally located opisthotic.

The jugular foramen is large, oval to circular in cross section, faces posteriorly with a very slight lateral inclination, and leads anteromedially into the posteroventral region of the cavum cranii. Between the fenestra ovalis and the jugular foramen is a posterodorsally oriented ridge that obscures most of the jugular foramen in lateral view. The borders of the jugular foramen are formed by the basioccipital ventrally and posteroventrally, the exoccipital posterodorsally, and the opisthotic anteriorly and anterodorsally.

Exoccipital (Figs. 3.8, 3.9, 3.10)

The exoccipital is a paired, complex element that is positioned dorsally and laterally to the basioccipital. It makes up the dorsolateral portion of the occipital condyle, as observed in SAM-PK-6238, and in all pareiasaurs. The exoccipitals have sutural contacts with the supraoccipital anteriorly, the opisthotics anterolaterally and the basioccipital ventrally.

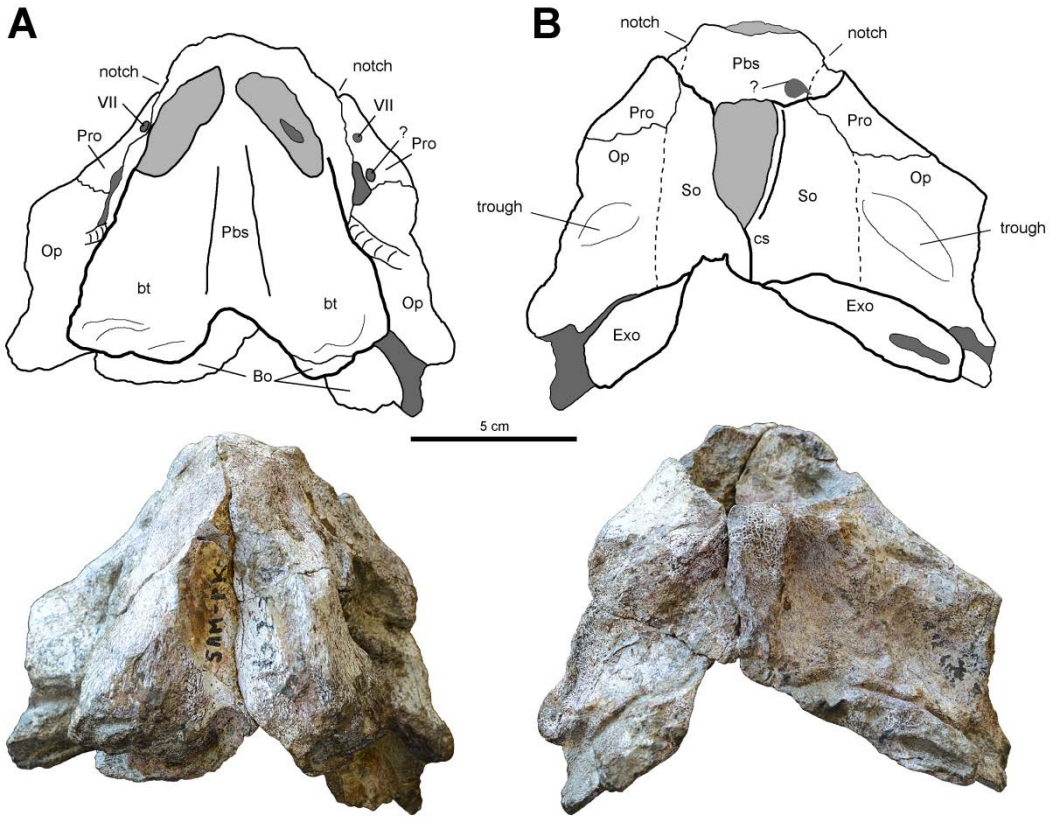


Figure 3.10: Photographs and interpretive drawings of the braincase of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in (A) ventral view, and (B) dorsal view. Anterior to the top of the page.

Above the condyle, the exoccipital forms the ventral and lateral borders of the large, square foramen magnum, which is slightly wider than high, and measures 20 mm in transverse width in the holotype and SAM-PK-6238.

The exoccipital extends laterally on either side of the foramen magnum. In the holotype, in dorsal view, the exoccipitals extend as thin, flat, horizontal plates of bone separated from the suparoccipital and the opisthotics by a deep transverse groove. The median supraoccipital forms the dorsal border of the foramen magnum, preventing the paired exoccipitals from meeting each other at the midline. These horizontal lateral flanges of the exoccipital extend far laterally. Medially, they are positioned along the posterior edge of the parocciptal processes of the opisthotics. Laterally they curve downwards to cover the posteroventral and ventral surface of the more distal portions of the paroccipital processes of the opisthotics.

In lateral view of the exoccipitals of holotype specimen (under the paroccipital processes of the opisthotics), show a long, anteriorly extending process that forms the posterodorsal border of the jugular foramen.

Supraoccipital (Figs. 3.9, 3.10)

The supraoccipital is a single, median bone, located posterodorsally on the braincase. It comprises a flat, horizontally oriented, thin plate of bone forming the posterodorsal roof of the braincase cavity and a thick, vertically oriented, pillar of bone (the dorsal ascending process) that connects the braincase to the skull roof.

The supraoccipital has sutural contacts with the prootics anterolaterally, the opisthotics laterally and the exoccipitals posteriorly. The bone is not horizontally flat but curves downwards at the lateral edges in occipital view.

The holotype preserves only the flat portion of the supraoccipital that covers the braincase cavity. Most of the dorsal ascending process of the supraoccipital is not preserved, except for a small preserved piece on the right side. A sharp, midline crest of the supraoccipital (the crista supraoccipitalis) extends posteriorly on the dorsal surface of the foramen magnum of the supraoccipital, from the posterior edge of the supraoccipital ascending bar, to the posterior edge of the supraoccipital. SAM-PK-6238 preserves the ascending bar of the supraoccipital on two small fragments of bone. The bar is diamond shaped in cross section and transversely wider than anteroposteriorly long.

Prootic (Figs. 3.9, 3.10)

The prootic is a relatively small bone of the braincase. It is a paired, curved element that forms the anterior and anterodorsal parts of the lateral walls of the braincase cavity. It is bounded ventrally and medioventrally by the parabasisphenoid, posterolaterally by the opisthotic and dorsally and mediodorsally by the supraoccipital. The paired prootics are prevented from meeting each other at the dorsal midline by the supraoccipital and ventrally by

the parabasisphenoid. The cavum cranii is well prepared and fully exposed in both the holotype and SAM-PK-6238 showing the fully ossified medial (internal) walls of the prootic that form part of the lateral walls of the braincase cavity.

Better preserved on the right side of the holotype than on the left, the short, horizontal suture between the prootic and the parabasisphenoid is very apparent. The indentation of the trigeminal (fifth) cranial nerve is present on the anterior margin of the braincase cavity of the prootic. The prootic-parabasisphenoid suture runs posteriorly from the just below this indentation of the trigeminal nerve to the anteroventral corner of the fenestra ovalis. A small foramen, representing the exit of the facial (seventh) cranial nerve is present above the horizontal prootic-parabasisphenoid suture, midway between the trigeminal (fifth) cranial nerve indentation and the fenestra ovalis.

Sutural contacts of the prootic with the opisthotic (viewed laterally) and suparoccipital (viewed dorsally) are revealed as edges of the slightly raised plates of the prootic bone on the holotype and as clear interdigitated sutures on SAM-PK-6238.

Opisthotic (Figs. 3.9, 3.10)

The opisthotic is a paired, elongated, relatively large and curved bone. It forms most of the paroccipital process that articulates the braincase with the skull roof. The holotype and SAM-PK-6238 show the opisthotic located on the posterolateral sides of the braincase and suturing with the prootic anteriorly, the supraoccipital laterally and the exoccipital posteriorly and posteroventrally. On the lateral walls of the braincase, the opisthotic is present between the prootic and the exoccipital. It creates a posterodorsally oriented sharp ridge and forms the anterior and anterodorsal borders of the jugular foramen and the posterior borders of the fenestra ovalis.

Neither paroccipital processes of SAM-PK-6238 are preserved, except for a small piece of the right distal portion that is sutured to the inner skull roof. On the

holotype specimen, the right paroccipital process is well preserved and broken into roughly two equally sized halves that fit together: the medial half is preserved articulated to the rest of the isolated braincase, the lateral half is preserved articulated to the inner skull roof. On the left side, only a very small medial portion of the paroccipital process is preserved on the braincase fragment.

The paroccipital process of the holotype and CGP JA 109 is a transversely expanded, roughly horizontal, plate-like projection that emerges from the lateral sides of the braincase, immediately above the fenestra ovalis and the jugular foramen. Medially, it has a small anterior contribution formed by the prootic, above the fenestra ovalis. Laterally and posteriorly, the paroccipital process is formed by the opisthotics. The exoccipital flange covers the posterior edge of the paroccipital process of the opisthotic (see Exoccipital). The posterior edges of the medial half of the paroccipital process curve steeply upwards to meet the exoccipital.

Medially, at the level of the foramen magnum, the paroccipital process forms a horizontally flat, thin, plate which has a long axis that is oriented laterally. It is low in dorsoventral height, and anteroposteriorly and mediolaterally expanded. The dorsal surface is concave and the ventral surface is convex. Laterally, this horizontal plate projects slightly downwards and forms a deep anteromedially elongated trough on the dorsal surface. The trough is also well defined in referred *Nochelesaurus* specimen SAM-PK-6238 and *Bradysaurus baini*, and is present but less distinct in *Embrithosaurus*. Immediately lateral to the trough, the blade of the opisthotic curves and turns steeply upwards. The distal portion of the paroccipital process is anteroposteriorly expanded (55 mm).

The distal portion of the paroccipital process of the opisthotic has a gently convex posteromedial surface. CGP JA 109 presents the same importantly diagnostic smooth and slightly convex posteromedial surface, with a dorsolaterally oriented swelling of the bone. In contrast in *Embrithosaurus* and

Bradysaurus baini, the posteromedial corner has a posteriorly projecting, dorsomedially oriented, knob like process, smaller in *Embrithosaurus* and larger in *Bradysaurus baini*.

The distal end of the paroccipital process of the opisthotic sutures with the ventral process of the supratemporal and the medial process of the squamosal on the inner skull roof. In occipital view, the paroccipital process is therefore u-shaped as in all other basal South African pareiasaurs.

Stapes

In the holotype and SAM-PK-6238, the stapes are not preserved.

3.5.4 Lower jaw

General Comments

The holotype of *Nochelesaurus* has only a partial right lower jaw preserving portions of the right dentary, splenial, surangular, angular, coronoid and prearticular. The articular is not preserved. Sutures are relatively easily identifiable. CGP JA 109 preserves only partial posterior portions of both lower jaw rami, articulated to the quadrates of the inner skull roof. SAM-PK-6238 preserves a complete lower jaw, consisting of separated left and right rami, with sutures on the lateral and medial surfaces easily identifiable. A small anteroventral section of the right ramus of SAM-PK-6238 is not preserved and plaster fills a large region of the left ramus.

The medial surface of the lower jaw is smooth but the lateral surface has a roughened mottled texture of numerous small projecting bumps and shallow depressions. In dorsal view, the complete lower jaw of SAM-PK-6238 is broad and anteriorly slightly pointed (Fig. 3.11). Posteriorly the rami curve slightly medially. The dorsal half of the lower jaw is vertical, high and narrow, and the ventral half is mediolaterally wider and projects ventrolaterally. The morphology

of lower jaw of *Nochelesaurus* is consistent with that of all other basal South African pareiasaurian taxa.

Transverse bone breaks on the lower jaw of the holotype and the well preserved right ramus of SAM-PK-6238 show that the elements of the lower jaw comprise vertically oriented overlapping sheet-like bones. The dentary, splenial, coronoid and prearticular comprise most of the medial surface, and the dentary and surangular most of the lateral. Ventrally the angular bone forms the horizontal, wide ventral surface of the lower jaw. The articular is the only robust bone of the pareiasaurian lower jaw and forms a strong articulation with the upper jaw of the skull as seen in SAM-PK-6238.

Severe dorsoventral compression has the affected the dorsal portion of the anterolateral aspect of the lower jaw fragment of the holotype, such that the alveolar ridge is flattened and laterally displaced and the teeth are flattened and directed outwards. All basal South African pareiasaurs have vertically oriented and slightly outwards pointing lower jaw teeth (10-20^0 from a vertical orientation) when undistorted, an observation correctly related to all pareiasaurs by Haughton and Boonstra (1930a). The lower jaw of SAM-PK-6238 is undistorted and is primarily used for this description, with the holotype secondarily used.

Dentary (Figs. 3.11, 3.12, 3.13, 3.14, 3.15)

The dentary is the largest bone of the lower jaw and forms most of the anterolateral portion. In lateral view the dentary has greater exposure than medially and covers the anterior two-thirds of the mandible. The dentary overlaps the splenial anteroventrally, the angular ventrally and the surangular posteroventrally. In medial view the dentary is nearly completely covered by the large, plate-like splenial posteroventrally and posterodorsally. The small coronoid bone covers the extreme posterodorsal portion of the dentary and a matrix-filled vertical cavity is present between the two bones.

SAM-PK-6238 shows the external anterior midline suture of the dentary with its partner, where externally a strongly fused mandibular symphysis is formed by the dentary as a midline vertical raised ridge. Internally, at the midline, the anteromedial portion of the dentary shows a horizontal narrow slit-like hole (foramen intermandibularis medius, Lee 1994, Lee *et al.* 1997) which extends into the meckelian canal. The dorsal border of this foramen is formed by the dentary and the ventral border by the splenial.

The dorsal section of the dentary shows the tooth row erupting from the lateral edge of the bone where 16 alveoli are present on the holotype fragment and 19 on each side of the complete rami of SAM-PK-6238. Just below the tooth row, preparation of the holotype has revealed the crista dentalis, a horizontal shelf of bone, on which four erupting replacement teeth are located within shallow, tooth sized depressions below the 1st, 3rd, 5th, and 10th exposed dentary teeth respectively. These shallow depressions are present under most teeth, but do not always contain visible exposed replacement teeth. The shelf is also present in SAM-PK-6238 and continues posteriorly to form the dorsal edge of the posterior dorsal fork of the splenial. The right lateral side of SAM-PK-6238 has a long horizontal groove and a large foramen dentofaciale majus (Lee *et al.* 1997).

Splenial (Figs. 3.11, 3.12, 3.13, 3.14, 3.15)

The splenial is an elongated bone located in the anterior part of the mandible. Bounded dorsally by the dentary, the splenial forms the ventral surface and most of the medial sides of the lower jaw anterior to the angular.

In lateral view, the splenial makes a thin horizontally elongated contribution to the ventrolateral edge of the lower jaw. Medially, the splenial has greater exposure as an overlapping plate and has a long anterodorsal horizontal suture with the dentary. Anteriorly, this suture occurs below the crista dentalis, and rises posteriorly to merge with the shelf.

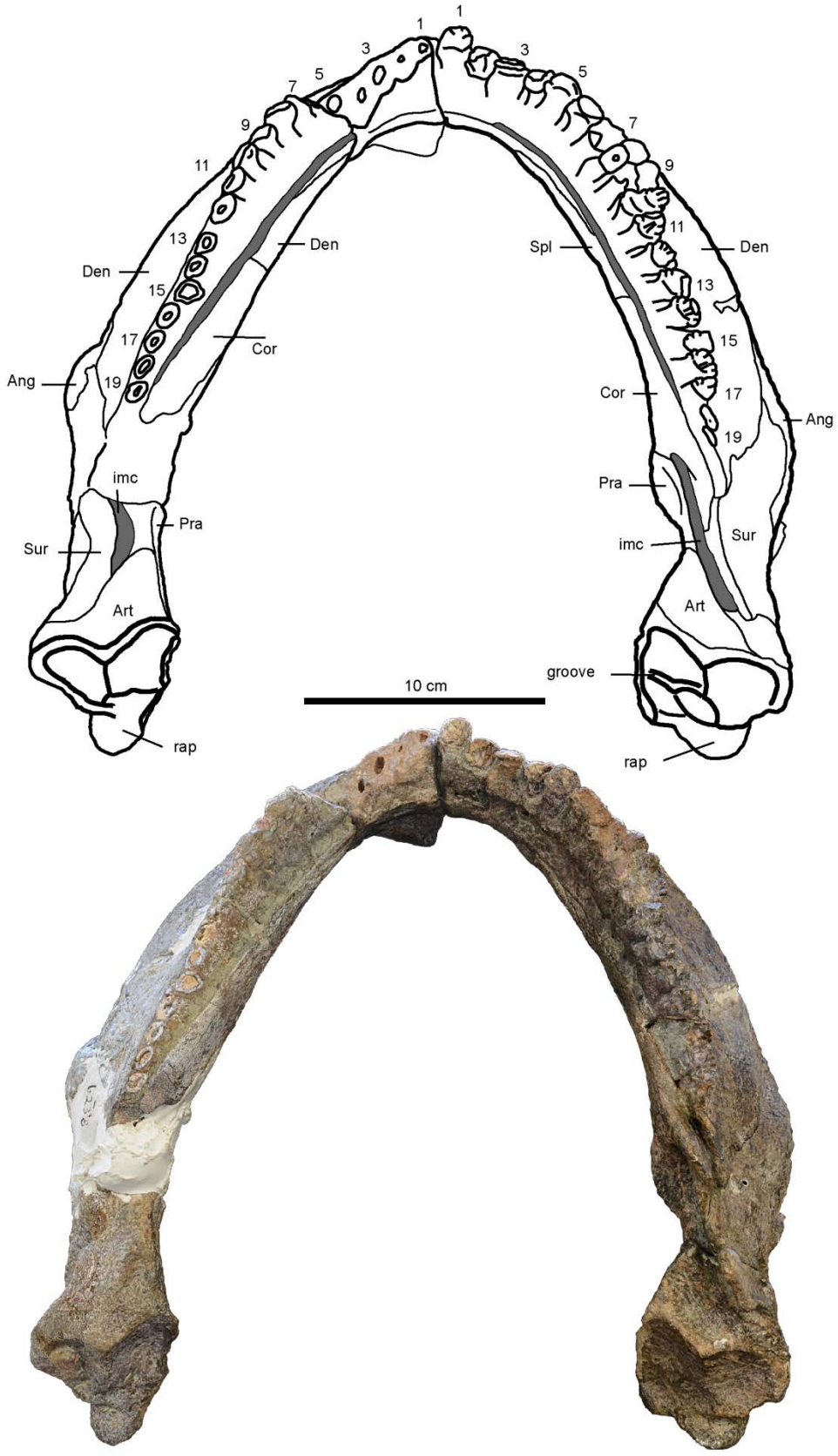


Figure 3.11: Photograph and interpretive drawing of the lower jaw of SAM-PK-6238 (*Nochelesaurus alexanderi*), in dorsal view.

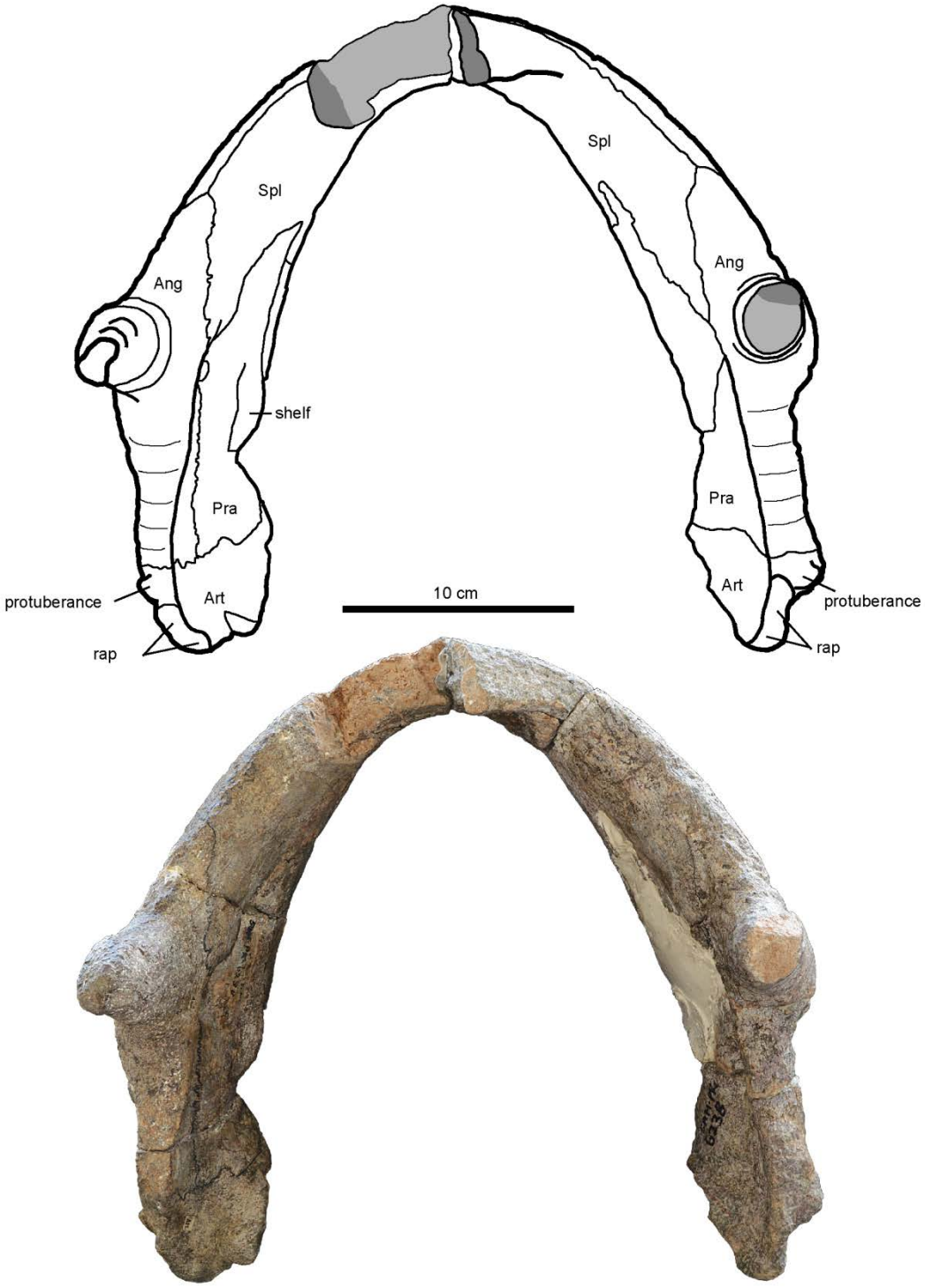


Figure 3.12: Photograph and interpretive drawing of the lower jaw of SAM-PK-6238 (*Nochelesaurus alexanderi*), in ventral view.

The splenial forms two forked flanges posteriorly: the dorsal flange maintains its height until it meets the coronoid with a vertical suture, the ventral flange projects further posteriorly and narrows posteriorly until it reaches the foramen intermandibularis caudalis where it forms the anteroventral border. The foramen intermandibularis caudalis is large in the holotype (20mm long, 15mm high), and slightly smaller in SAM-PK-6238 (15mm long, 12mm high).

Anteriorly, at the midline, the partially preserved left splenial of SAM-PK-6238 sutures vertically with its partner element and forms the ventral portion of the strongly ankylosed mandibular symphysis, as in all other basal South African pareiasaurs. The midline ventral portion of the mandibular symphysis creates a significant mentum that projects posteroventrally and internally it forms a sharp, raised vertical ridge.

Angular (Figs. 3.11, 3.12, 3.13, 3.14, 3.15)

The angular is a mediolaterally narrow, anteroposteriorly elongated, with a dorsoventrally low main body. Posteriorly the bone forms most of the flat, ventral surface of the lower jaw. On the lateral surface the angular sutures with the dentary dorsally and the surangular posterodorsally. On the medial surface the angular contacts the splenial anterodorsally, the prearticular dorsally and between them forms the posteroventral border of the large foramen intermandibularis caudalis. The posterior portion of the angular is not preserved in the holotype but is in SAM-PK-6238 where the angular contacts the articular posteriorly with horizontal transverse suture. The angular makes a slightly larger contribution to the lateral surface of the lower jaw, than it does to the medial, where it extends higher laterally.

The angular is a flat horizontal bone. Anterior to the angular boss, the lateral and medial edges curve gently upwards to produce a smooth, even curve. Posterior to the angular boss, the medial edge of SAM-PK-6238 has a 90^0 bend and extends upwards and then inwards to create a ledge on the medial surface of the lower

jaw. This long horizontal medial ledge of the posterior angular continues on the articular and is also present in the holotype of *Embrithosaurus*.

On the ventral surface of the lower jaw the angular tapers anteriorly to a sharp point bounded laterally by a long suture with the dentary and medially with the splenial. On the ventral surface of the holotype, the ”angular boss” is not preserved and it is broken off near its base, as is often the case with specimens of basal South African pareiasaurs. The cross section of the break reveals is anteroposteriorly elongated. SAM-PK-6238 preserves the complete right angular boss and a partial left one. The right angular boss is long (55 mm), horn-like and tapers distally. It is directed posteroventrally and slightly medially and forms a low, indistinct rim around the circumference about half way along its length (Fig. 3.14). Distally it terminates with a relatively blunt tip (20mm wide) that faces posteroventrally.

The angular boss of *Embrithosaurus* is very similar to that of *Nochelesaurus* (SAM-PK-6238). It is also posteroventrally directed, with a slightly raised rim of bone before the blunt distal tip. The holotype of *Bradysaurus baini* has relatively small angular boss for the large size of the skull.

Both rami of SAM-PK-6238 show a long, anteroventrally oriented, shallow groove on the lateral surface of the angular, just below the intersection of the angular, surangular and dentary. This groove is also present on the holotype of *Embrithosaurus*. Behind this groove, above the angular boss, the angular is swollen and bulges laterally.

Coronoid (Figs. 3.11, 3.12, 3.13, 3.14, 3.15)

The coronoid is the smallest bone on the lower jaw. It is partially preserved on the holotype as a thin, flat, vertical and anteroposteriorly elongated bone located on the medial side of the lower jaw. SAM-PK-6238 preserves the complete right coronoid. In medial view the coronoid shows a long horizontal suture with the prearticular ventrally and anteriorly a short vertical slightly

curved suture with the splenial. Posterolaterally the vertical coronoid plate is almost completely overlapped laterally by the dentary (anteriorly) and the surangular (posteriorly).

Anteriorly the coronoid is at the same level as the alveolar ridge on the dentary, but posteriorly it swells and increases in height to form the coronoid process posterior to the mandibular tooth row. The coronoid process is mostly not preserved in the holotype, reaching a level as high as the distal tips of the tooth crowns. In lateral view, the coronoid process of SAM-PK-6238 rises well above the dentary. Medially, the coronoid process forms the vertically oriented anterolateral and lateral rim of the adductor fossa, a flat bowl-like depression located behind the tooth row on the dorsal and medial surface of the mandible. The adductor fossa's anteromedial rim and ventromedial floor is formed by the prearticular as a flat surface depression.

Posterior to the adductor fossa the intra-mandibular cavity is present in SAM-PK-6238 as a narrow but vertically deep cavity which opens dorsally. Its medial wall is formed by the prearticular and its lateral wall by the surangular. The articular forms the posterior and posteromedial walls.

Prearticular (Figs. 3.11, 3.12, 3.13, 3.14, 3.15)

The prearticular is a flat sheet-like bone located on the posterior half of the medial surface of the lower jaw. In medial view, it wedges between the two forked flanges of the splenial, which form its anterior, anterodorsal, and anteroventral sutural contacts. Ventrally the prearticular forms a long, horizontal ventral sutural contact with the angular which ends anteriorly at the foramen intermandibularis caudalis where the prearticular forms the dorsal half of the margin of this large foramen. Dorsally the prearticular shows a short horizontal sutural contact with the coronoid.

The posterodorsal part of the prearticular is not preserved in the holotype. Here, SAM-PK-6238 preserves a prominent horizontal and slightly posteroventrally

oriented shelf that forms the floor of the adductor fossa. This feature is also present in the holotype of *Embrithosaurus*, and all basal South African pareiasaur specimens, and other pareiasaurs (e.g. *P. nasicornis*, Lee *et al.* 1997).

Surangular (Figs. 3.11, 3.12, 3.13, 3.14, 3.15)

The holotype of *Nochelesaurus* preserves only a very small piece of the right surangular. Specimen SAM-PK-6238 shows the surangular to cover most of the posterior half of the lateral surface of the lower jaw. The surangular is a flat, vertically thin, slightly curved plate of bone that forms a tapering wedge of bone anteriorly where it sutures with the dentary anterodorsally and the angular anteroventrally and ventrally. Posteriorly it sutures with the articular with a curved vertical contact. Specimen SAM-PK-6238 has a deep elongated fossa on the posteroventral corner of the external surface of the surangular, which is oval and anteroposteriorly elongated, (33 mm long, 17 mm high, 10 mm deep). This large fossa is unique to specimen SAM-PK-6238 and probably does not represent a genuine diagnostic feature of *Nochelesaurus* as it is not present on the right surangular of specimen CGP JA 109 where the lower jaw is smooth and flat in this region.

Articular (Figs. 3.11, 3.12, 3.13, 3.14, 3.15)

The articular is not preserved on the lower jaw of the holotype. The articular of SAM-PK-6238 is a robust and complex bone forming the posterior end of the lower jaw.

Anteriorly the articular narrows and extends into the intra-mandibular cavity. This anterior portion wedges between the plate-like surangular and prearticular. Anteroventrally it sutures with the angular. Posteriorly the articular widens and is triangular in dorsal view. The dorsal surface of the posterior portion of the angular is horizontally flat and forms the craniomandibular joint, termed the area articularis mandibularis (Lee 1994) or glenoid fossa (Tsuji 2013), for articulation with the quadrate.

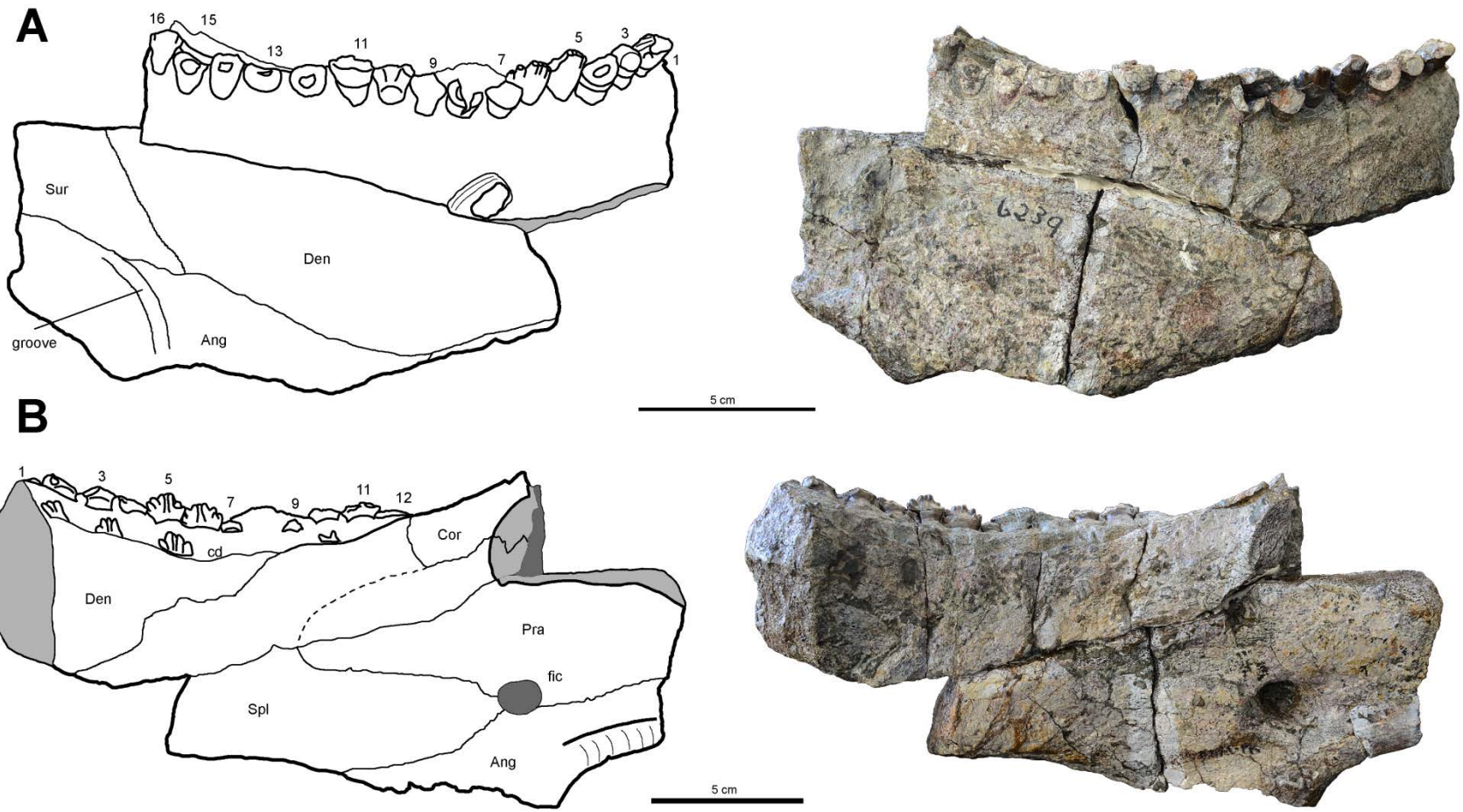


Figure 3.13: Photographs and interpretive drawings of the right lower jaw fragment of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in (A) lateral view, and (B) medial view.

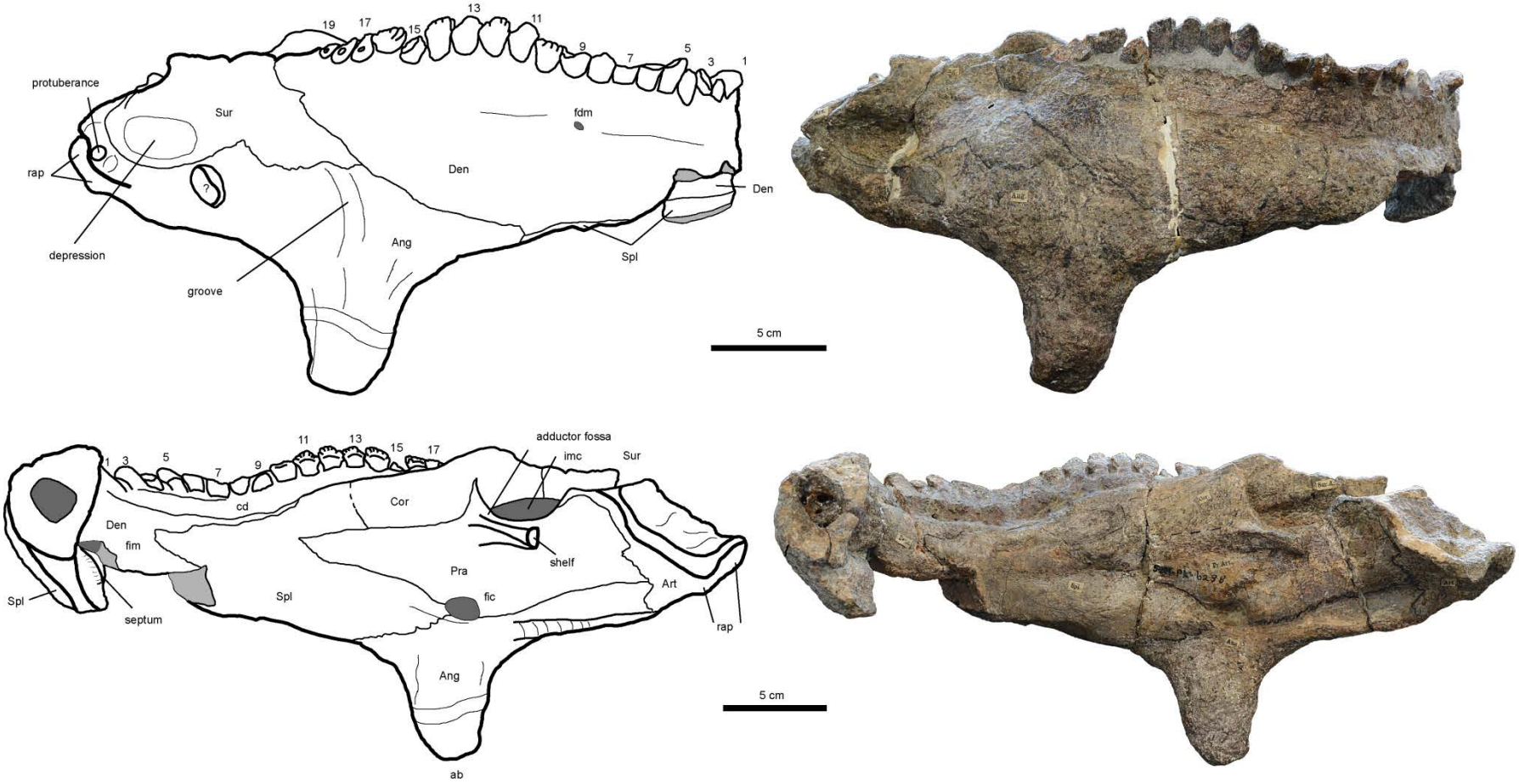


Figure 3.14: Photographs and interpretive drawings of the right lower jaw of SAM-PK-6238 (*Nochelesaurus alexanderi*), in (A) lateral view, and (B) medial view.

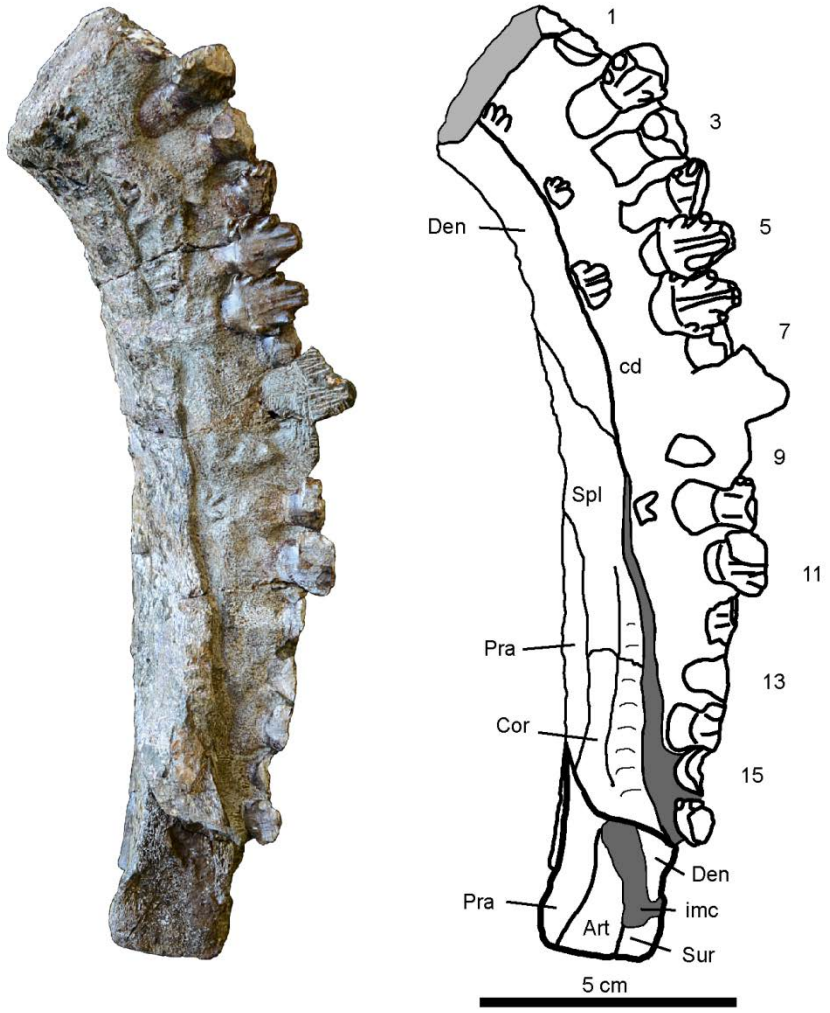


Figure 3.15: Photograph and interpretive drawing of the right lower jaw fragment of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in dorsal view. Anterior to the top of the page.

The medial and lateral articular cotyles are two shallow, concave depressions, that face posterodorsally, and are at a level well below the tooth row. The medial cotyle (35 mm wide, 47 mm long) is much larger than the lateral cotyle (25 mm wide, 32 mm long), and has a transverse groove crossing its face, better preserved on the right. The posteromedial corner of the medial cotyle extends medially as flat, horizontal flange. The cotyles are separated by an anteroposterioly oriented sharp edged ridge, and the anterior, lateral and posterior rim of each cotyle is thickened. The well preserved medial and lateral cotyles of the holotype of *Bradysaurus baini* have very similar dimensions and measurements to SAM-PK-6238.

Behind the median longitudinal ridge that separates the cotyles, the posterior edge of the articular forms a large retroarticular process. This process (termed the “dorsal lump” by Lee 1997b) is posterodorsally oriented, 12 mm wide, 40 mm high, and projects posteriorly 10 mm beyond the posterior edge of the cotyles. Its dorsal surface produces an upturned hook or flange and is slightly higher than the level of the longitudinal ridge that separates the cotyles.

On the posteroventral edge of the articular, underneath the lateral cotyle, is a small, round protuberance, 8mm wide, visible in ventral (Fig. 3.12) and lateral views (Fig. 314).

3.5.5 Marginal dentition

General Comments

Most of the upper jaw and lower jaw teeth of the holotype are poorly preserved and are broken off about midway between the base and the apex of the crowns. On the right upper jaw, the third premaxillary and first and second maxillary tooth have most of their crowns preserved (Fig. 3.16) and on the lower jaw the fifth and sixth teeth on the right are well preserved (Fig. 3.17).

The upper jaw teeth of SAM-PK-6238 are extremely poorly preserved, with all crowns broken off, except for the first and third maxillary teeth on the left side, which are partially preserved. On the lower jaw, the mandibular teeth on the left side are broken off at the base of the crown and on the right the crowns of the tenth to seventeenth mandibular teeth are partially preserved (Fig. 3.18).

Specimen CGP JA 109 has the right maxillary teeth preserved, most broken off at the base of the crown, apart from three teeth that are better preserved but unprepared.

Only sixteen mandibular teeth are present on the partially preserved dentary of the holotype, which represents most of the right lower jaw. The complete lower jaw of SAM-PK-6238 has nineteen mandibular teeth on each side.

The holotype of *Nochelesaurus* and SAM-PK-6238 have three premaxillary teeth either side of the midline. These are the largest teeth of the upper jaw and the both the upper and lower jaw teeth decrease in size posteriorly. The right maxilla of the holotype and SAM-PK-6238 each preserve 15 teeth and the left maxilla of SAM-PK-6238, which is missing a small posterior section, has 14. The upper jaw of *Nochelesaurus* thus bears a total of 18 teeth on either side.

Upper jaw teeth (Fig. 3.16)

In both lingual and labial view, the upper jaw teeth of the holotype of *Nochelesaurus* are oval, dorsoventrally elongated, and higher than wide. This shape is similar to shape of the teeth of *Bradysaurus baini*, and contrast with the wider teeth of *Embrithosaurus*. The premaxillary and maxillary teeth of the holotype and SAM-PK-6238 overlap each other significantly. Labially, the posterior margin is fully exposed and the anterior margins are partly covered by the posterior margin of the adjacent tooth.

The labial surface of the upper jaw teeth are convex and the lingual surfaces are flat and very slightly concave.

There are seven to eight cusps on the upper jaw teeth of the holotype of *Nochelesaurus*. As with the lower jaw teeth, the marginal cusps on the upper jaw teeth are placed irregularly around the crown, as the spaces between cusps varies. At the distal apex of the crowns of the 3rd premaxillary and the 1st maxillary teeth of the right upper jaw, the cusps are sheared-off. The 1st maxillary tooth reveals that three central cusps, placed very close together, were present on a long, isolated trident. These two teeth each show two lateral cusps on the mesial and distal margins of the crown, with large gaps or spaces between them, making a total of seven cusps per tooth. The lowest of the mesial and distal marginal cusps are positioned 4 mm above the base of the tooth. Interestingly, an additional very low and very small marginal cusp is present at the base of the mesial (anterior) margin of the crown of the 2nd, 4th and 5th right maxillary tooth of the holotype (Fig. 3.16, cusp 1), meaning at least 8 cusps were

present in certain teeth. Poor preservation make it impossible to determine the number of cusps of the upper jaw teeth of SAM-PK-6238. The distal (posterior) margin of these holotype teeth, lack a corresponding very low, cusp at the base of the crown, creating a non- symmetrical cusp arrangement between the mesial and distal margins. *Embrithosaurus* and *Bradysaurus baini* present symmetrical cusp arrangements on their maxillary teeth.

Three to five vertical ridges with shallow grooved ridges are present on the lingual surfaces of the 3rd premaxillary and 1st right maxillary teeth of the holotype, which emanate down from the three cusps of the distal tip (the central three ridges) and sometimes the first lateral cusps either side (when five ridge are present).

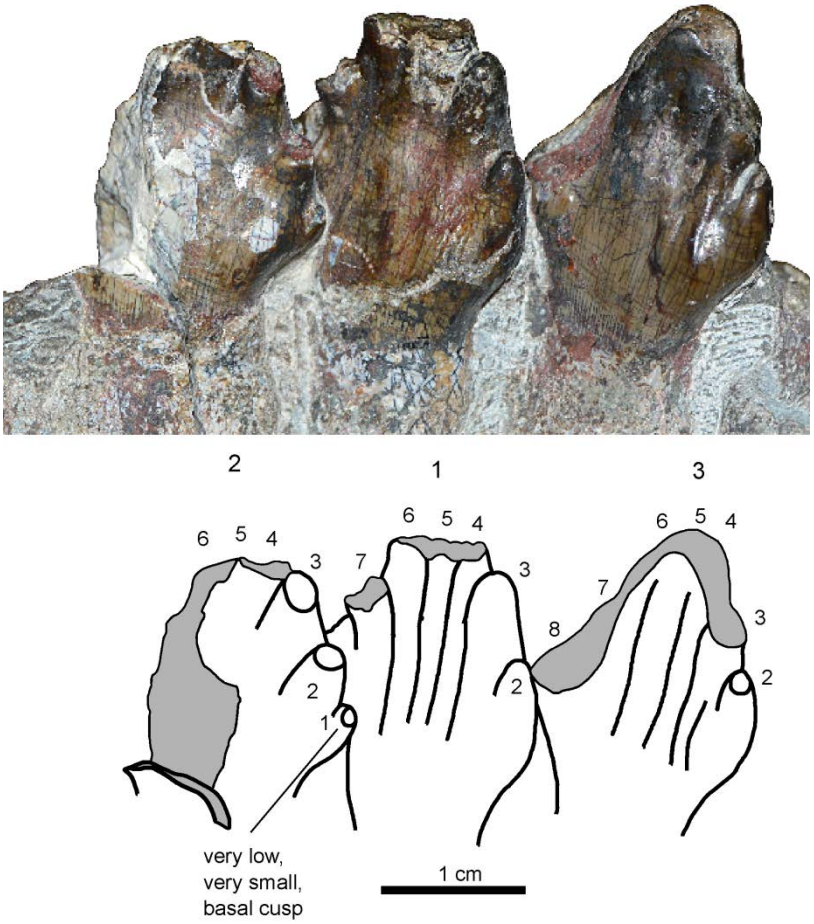


Figure 3.16: Photograph and interpretive drawing of upper right 3rd premaxillary and 1st and 2nd maxillary teeth of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in medial view.

Lower jaw teeth (Figs. 3.17, 3.18)

The crowns of the lower jaw teeth are labio-lingually flattened, leaf-shaped, and bear a number of cusps on the margins.

In lingual view, the dentary teeth of the holotype and SAM-PK-6238 are dorsoventrally elongated, higher than wide, relatively tall, and relatively narrow. This dorsoventrally elongated shape is similar to the elongated shape seen in *Bradysaurus baini* and very different from the shorter and wider shape of *Embrithosaurus*.

Neighbouring teeth are not oriented in the same plane as the anterior and posterior margins of the crowns overlap each other, obscuring the marginal surfaces. There is no consistent pattern and either of the anterior or posterior margins may be visible or obscured. The overlap is greater in SAM-PK-6238 than in the holotype.

The number of cusps varies on different mandibular teeth of the holotype specimen. The 5th right mandibular tooth has eight cusps and the 6th has ten. Specimen SAM-PK-6238 has at least eight cusps on the 16th tooth on the right side and at least seven on all preserved teeth.

The cusps are arranged irregularly around the crown, as different sized gaps exist between cusps located in different positions. In the holotype the apex of the crown has three central cusps, set very close together, with no gaps between them. All three cusps are situated on a long, narrow, isolated trident. The central cusp is the longest and is slightly higher and the two lateral cusps are the same length. On either side of the three cusp central complex, are two additional lateral cusps, with large gaps between each other and which are separated from the three cusp central complex by a large gap. This irregularly spaced, symmetrical arrangement of seven cusps, matches the condition present in specimens of *Bradysaurus baini*.

Additionally *Nochelesaurus*, has a very low and small cusp at the base of the mesial margin of the crown in all well preserved teeth. These are clearly identifiable in the second, fourth, fifth, sixth, tenth, eleventh, and sixteenth right dentary teeth of the holotype (Fig. 3.17) and the 16th right dentary tooth of SAM-PK-6238 (Fig. 3.18). The 14th, 13th and 12th right dentary teeth of SAM-PK-6238 show broken enamel where the small basal cusps may have been (Fig. 3.18). The distal margin of these teeth lack a corresponding low cusp at the base of the crown, which thereby creates a non- symmetrical cusp arrangement between the mesial and distal margins. Interestingly, one specimen of *Bradysaurus baini* (NHMUK R49426) has a similar low cusp, but on the base of the posterior (distal) margin of the crown of a lower jaw tooth, also creating a non-symmetrical cusp arrangement. This means that both *Nochelesaurus* and *Bradysaurus* can present non-symmetrical cusp arrangements on mandibular teeth. *Embrithosaurus* alone presents symmetrical cusp arrangements on its mandibular teeth.

On the lower jaw teeth of the holotype of *Nochelesaurus* are two medially positioned, very small, vertically pointed cusps, near the base of the distal margin of the crown, present on 2nd and 6th right dentary tooth of the holotype (Fig. 3.17), but cannot be confirmed on all teeth due to poor preservation. Such medial cusps cannot be identified on SAM-PK-6238, due to poor preservation. Two specimens of *Bradysaurus baini* also present very small, medially positioned cusps: on the 6th right dentary tooth of specimen SAM-PK-K11638 and on a right dentary tooth of NHMUK R49426. These medially positioned cusps are not present on any specimens of *Embrithosaurus*.

An incipient horizontal cingulum ridge is present on certain well preserved lower jaw teeth of the holotype (the 5th and 6th right teeth) and SAM-PK-6238 (the 12th right tooth) where it crosses the base of the tooth. On the holotype, the two small, medial cusps are positioned on the cingulum ridge. Another important feature of the lower jaw teeth of *Nochelesaurus* is the presence of three vertical raised ridges, on the holotype, separated by deep grooves.

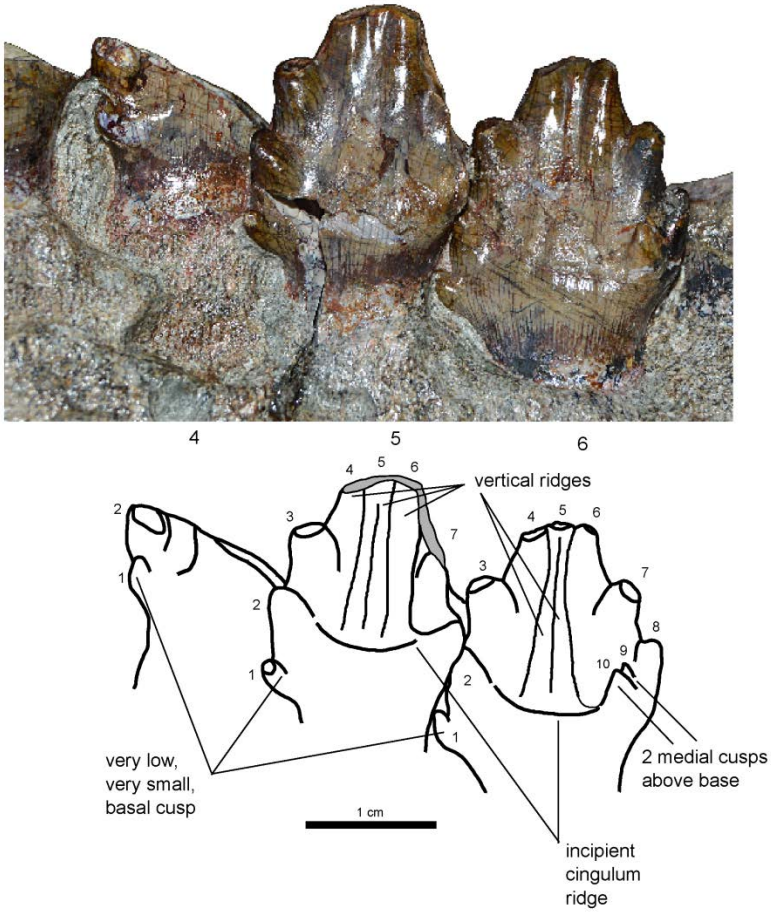


Figure 3.17: Photograph and interpretive drawing of 4th, 5th and 6th lower right mandibular teeth of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in medial view.

These ridges extend ventrally from each of the three central cusps on the apex of the crown to the slightly swollen base of the crown. Three undeveloped, erupting replacement teeth located below the 1st, 3rd and 5th mandibular teeth also show these vertical ridges. SAM-PK-6238 has only one distinct vertical ridge on the 11th, 14th and 16th right maxillary teeth. A specimen of *Bradysaurus baini* (NHMUK R49426) has three high distinct vertical ridges. It appears that only *Embrithosaurus* lacks a distinct lingual vertical ridge and instead has a smooth, low, horizontally triangular bulge at the base of the lingual surface of each mandibular teeth.

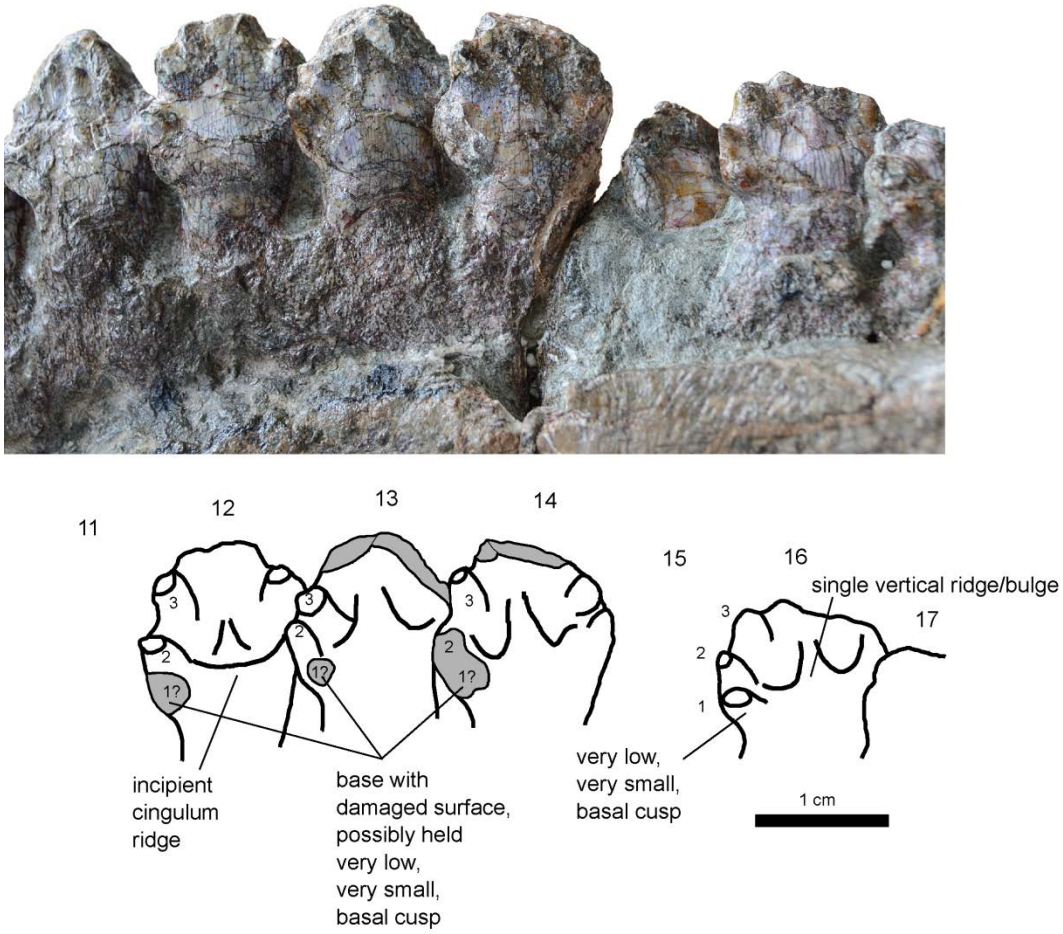


Figure 3.18: Photograph and interpretive drawing of 11th to 17th lower right mandibular teeth of SAM-PK-6238 (*Nochelesaurus alexanderi*), in medial view.

4. CHAPTER FOUR: POSTCRANIAL DESCRIPTION OF *EMBRITHOSAURUS SCHWARZI*

4.1 Introduction

Broom (1903) described the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034) in a brief paper (originally mistakenly assigning it to *Pareiasaurus serridens*). Noting the skull as crushed and with very few cranial sutures identifiable, Broom (1903) chose to focus his description primarily on the postcranium. Even so, the postcranial description is brief, as Broom (1903) noted that most of the new skeleton closely resembled that of the very complete *Pareiasaurus/Bradysaurus baini* (NHMUK R1971), recently well described by Seeley (1892) and that another detailed pareiasaurian postcranial description was unnecessary. Consequently, Broom provided only very brief descriptions of the vertebrae, scapulocoracoids, cleithra, clavicles, interclavicle, humerus (right), tibia, fibula, and a large astragalocalcaneum. However, he did describe the radii, ulnae, femora and the pelvis in more detail as he noticed several differences in his specimen compared to Seeley's (1892) very complete *P. baini*. Rough drawings of most of the postcranial elements were produced by Broom (1903: Plate XV, Figs 1 - 24) including a detailed full body restoration of the specimen in a living posture (Broom 1903, Plate XVI; and here Fig. 3.1) which he subsequently used in future publications as a model of a complete *Pareiasaurus serridens* (e.g. Broom 1913c).

Noting differences between Broom's (1903) specimen and the holotype of *Pareiasaurus serridens* (NHMUK R4063), Watson (1914b) assigned Broom's specimen as the holotype of a new genus and species *Embrithosaurus schwarzi* and provided a brief diagnosis. Since then, *Embrithosaurus schwarzi* has been retained as distinct and valid by all subsequent taxonomic workers, who unfortunately provided only brief diagnoses in their taxonomic reassessments, and usually only based on cranial features (Haughton and Boonstra 1929, Boonstra 1934a, Boonstra 1969, Kuhn 1969, Lee 1994, 1997a, Van den Brandt 2016).

The cranium of the holotype of *Embrithosaurus schwarzi* was recently re-described in detail by Van den Brandt (2016, Van den Brandt *et al.* 2019) who also provided an updated cranial diagnosis, but this has not produced a complete understanding of the taxon as the postcranium was not included in the study. Lee (1994, 1997a) was the first to publish explicit postcranial autapomorphies for *Embrithosaurus schwarzi*, consisting of three pelvis features, although most of these pelvic characters had already been documented by previous authors (e.g. Watson 1914b, Haughton & Boonstra 1930b). A detailed anatomical description of the postcranial elements was not produced by Lee.

Embrithosaurus schwarzi was included in the series of 'Pareiasaurian Studies' papers produced by Haughton and Boonstra between 1929-1934, with each paper dedicated to a particular postcranial anatomical region.

This chapter aims to re-describe in detail the postcranial elements of *Embrithosaurus schwarzi* using the holotype and referred specimens. Particular emphasis is placed on describing distinguishing features of the genus, compared to the anatomically similar co-occurring *Tapinocephalus* AZ pareiasaus, such as the anatomy of the pelvis. Anatomical features of historical discussion and contention, such as the morphology of the ulna, the sacral vertebrae and the osteoderms are also described in this chapter and discussed in detail in Chapter 7 (Discussion). Postcranial anatomical features related to pareiasaurian phylogenetic characters and scores also receive particular attention in this chapter.

4.2 Material

4.2.1 Holotype

Refer to Chapter Two, Material and methods

4.2.2 Referred material

Refer to Appendix A for a list of referred specimens of *Embrithosaurus schwarzi*.

4.2.3 Comparative material

Refer to Chapter Two, Material and methods.

4.2.4 Literature consulted

Refer to Chapter Two, Material and methods.

4.2.5 Preservation and preparation

Refer to Chapter Two, Material and methods.

4.2.6 Holotype horizon and locality

Refer to Chapter Two, Material and methods.

4.3 Systematic Palaeontology

REPTILIA Laurenti, 1768

PARAREPTILIA Olsen, 1947

PAREIASAURIA Seeley, 1888

PAREIASAURIDAE Cope, 1896

EMBRITHOSAURUS Watson, 1914

Embrithosaurus schwarzi Watson, 1914

4.4 Postcranial description

This description pertains primarily to the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034). References to other *Embrithosaurus* specimens are specifically noted in the text.

4.4.1 Shoulder girdle

The shoulder girdle of pareiasaurs comprises paired scapulocoracoids, cleithra, clavicles and a single median interclavicle (Boonstra 1932c). SAM-PK-8034 preserves a partial left scapulocoracoid (Figs. 4.2, 4.3), with an articulated partial left proximal cleithrum and partial left lateral clavicular fragment. A separate large fragment comprising a partial right interclavicle and clavicle is also preserved (Fig. 4.4).

Scapulocoracoid (Figs. 4.1 4.2, 4.3; Table 4.1)

The scapulocoracoid comprises the elongated scapula blade, and the anterior and posterior coracoids which form most of the flat coracoid plate. Apart from the vertical suture between the anterior coracoid and the posterior coracoid on the lateral surface (Fig. 4.3) the sutures between these three elements are strongly fused and cannot be determined, as is often the case in large, and therefore presumably adult pareisaurian specimens (Boonstra 1932c, Benton 2016).

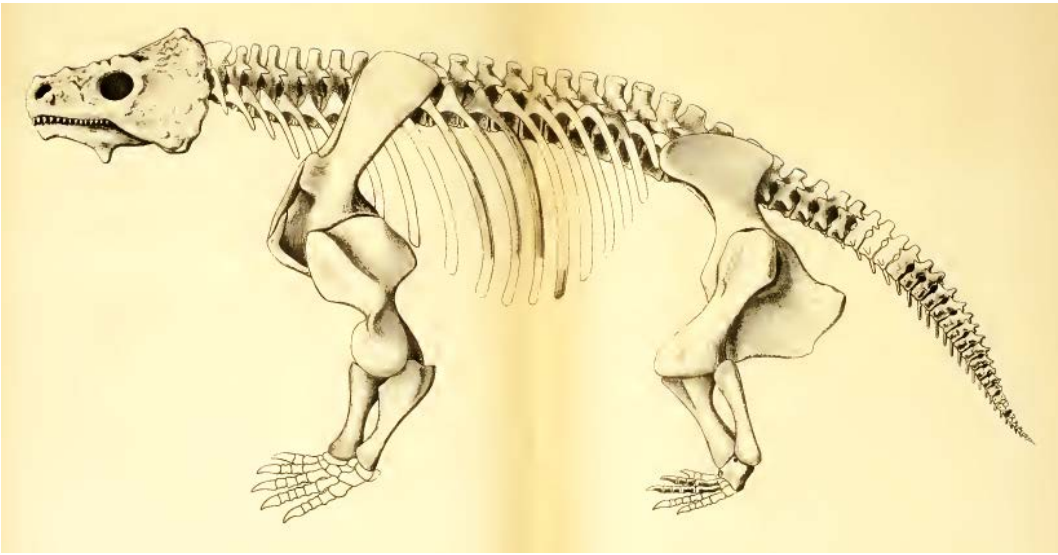


Figure 4.1: Full body reconstruction of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034) by Broom (1903). Most of the skeleton is shown as preserved (shaded elements). Unshaded elements (not preserved) include the manus, most of the pes (except for two digits), most of the ribs, a section of three anterior caudal vertebra, and several isolated posterior caudal vertebrae.

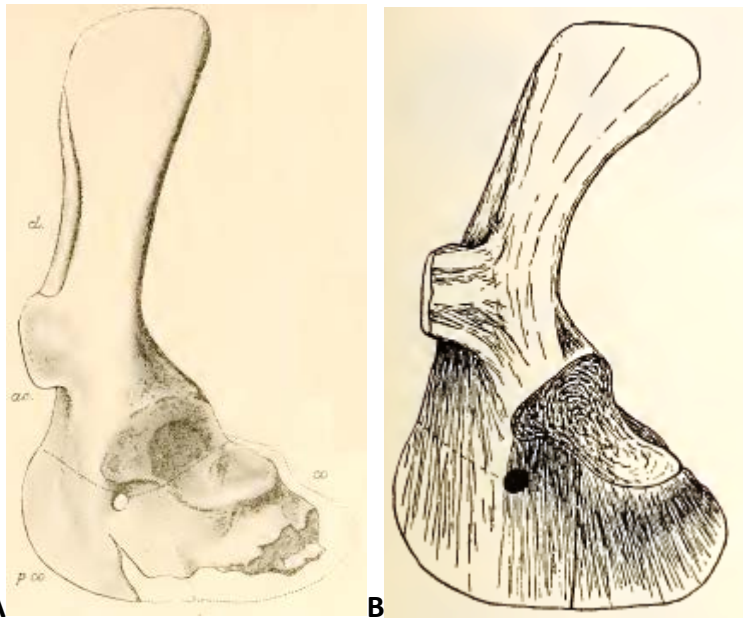


Figure 4.2: Interpretive drawings of the left scapulocoracoid of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034) in lateral view, (A), by Broom (1903). **ac**, acromion**; cl**, cleithrum; **co**, coracoid; **p.co**, precoracoid, and (B), by Boonstra (1932c). Note the acromion process (ac) and dorsal scapula blade are no longer preserved (Fig. 4.3).

Broom (1903: Plate XV, Fig 1; here Fig 4.2A) and Boonstra (1932c: Fig 18; here Fig. 4.2B) figured the left scapula blade as complete, but a large portion of the dorsal distal end has since been broken off and is now lost (Fig 4.3). The base of the scapula blade carries the acromion process (broken off and not preserved apart from a small dorsal piece) Above the dorsal edge of the acromion process, the scapula blade is constricted, oval in cross section, anteroposteriorly 100 mm wide and mediolaterally 50 mm thick. Using the figures provided by Broom and Boonstra I estimate the complete scapula blade to have been approximately 425 mm long, including the acromion process, which would be approximately twice the maximum anteroposterior diameter of the glenoid fossa (210 mm) (Turner *et al*. 2015 character 87). Using the figures provided by Broom and Boonstra, the dorsal end of the scapula blade is anteroposteriorly expanded or flared to approximately 200 mm, with the pronounced distal flaring creating curved preaxial and postaxial margins (Turner *et al*. 2015 character 88).

Over most of the extent of the preserved mid to proximal scapula blade of the holotype, the blade is wide and forms a flat, thin plate, only +-20 mm

mediolaterally thick. Dorsoventrally, the blade is gently convex and bulges laterally (to cover the chest of the animal, Boonstra 1932c). Distortion has bent part of the blade medially, producing a significant medial "kink" in the otherwise typical lateral curvature (Fig. 4.3).

On the medial surface of the scapula blade, is a low, medially projecting, oval process (10 mm high) covering the anterior half of the medial blade, 20 mm above the distal tip of the clavicle (Fig. 4.3B). Specimen CGP CBT 112 also shows a similar large, wide low process at this position.

Broom (1903) figured a large, raised and projecting acromion process on the anterior margin of the scapula blade, situated between level of the dorsal edge of the glenoid cavity and the ventral edge of the cleithrum. A large irregular region of the proximal scapula blade is damaged and not preserved. Only a small portion of the dorsal edge of the acromion process is now preserved, at the ventral cleithrum contact. As seen in Broom's (1903: Plate XV, Fig 1, here Fig. 4.2A) and Boonstra (1932c: Fig 18; here Fig. 4.2B) illustrations, and in all large basal South African pareiasaurs, the acromion process was very large, rectangular and wide (estimated to be approximately 100 mm dorsoventrally) and projecting (Turner *et al*. 2015 character 89).

The glenoid fossa is an irregular sigmoidal concavity. It is anteroposteriorly elongated (210 mm long, 80 mm high) and obliquely anterodorsally oriented (20^0 above the horizontal axis). The fossa is defined by a sharp rim of bone forming the border of the glenoid. The fossa is bipartite as it comprises two main internal facets for articulation with the head of the humerus: 1) a posterior facet on the internal ventral surface, and 2) an anterior facet on the internal dorsal surface.

The posterior facet is formed above the bulging posteroventral rim of the glenoid fossa which projects horizontally laterally to form a shelf-like buttress. The posterior internal facet is horizontally oriented and faces dorsolaterally and itself comprises an anterior portion that faces slightly more anteriorly and a posterior portion that faces slightly more posteriorly.

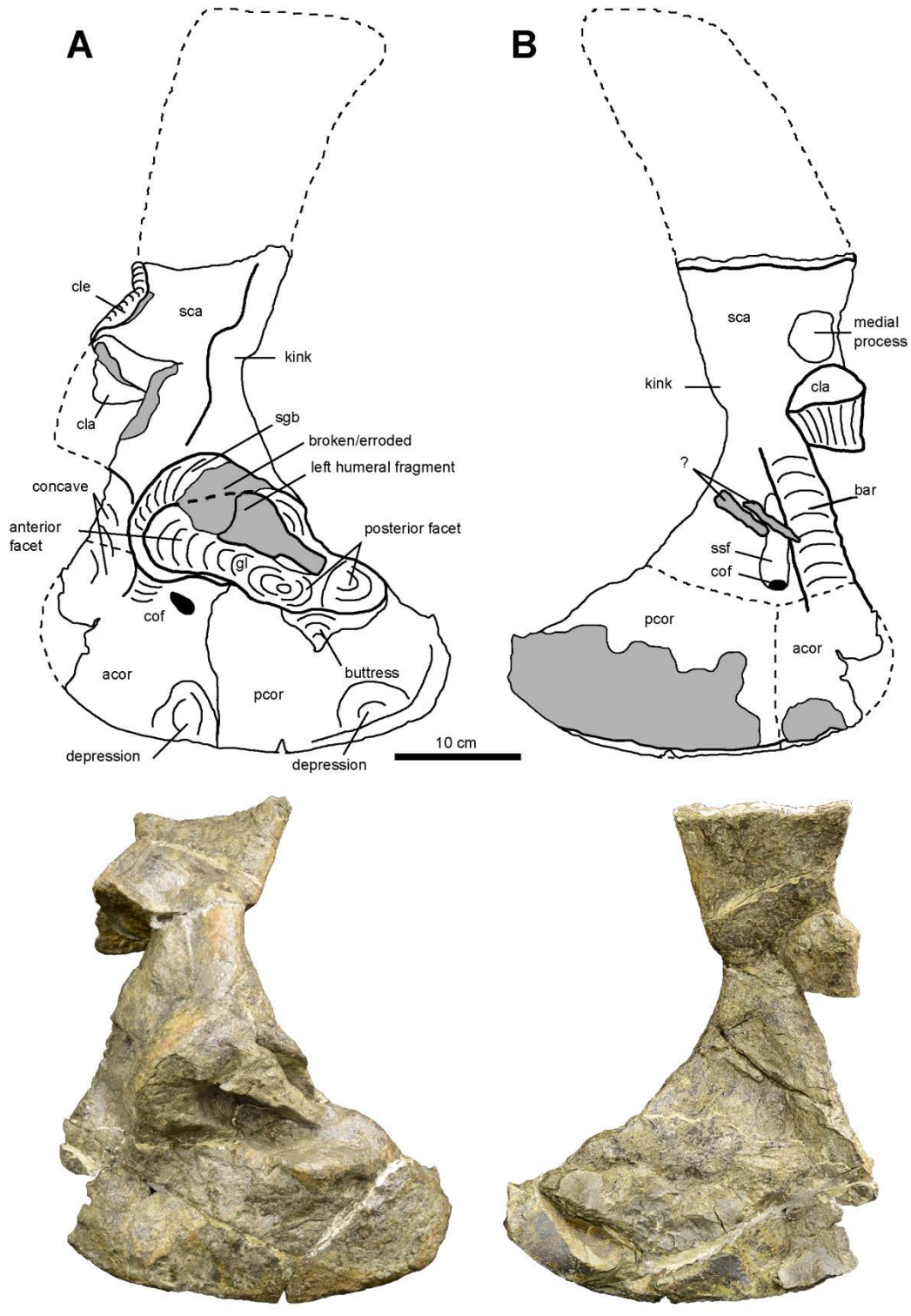


Figure 4.3: Photographs and interpretive drawings of the left scapulocoracoid of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in lateral view, and (B), in medial view. Dorsal to the top of the page.

At the anteroposterior midpoint, the glenoid fossa twists to face laterally, is very shallow, and the dorsal and ventral rims are narrow, low, and sharp edged. The anterior facet is formed by the greatly thickened anterodorsal rim (supraglenoid buttress) of the fossa which is more pronounced than the posterior shelf-like buttress, and creates an overhang. Overall, the entire internal facet of the glenoid faces laterally, and slightly posteroventrally. Above and behind the supraglenoid buttress**,** the holotype is damaged, but specimen CGP CBT 112 shows a vertical groove, which is also seen in *Bradysaurus* and *Nochelesaurus* specimens.

Broom (1903) noted an extremely unusual "vertical dividing ridge" (Broom 1903: 131) in the left glenoid fossa and went on to explain that this strange morphology must have allowed for only vertical and rotary movements of the articulated humerus, with little or no anteroposterior movement possible. Additional preparation revealed that this vertical ridge is a dislodged piece of the distal head of the left humerus (Fig. 4.3A), and it matches perfectly with bone break marks on the left humeral head. Specimen CGP CBT 112 shows the typical low and oblique ridge in the centre of the fossa, also seen in the holotypes of *Nochelesaurus* and *Bradysaurus*.

The coracoid plate is anteroposteriorly expanded (350 mm long) and flat (only 30 mm deep). The ventral border is nearly horizontal, and the anterior and posterior sides curve upwards. The anteroventral margin of the left anterior coracoid is damaged and a small section is not preserved. The ventral and anterior margins of the coracoid plate are relatively smooth and lack the numerous small thickenings (coracoid rim buttresses) reported for *Bunostegos* (Turner *et al.* 2015). On the lateral surface of the coracoid plate are two depressed regions (Fig. 4.3A) with three gently raised regions adjacent, as seen in *Nochelesaurus* and *Bradysaurus*. The lateral exit of the large coracoid foramen is 20 mm below

the ventral rim of the anterior facet of the glenoid fossa. It is an anterodorsally elongated foramen, which tapers anteriorly to a point.

Assuming a vertical posterior edge of the scapula blade, the dorsal edge of the posterior coracoid is relatively horizontal and forms an angle of about 120^0 (SAM-PK-8034 holotype) or 125^0 (CGP CBT 112) with the posterior border of the scapula (Turner *et al*. 2015 character 90).

In medial view, the inner surface of the scapulocoracoid is smooth but retains much obscuring matrix ventrally (Fig 4.3B). The subscapular fossa is shallow (60 mm high, 30 mm wide, 10 mm deep) and located behind a 45 mm thickened cylindrical swelling of the anterior border of the scapula (Fig. 4.3B "bar"). The large specimen CGP CBT 112 has a much larger subscapular fossa measuring 90-100 mm high, 35 mm wide and 20 mm deep.

The subscapular fossa has an unidentified bone resting obliquely across its dorsal portion. The opening of the oval coracoid foramen is in the ventral-most portion of the subscapular fossa, and the ventral border of the coracoid foramen is slightly raised. From the medial surface of the scapula, the foramen passes ventrally and slightly laterally through the coracoid plate to exit on the lateral surface. Turner *et al*. (2015) in their description of *Bunostegos*, consider that the orientation of the path of the foramen may be phylogenetically important as it varies from a lateral to more ventral orientation in different pareiasaurs.

Cleithrum (Figs. 4.1, 4.2, 4.3)

The cleithrum has atrophied and may not have been functional in pareiasaurs (Boonstra 1932c). In SAM-PK-8034 a partial right cleithrum is present and is vertically long, anteroposteriorly flattened, forming a thin plate on the anterior edge of the vertical scapula blade. Dorsally, it is partially fused with the scapula blade, being more distinct and separate ventrally. It extends and narrows dorsally from the dorsal edge of the acromion process. Its dorsal end is not preserved but the figures provided by Broom (1903: Plate XV, Fig 1, here Fig.

4.2A) and Boonstra (1932c: Fig 18; here Fig. 4.2B) indicate that it did not reach the dorsal edge of the scapula (Turner *et al*. 2015 character 91).

Interclavicle (Fig. 4.4)

As in all pareiasaurs, the interclavicle is a T-shaped bone comprising a thin and flat median stem and two laterally projecting thin and flat extensions ("lateral arms"). Only a fragment of the right lateral extension of the interclavicle of SAM-PK-8034 is preserved (Fig. 4.4). This has an anterior surface that is deeply grooved for the reception of the posterior process of the right clavicle. Medially, in cross section, the interclavicle is thick and is longer anteroposteriorly than high. Laterally the bone gradually narrows in anteroposterior width as the anterior surface remains at the same level but the posterior side tapers strongly and curves anteriorly, and flattens at the end where it has a rounded edge.

Clavicles (Figs. 4.3, 4.4)

The paired clavicles are a long, flat bones which extends laterally from near the median plane, to just lateral of the dorsal surface of the acromion process of the scapula. A small piece of the dorsal end of the left clavicle (80 mm long) is attached to the scapulocoracoid (Fig 4.3). This dorsal end of the clavicle articulates primarily with the acromion process of the scapula. Beyond the acromion process, the dorsal tip of the clavicle flattens and articulates with the cleithrum dorsally and the scapula blade posterodorsally. At the level of the articulation with the dorsal edge of the acromion process, the bone is 50 mm wide, but distally the clavicle bulges and flares to 70 mm in width and then curves to produce a rounded blunt distal edge (Fig 4.3).

A larger partial right clavicle is preserved, badly weathered and eroded, articulated to the dorsal surface of the right extension of the interclavicle fragment (Fig. 4.4). The lateral half of the right clavicle is flat, high (70 mm dorsoventrally) and narrow (20 - 30 mm anteroposteriorly) and the lateral-most edge is broken off. The medial half of the bone tapers towards the midline (Fig.

4.4). At the midline, in cross section (Fig. 4.4) the right clavicle is triangular with a sharp, posteriorly tapering posterior process (20 mm high) that fits into the corresponding groove on the anterior surface of the right interclavicle's lateral

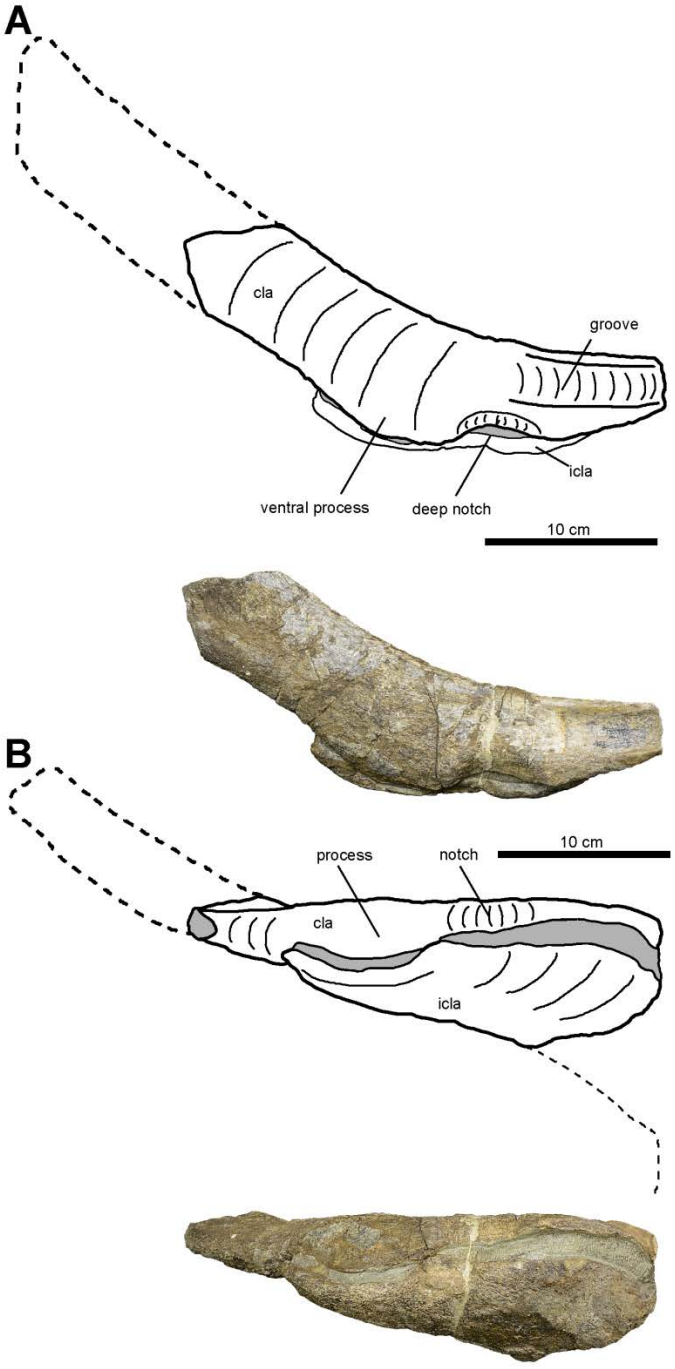


Figure 4.4: Photographs and interpretive drawings of the right clavicle and interclavicle of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in anterior view, and (B), in ventral view. Dorsal to the top of the page.

extension. The anterior surface of the median half of the right clavicle has a deep groove which dissipates laterally at a point where a wide notch is present (also present on CGP CBT 112) on the ventral edge of the clavicle (Fig 4.4). Lateral to this notch, there is a wide, ventral process (80 mm wide, 20 mm high on the holotype, that occludes tightly with a corresponding bowl shaped depression at the lateral end of the anterior surface of the interclavicle.

4.4.2 Forelimbs

Humerus (Figs. 4.1, 4.5, 4.6, 4.7; Table 4.2)

Embrithosaurus and all large middle Permian South African pareiasaurs have been reconstructed with the humerus in the horizontal position, parallel to the ground (Boonstra 1932c, Lee 1997a), as these authors postulate that a horizontal humeral posture accounts best for the articulations and allowable movement made between the head of the humerus and the glenoid cavity of the scapulocoracoid. I therefore use the directional vector terms proximal, distal, dorsal, ventral, postaxial (posterior) and preaxial (anterior) in terms of a horizontal orientation for the humerus, with the intercondylar fossa (ulnar fossa, olecranon fossa) of the distal humerus facing dorsally.

The 420 mm long right humerus of the holotype is very well preserved. It is complex, robust, with a short, narrow, cylindrical shaft (60-70 mm in diameter) and expanded proximal and distal ends. Only about 50% of the left humerus is preserved as most of the postaxial half is missing. Accordingly the right humerus is used for this description.

The proximal end of the humerus comprises a flattened strip for articulation with the glenoid cavity. The distal end comprises the complex trochlear joint with facets on the dorsal and ventral surfaces, for articulation of the radius and ulna. The proximal and distal expansions of both humeri of the holotype are not in the same plane but are “twisted” at the shaft so that the planes are nearly at right angles to each other, subtending an angle of 70-80^0 (Fig 4.7) (Turner *et al.* 2015

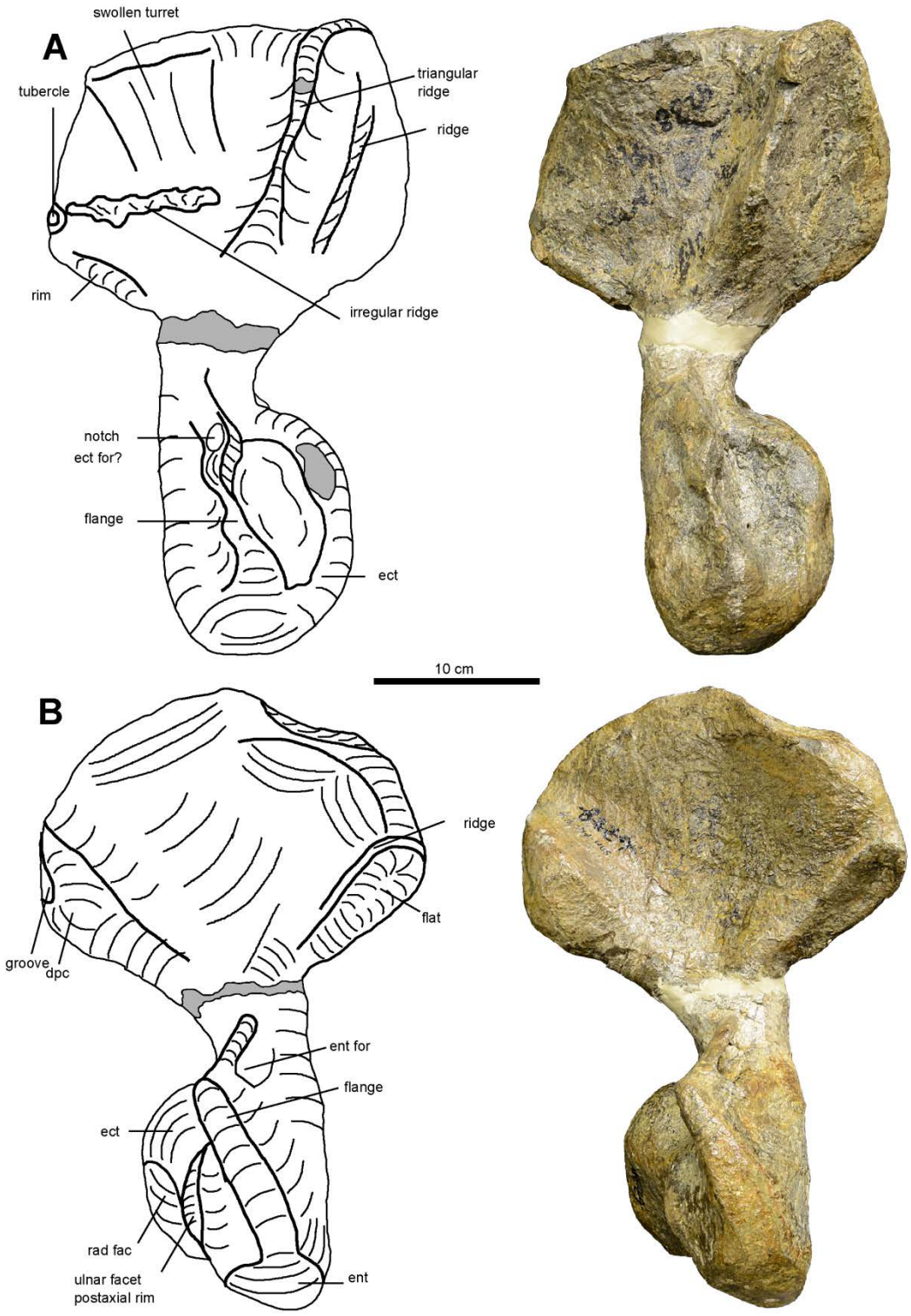


Figure 4.5: Photographs and interpretive drawings of the right humerus of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in anterior view and (B) in posterior view. Medial to the top of the page.

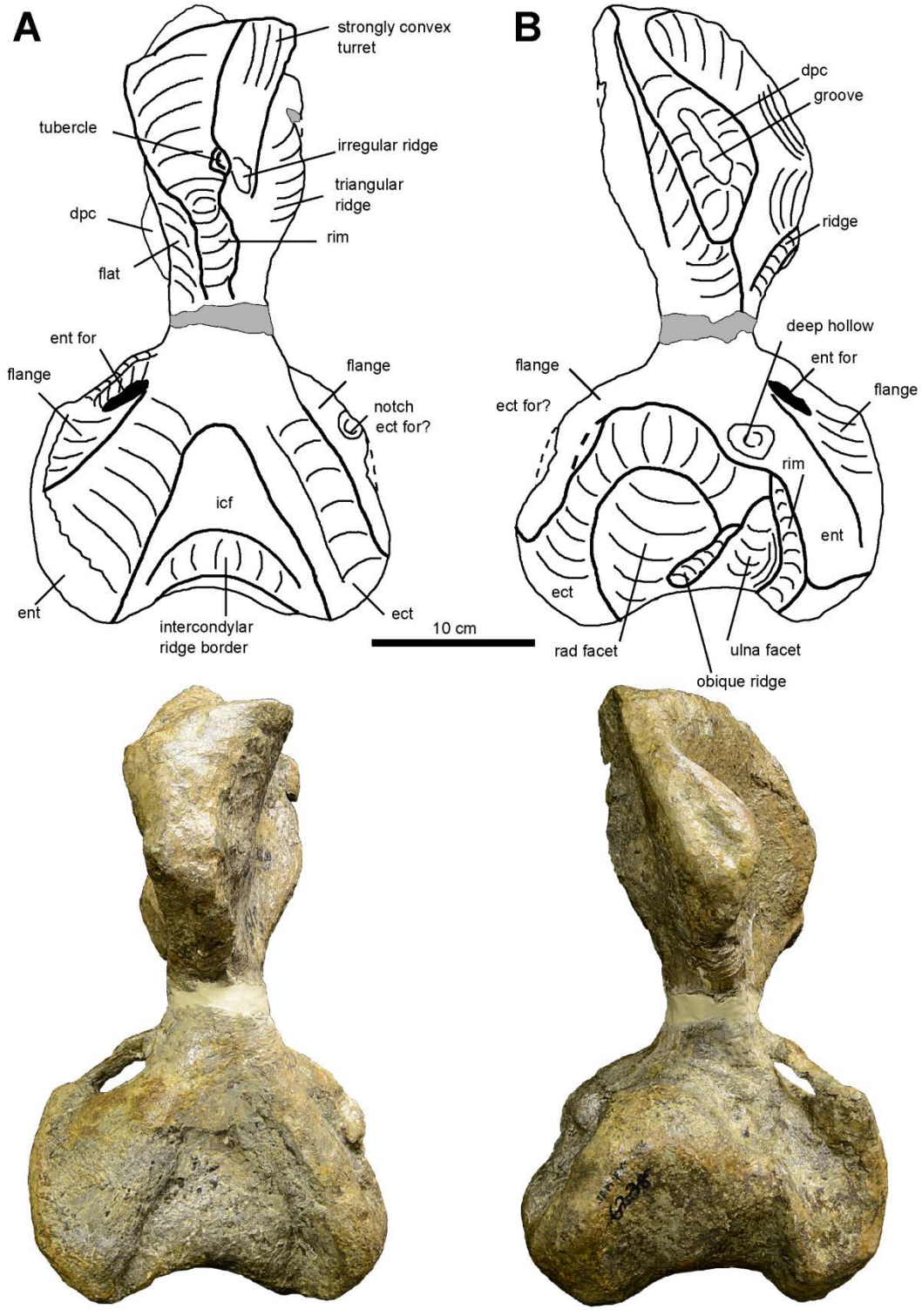


Figure 4.6: Photographs and interpretive drawings of the right humerus of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in dorsal view, and (B), in ventral view. Medial to the top of the page.

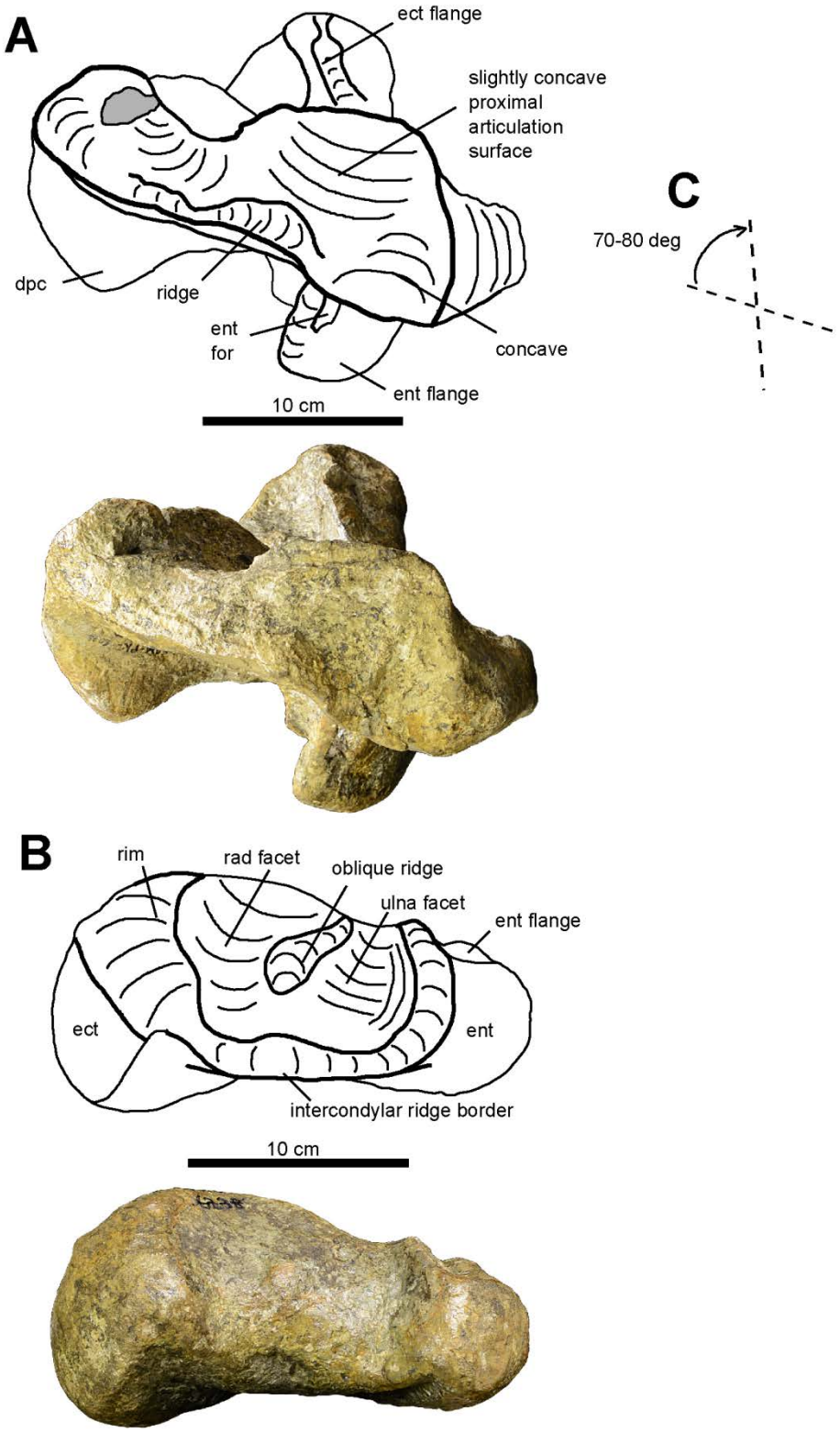


Figure 4.7: Photographs and interpretive drawings of the right humerus of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A) and (C), in proximal view, and (B), in distal view. (C) illustrates the angle between the proximal and distal expansions as 70-80^0. Ventral to the top of the page.

character 92). *Embrithosaurus* specimen FMNH UR 2443 shows twisting of 60^0 between the proximal and distal humeral expansions.

The entepicondyle and ectepicondyle form large robust processes (230 mm in anteroposterior width) with the ectepicondyle larger than the entepicondyle (Fig. 4.6) (Turner *et al.* 2015 character 99).

The preaxial ectepicondyle has a wide, expanded and flared flange, with an irregular margin (Turner *et al.* 2015 character 93) that extends preaxially. The edge of the flange is damaged, and irregularly notched, and a small portion of the preaxial edge is not preserved (also noted by Broom, 1903). The ectepicondylar foramen (present in all pareiasaurs according to Lee 1997b: 237) is present on the ectepicondylar flange in an irregular notch (Fig. 4.6A) (Turner *et al.* 2015 character 94).

The postaxial entepicondyle also has a flared flange that extends far postaxially. It is much thicker and wider than the ectepicondylar and has a notable sharp, right-angled, edge on the postaxial proximal corner (Turner *et al.* 2015 character 95)**.** A large and completely enclosed entepicondylar foramen is present in the entepicondylar flange (40 mm long, 20 mm wide, 20 mm deep). It is slit-like and elongated, with a very thin and delicate, flattened, medial, margin forming a bridge (Turner *et al.* 2015 character 96). This entepicondylar foramen is positioned so that it is visible (completely open and can been seen directly through) when the distal expansion of the humerus is viewed dorsally (Fig. 4.6A) (Turner *et al.* 2015 character 97).

On the distal dorsal surface of the humerus, between the two epicondyles, is a large shallow triangular depression, the intercondylar fossa for the articulation of the olecranon process of the ulna (Fig 4.6A). Even though the ulna of the holotype of *Embrithosaurus* does not have an olecranon process, the humerus presents this distinct, albeit shallow (20 mm deep), intercondylar fossa (Turner *et al.*2015 character 103). The triangular intercondylar fossa is much wider than the width of the proximal ulna (olecranon process) (Turner *et al.* 2015 character 104)

and is demarcated by straight, raised edges preaxially and postaxially and a gently concavely curved, wide and low, but distinct, swollen transverse ridge (intercondylar ridge border) on the dorsal distal margin. This ridge separates the fossa from the articular radial and ulna facets of the humerus (Turner *et al.* 2015 character 102).

On the ventral surface of the humerus, between the two epicondylar flanges are two articular facets: the radial and ulnar facets (Fig. 4.6B). The radial condyle (Lee 1997a) or capitellum (Boonstra 1932c) is positioned preaxially and is a large, round, bulbous swelling, with a large, shallow depression, the radial facet (Fig. 4.6B, 4.7). The ulnar condyle is positioned postaxially and is much smaller and comprises a deeper, proximally tapering, elongated triangular groove, the ulnar facet (trochlear ulnar groove, ulnar articulation surface) which is bordered on its postaxial (posterior) side by a long, sharp-tipped rim of bone (Fig. 4.6B, 3.7) (Turner *et al.* 2015 character 101). The ulnar facet and its postaxial rim border on the ventral surface of the humerus, together form the articulation (trochlea) for the ulna (Lee 1997b:238). On the ventral surface of the humerus, the radial and ulnar facets are separated by an oblique, low ridge (Fig. 4.6B) which dissipates distally (Fig. 4.7B) and does not reach the border of the intercondylar fossa on the distal dorsal edge of the humerus. Figure 4.7B shows the radial and ulnar facets are prevented from extending round onto the distal side of the humerus by the intercondylar ridge border (Turner *et al.* 2015 character 100). The two epicondyles do not project distally far beyond the radial and ulnar articulation surfaces, extending only about 25 mm (Fig. 4.6) (Turner *et al.* 2015 character 98).

The proximal half of the humerus forms a wide, plate-like and roughly square blade with an anteroposterior length of only 250 mm (including the delto-pectoral crest). The anterior side of the proximal blade is gently convex and is crossed by a prominent diagonally oblique ridge that dissipates distally before reaching the shaft of the humerus (Fig. 4.5A). There is a ridge either side of the prominent oblique ridge: preaxially a much less prominent thin, straight ridge;

and postaxially a rugose irregular ridge, with a tubercle and swollen rim are also present.

The posterior side of the blade is concave (Fig. 4.5B). On the proximal ventral surface is the delto-pectoral crest, which extends distally from the proximal head of the humerus, curves postaxially and thickens to form a bloated, knob-like structure, with straight preaxial margin and curved postaxial margin, with a slightly convex ventral surface with a long, shallow groove (Fig. 4.6B).

The articular facet of the humerus forms a strip-like surface on the proximal margin of the humerus and is 210 mm in anteroposterior length and slightly s-shaped as the anterior portion curves ventrally and the posterior portion dorsally (Fig. 4.7A). The generally flat articular surface also widens considerably anterodorsally to 90 mm, more than twice the posteroventral width of 40 mm, supported by the proximal blade which is swollen to form a strongly convex turret on the preaxial side (Fig. 4.5A). The edges are slightly raised and the centre slightly depressed to form a shallow concavity, morphology that Turner (*et al.* 2015) ascribe as evidence of a large cartilaginous cap in *Bunostegos*.

Radius (Figs. 4.1, 4.8; Table 4.3)

For descriptive purposes the radius and ulna are assumed to have been oriented vertically in life. Both radii of SAM-PK-8034 are preserved but the left is deeply eroded all round and as a result appears smaller than the much better preserved right radius. The 231 mm long right radius is robust and stout, with a narrow shaft (40 mm anteroposteriorly x45 mm mediolaterally), oval to rectangular in cross section. The proximal and distal ends are mediolaterally expanded, proximally to 110 mm and distally to 100 mm. The radius is overall straight, but is slightly curved to bulge slightly anteriorly. The distal half of the posterior side of the radius presents a shallow concave region with well-defined borders (Fig. 4.8B).

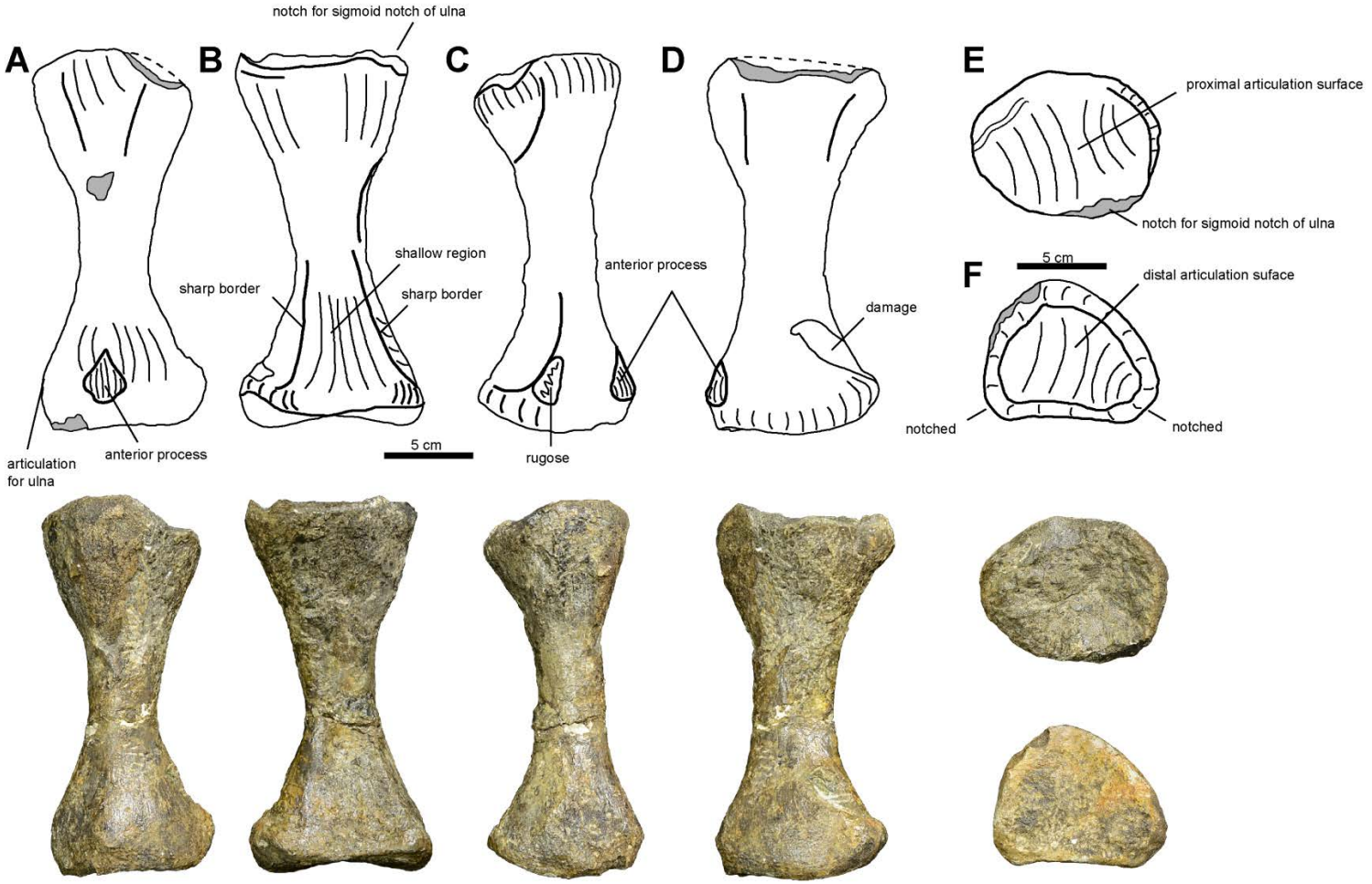


Figure 4.8: Photographs and interpretive drawings of the right radius of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in anterior view, (B), in posterior view, (C), in lateral view, (D), in medial view, (E), in dorsal view, (F), in ventral view. Dorsal to the top of the page in (A), (B), (C) and (D). Anterior to the top of the page in (E) and (F).

In cross section, the proximal (dorsal) articulation surface of the radius is ovoid, with a deep concavity for articulation with the radial condyle of the humerus (Fig. 4.8E). The edges are slightly raised and a small notch for articulation with the sigmoid notch of ulna is present on the posterolateral corner (Fig. 4.8F).

In cross section, the distal (ventral) articulation surface forms an isosceles triangle and a flat surface with a shallower concavity (Fig. 4.8F). The posterior side forms the straight, long axis of the triangle. The anteromedial and anterolateral sides are slightly shorter, roughly equal, and convexly bulging. The posterolateral and posteromedial corners are notched.

Assuming a horizontal proximal articulation surface, the distal articulation surface of the radius is oblique, and creates an angle of about 20^0 above a horizontal plane (Fig. 4.8C, D) similar to *Nochelesaurus* and *Bradysaurus*.

As noted by Broom (1903) there is a small, triangular, anterior process on the anterior surface of the radius (Fig. 4.8A, C, D) positioned 10 mm above the ventral edge. On the lateral side of the radius, a rugose region, for the articulation with the ulna is present, extending 10 - 20 mm above the ventral edge (Fig. 4.8C). On the medial side (Fig. 4.8D) is a damaged area creating the false impression of a sharp edged fossa, positioned 40 mm above the ventral edge, perhaps similar to the triangular fossa documented at the same position in *Bunostegos* (Turner *et al.* 2015).

The mediolaterally expansion of the proximal and distal ends of the radius are not in the same plane, but form an angle of 45^0 to each other.

Ulna (Figs. 4.1, 4.9, 4.10, 4.11; Table 4.4)

The left ulna of SAM-PK-8034 is very poorly preserved and badly eroded, however, the right ulna is well preserved. It is 295 mm in dorsoventral length, and mediolaterally flattened, more so distally than proximally as the proximal half of the ulna is much more robust than the distal half.

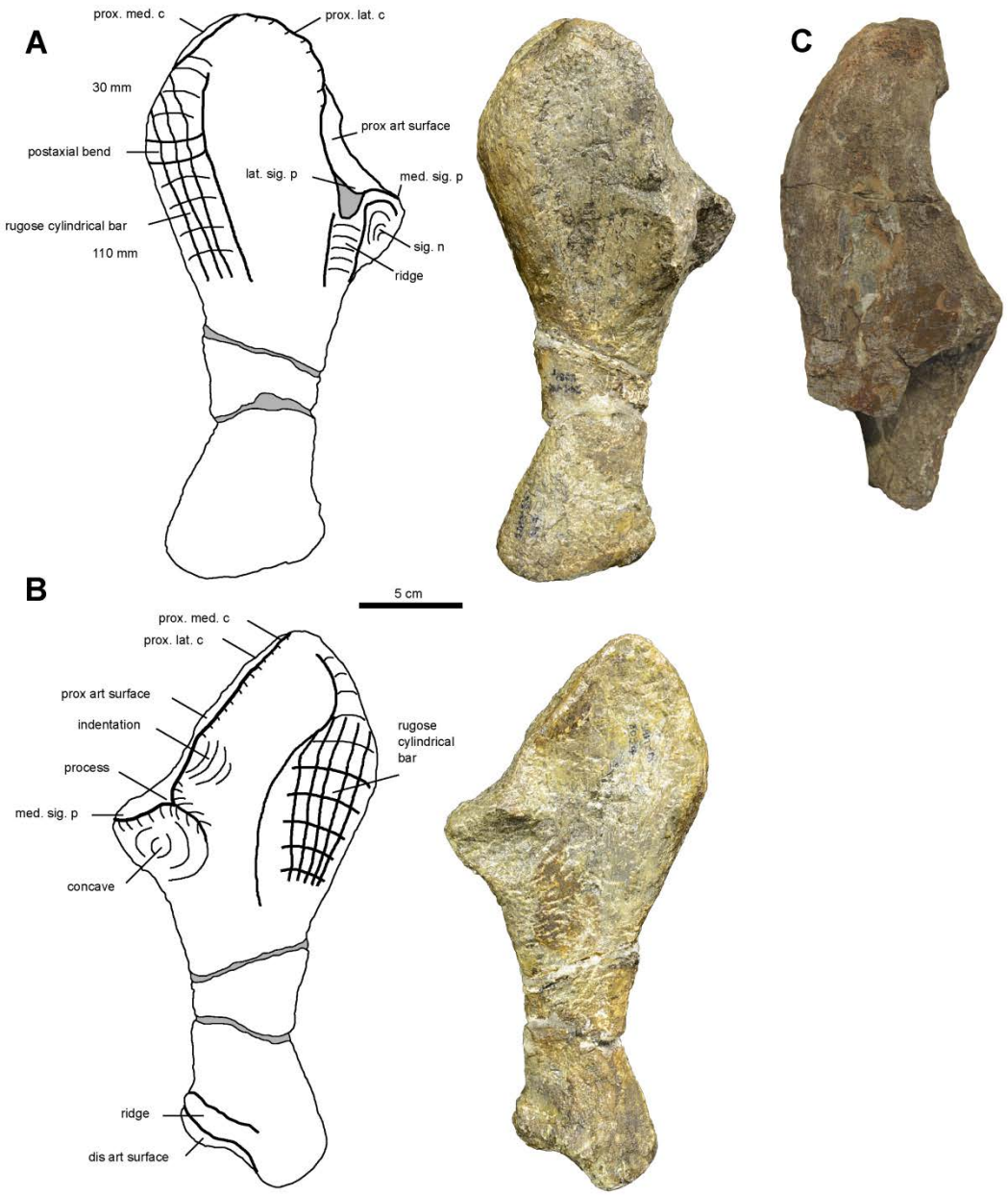


Figure 4.9: Photographs and interpretive drawings of right ulnae of *Embrithosaurus schwarzi*, (A), the holotype (SAM-PK-8034) in lateral view, (B), the holotype (SAM-PK-8034) in medial view, and (C), FMNH UR 2443 in lateral view (note the olecranon process, with partial right radius attached). Proximal to the top of the page.

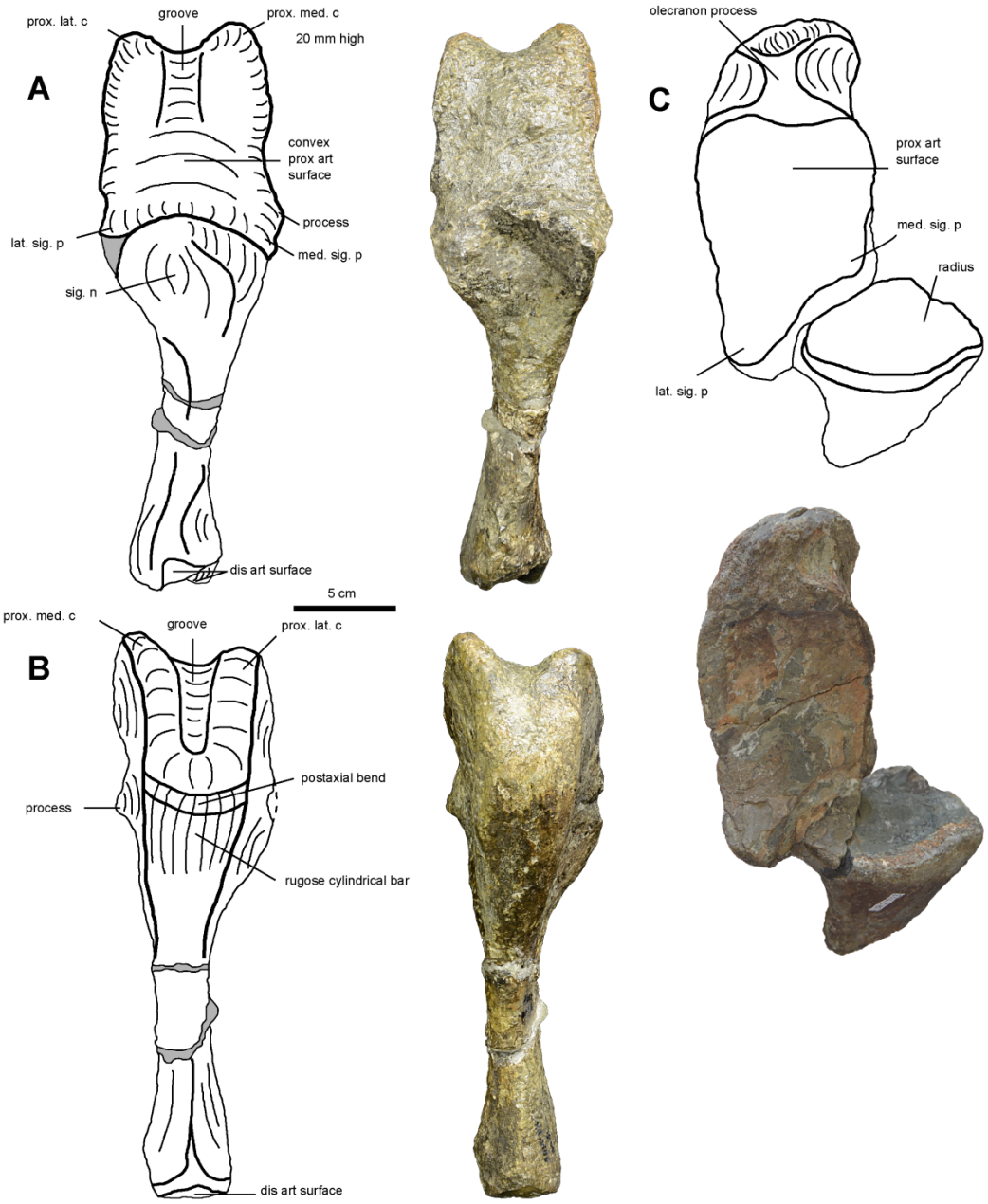


Figure 4.10: Photographs and interpretive drawings of right ulnae of *Embrithosaurus schwarzi*, (A), the holotype (SAM-PK-8034) in anterior view, (B), the holotype (SAM-PK-8034) in posterior view, and (C), FMNH UR 2443 in anterior view (with partial right radius attached). Proximal to the top of the page.

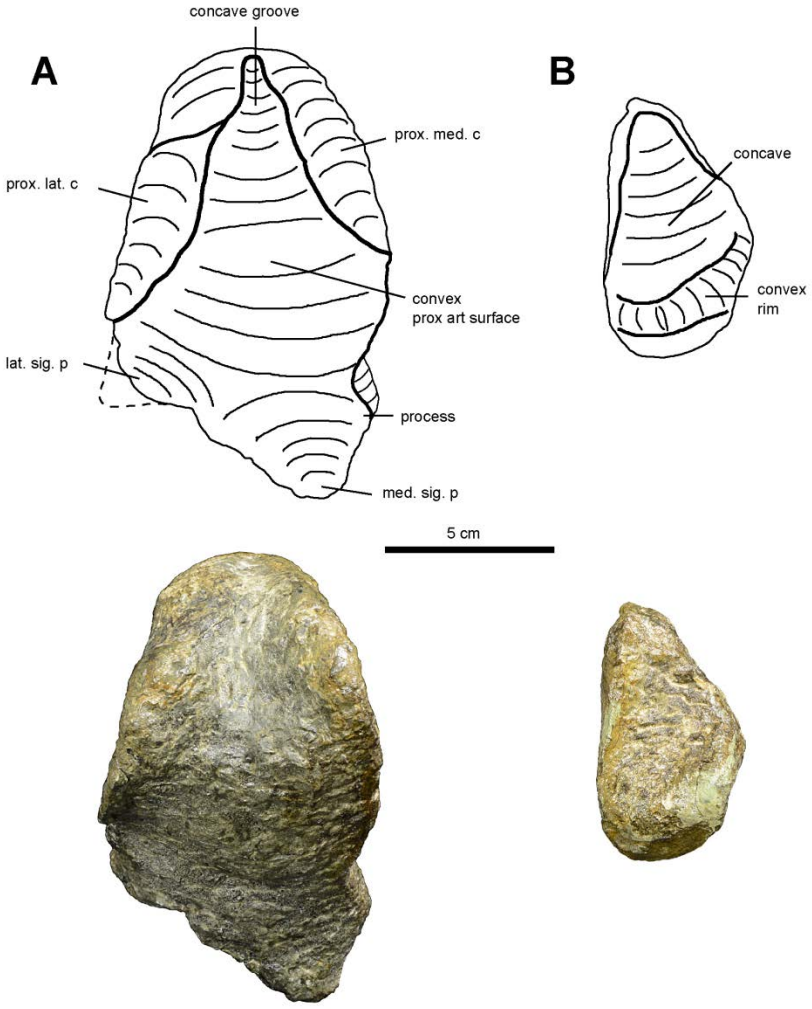


Figure 4.11: Photographs and interpretive drawings of the right ulna of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in proximal view, and (B), in distal view. Posterior to the top of the page in (A). Anterior to the top of the page in (B).

The straight postaxial margin of the ulna is thickened and swollen to form a cylindrical bar (110mm dorsoventrally), which thickens proximally. This postaxial bar is covered laterally, medially and postaxially (posteriorly) with prominent long rugose ridges that supported muscular attachment (Boonstra 1932c). Proximally, the rugose bar reaches a bend on the postaxial side of the ulna (Fig. 4.9), and the rugosity extends only 20-30 mm obliquely dorsally, above the bend. Anterior to the bar, the medial and lateral surfaces of the ulna are generally flat with shallowly concave vertical depressions, that emphasis the bar. Distally, the shaft of the ulna narrows before widening towards the distal end.

The anterior two-thirds of the small distal articular surface is deeply concave and the posterior third convex. The edges are sharp and slightly raised (Fig. 4.11B).

The large proximal articulation surface articulates with the groove-like ulnar condyle of the humerus. This articulation surface has been historically slightly over prepared. It forms a flat to gently convex rectangular pad, facing anterodorsally, with sharp edged margins (Fig. 4.10A)

Distally, the proximal articular surface shows two triangular, ledge-like sigmoidal processes, which create the dorsal borders of the sigmoidal (radial) notch (Figs. 4.10, 4.11). The medial process is larger. Broom (1903) noted that the lateral process was damaged during preparation and was therefore larger and projected further than currently preserved and the shape of its termination point cannot be determined. The medial process terminates with a relatively sharp point. A separate, small process is present on the border of the articular surface, 30 mm medial to the medial sigmoidal process. The sigmoidal notch is a relatively deep concave facet, which articulates with the proximal end of the radius.

Proximally, there is no olecranon process. Instead, the convex anterodorsally facing articular surface**,** forms a shallow and concave groove between two sharp, raised olecranon crests dorsally and posteriorly (Figs. 4. 3.10, 4.11) (Turner *et al.* 2015 character 105). As observed by Boonstra (1932c), there is no anterodorsal limiting ridge, and no olecranon process or shelf preventing the gently convex anterodorsal articular surface from extending proximally onto the proximal side of the ulna. The proximal lateral and proximal medial crests are 40 mm apart and the groove between them is up to 20 mm deep. The medial crest is slightly larger. The shallow groove extends 30-40 mm posteriorly onto the posterior (postaxial) side of the ulna (Fig. 4.10B), where the distance between the crests narrows to 20 mm before the crests and the groove dissipate just before reaching the postaxial bend of the cylindrical postaxial bar. There is no posterodorsal limiting ridge. Apart from these two low olecranon crests, either side of the groove of the proximal articulation surface, there is no dorsally

projecting olecranon process on the proximal end of the ulna (Turner *et al.* 2015 character 106).

Referred *Embrithosaurus* specimen FMNH UR 2443, unambiguously identified as *Embrithosaurus* through the dimensions of the pelvis, has a large and prominent olecranon process (Figs. 4.9, 4.10), 40 mm dorsoventrally high, extending anteriorly 20 mm, which is very similar to that of the holotype of *Bradysaurus baini*. The olecranon process is formed anterodorsally by two overhanging, concavely curved projections of the lateral and medial surfaces of the ulna, that meet each other anteriorly, forming a limiting ridge ("lip-like" overhanging ledge) above the proximal articulation surface of the ulna (Turner *et al.* 2015 character 105). *Embrithosaurus* specimen CGP CBT 112, also has a large, prominent olecranon process on the right ulna, 25 mm dorsoventrally high, extending anteriorly 15 mm beyond the articular surface.

Carpus and Manus (Fig. 4.1)

Broom (1903:132) reported for SAM-PK-8034 that "a considerable number of isolated phalanges and metacarpals were found with, but with no indication as to which digits they belong". Two complete isolated digits are preserved for SAM-PK-8034 as well as several misplaced phalanges and small carpal bones. Boonstra (1929a) in his paper on the pareiasaurian manus, published a photograph of these two isolated digits for SAM-PK-8034 (Boonstra 1929a: Plate VII, Fig. 2), correctly stating that each comprise a metacarpal and three phalanges, including the terminal claws. From Broom's (1903) full body restoration (Broom 1903: Plate XVI, and here Fig. 4.1), Boonstra (1929a) who worked on several pareiasaurian mani, noted the manus phalangeal formula for SAM-PK-8034 as 2, 3, 4, 5, 4 which I accept.

4.4.3 Hindlimbs

Femur (Figs. 4.1, 4.12, 4.13, 4.14; Table 4.5)

The distal half of the left femur is well preserved but the proximal half is deeply weathered on all sides apart from the proximal articular surface. The right femur is very well preserved, was illustrated by Broom (1903, Plate XV, Figs. 15, 16) and forms the basis of this description.

Haughton and Boonstra (1930b) note the pareiasaurian femur as generally obliquely outwardly oriented in life position. The femur of *Embrithosaurus* is 410 mm long, with an expanded proximal end (210 mm anteroposteriorly wide), an oval shaft (110 mm anteroposteriorly x 70 mm dorsoventrally), and a two robust distal condyles (170 mm anteroposteriorly wide) distally. The torsion of the planes between the proximal and distal articulations is 30^0.

The head of the femur is large and robust, and the (proximal articulation surface) is slightly convex, facing primarily proximally. In proximal view (Fig. 4.14B), the articular surface is a convex, elongated “tear-drop” shape which narrows postaxially to a slight notch that separates the proximal surface from the major trochanter on the postaxial side of the femur. The dorsal and ventral margins of the surface are right angled and form a slightly raised rim and the surface does not encroach round onto the ventral or dorsal sides of the femur. The proximal articulation surface of the femoral head is not flat but convex and is more strongly curved as the femur head expands anteriorly (preaxially) away from the shaft of the femur, and curves gently distally (laterally outwards) until the surface terminates at a 90^0 right angle (Fig. 4.12). (Turner *et al.* 2015 character 120).

The preaxially expanded femoral head creates an angle of 40^0 from the plane of the femoral shaft (Fig. 4.12). According to Haughton and Boonstra (1930b) a relatively low or shallow femoral head expansion, such as only 40^0, is the primitive condition, which supports an oblique femur and more sprawling

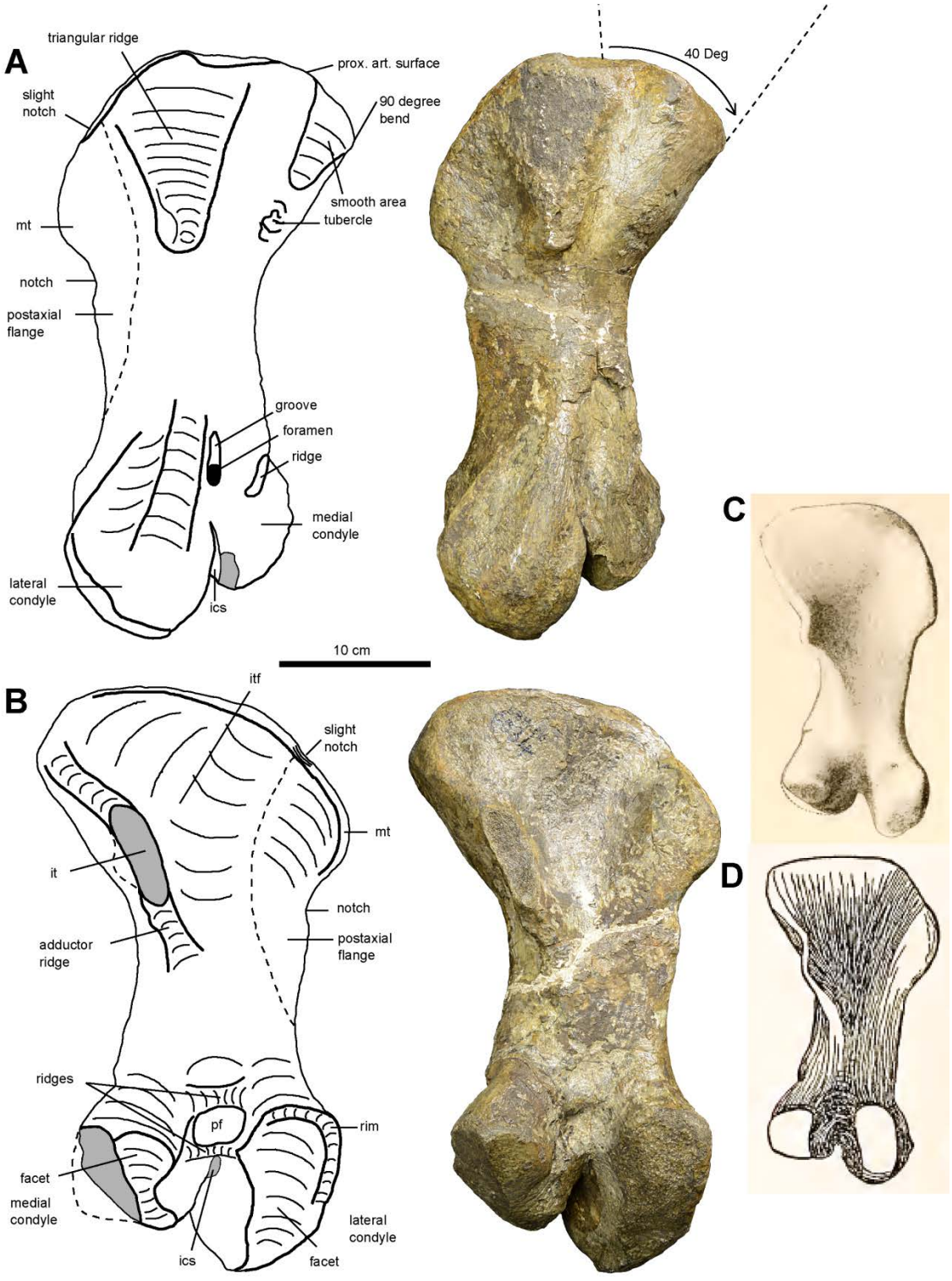


Figure 4.12: Photographs and interpretive drawings of the right femur of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in dorsal view, (B), in ventral view, (C), in ventral view by Broom (1903), and (D) in ventral view by Haughton and Boonstra (1930b). Proximal to the top of the page.

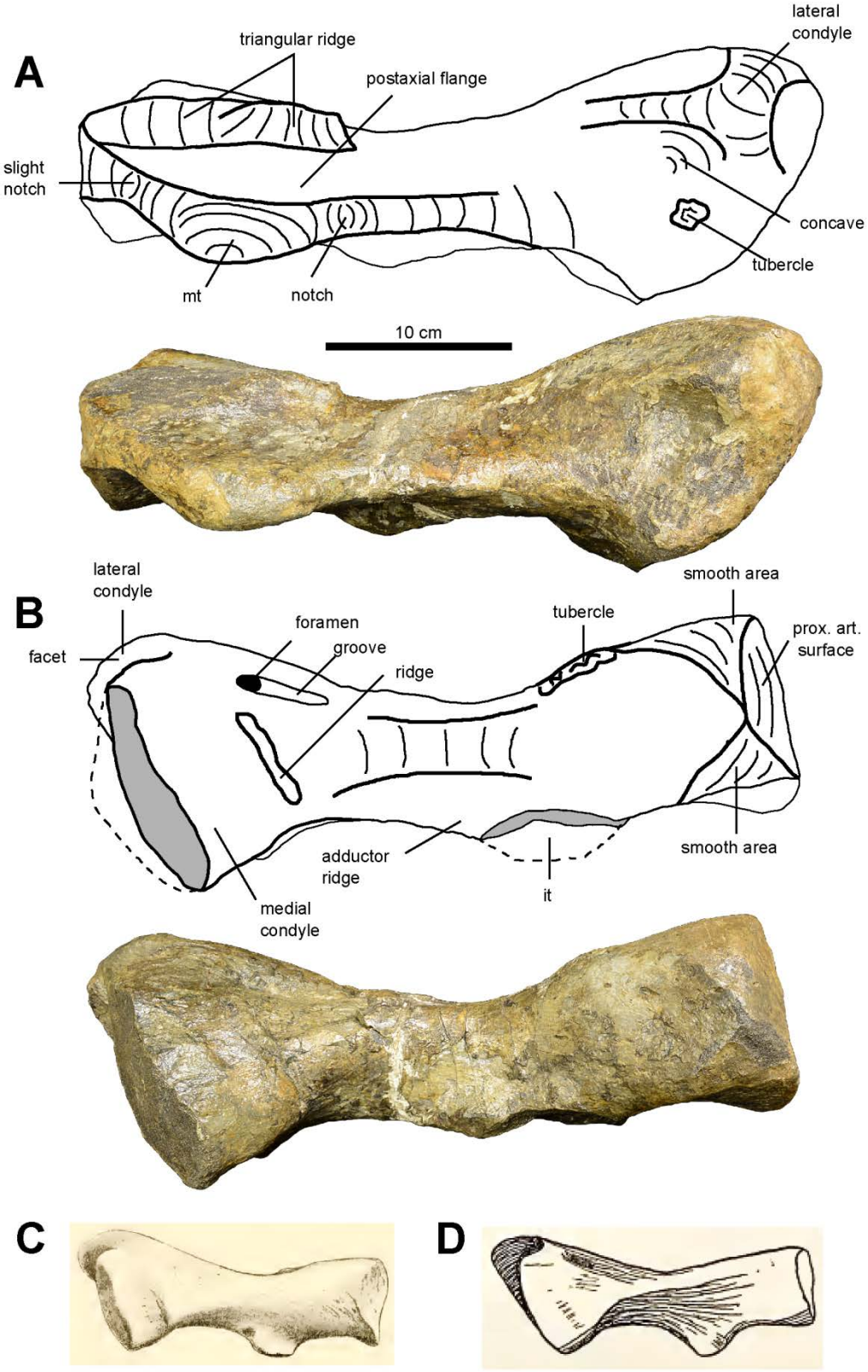


Figure 4.13: Photographs and interpretive drawings of the right femur of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in posterior view, (B), in anterior view, (C) in anterior view by Broom (1903), and (D) in anterior view by Haughton and Boonstra (1930b). Dorsal to the top of the page.

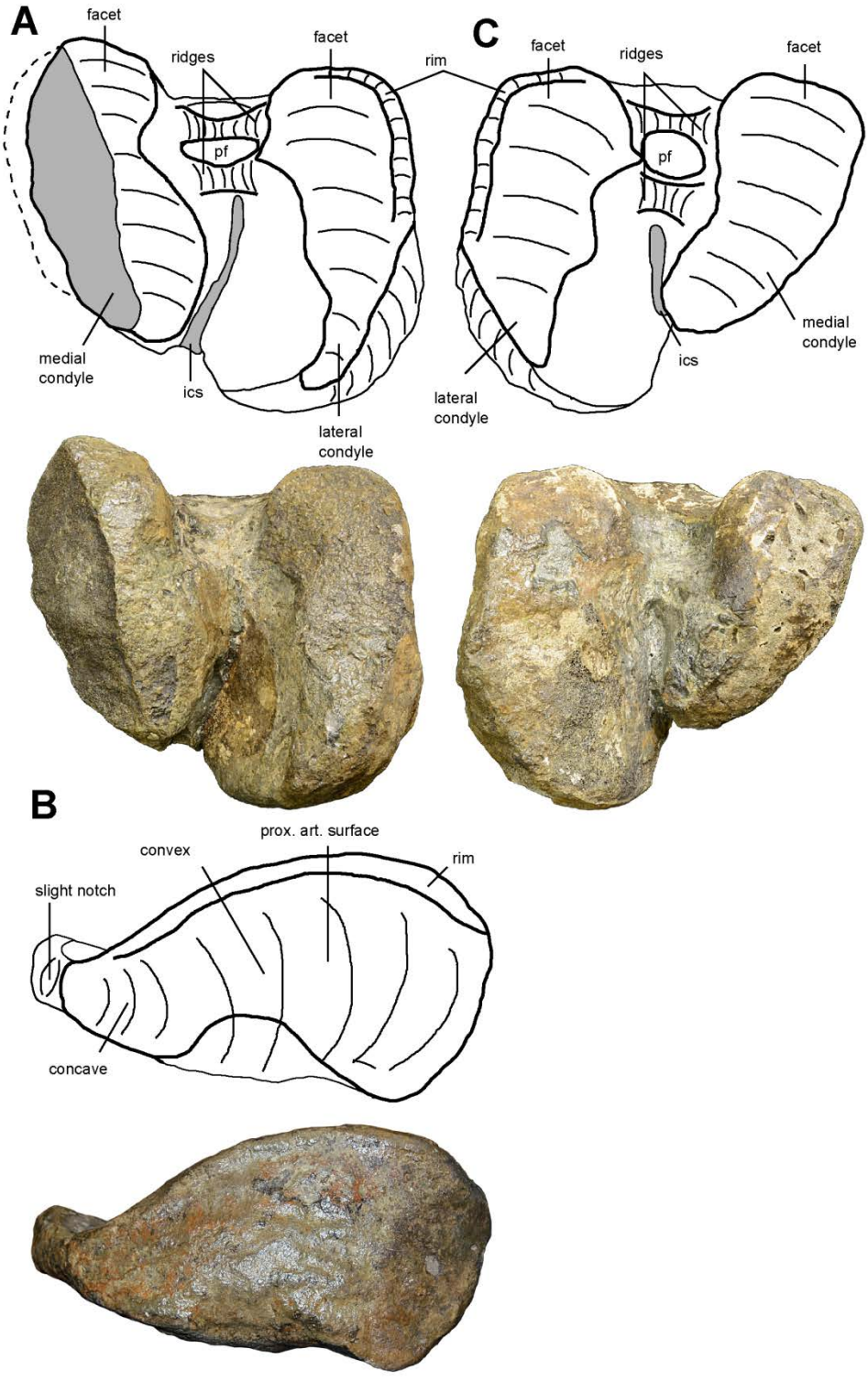


Figure 4.14: Photographs and interpretive drawings of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), right femur in distal view, (B), right femur in proximal view, (C), left femur in distal view. Ventral to the top of the page.

and less upright hind limb posture.

The major (external) trochanter is a distinct, well developed, knob-like swelling on the postaxial flange (Turner *et al.* 2015 character 121). It is directed posteroventrally and projects the furthest (30 mm) postaxially (posteriorly) of all South African middle Permian pareiasaurs, beyond the shaft of the femur. However, dorsoventrally, the major trochanter is the same thickness (35 mm) as in most South African middle Permian pareiasaurian specimens, which is much thicker than the 20 mm thick postaxial flange on which it is positioned. The major trochanter is formed between two notches: a shallow notch on the proximal-postaxial corner of the femur separates the major trochanter from the proximal articulation surface of the head, and a more distinct and deeper notch on the postaxial flange, which separates the major trochanter from the postaxial shaft.

The postaxial flange forms a wide and flat plate and proximally includes the major trochanter. Posteriorly and slightly ventrally oriented, the flange extends distally from the proximal-postaxial border notch of the major trochanter for the entire length of the shaft of the femur, tapering distally, it merges imperceptibly with the shaft of the femur, terminating just before the large lateral distal (fibular) condyle (Turner *et al.* 2015 character 123). The postaxial edge of the flange is straight to slightly convex in dorsal and ventral view (Fig. 3.12), and not slightly concave as maintained by Lee (1997b:247). The preaxial edge of the shaft of the femur is straight. Therefore the shaft of the femur appears anteroposteriorly consistently wide along its entire length and is not constricted (Turner *et al.* 2015 character 124). In dorsoventral thickness, the flange is 20 mm thick proximally, immediately distal of the protruding trochanter major, and thickens distally to 40 mm.

A large, rugose low, triangular ridge for muscular attachment covers most of the dorsal surface of the proximal portion of the femur between the major trochanter and the preaxial edge of the femur (Fig. 4.12A). The ridge is low

proximally and rises distally. A small irregular tubercle is present anterior to this ridge, on the preaxial border.

In ventral view, the proximal portion of the femur is deeply concave forming the intertrochanteric fossa between the major trochanter and the internal trochanter. Since Broom's (1903) original description and illustrations, most of the internal (minor) trochanter near the preaxial edge of the femur has been sheared-off and only a long broken edge remains (75 x 22 mm). Broom's illustrations of the complete internal trochanter in ventral view (Broom 1903: Plate XV, Figs. 16 and here Fig. 4.12C) show that the proximal region is gently curved, such that the preaxial (anterior) side is concave and the postaxial (posterior) side is convex (Turner *et al.* 2015 character 125). *Embrithosaurus* specimens FMNH UR 2443 and CGP CBT 112 also have gently curved internal trochanters. Broom's preaxial (anterior) view (Broom 1903: Plate XV, Fig. 17 and here Fig. 4.13C) show the internal trochanter of the holotype protruding ventrally perpendicular out of the femur, forming a raised curved shelf that extends far ventrally, to about 30 mm beyond the femur shaft (drawn in dotted in Fig 4.13B.). From the broken edge of the internal trochanter, a long, thick and straight adductor ridge continues distally, tapering off into the femur. The distal portion of the adductor ridge is very rugose (it is smoother and narrower in the holotypes of *Bradysaurus baini* and *Nochelesaurus alexanderi*). There is a large anterior (preaxial) process or bend in CGP CBT 112 (not present in *Nochelesaurus* or *Bradysaurus baini*). Broom (1903: Plate XV, Fig. 17 and here Fig. 4.13C) shows this anterior process.

A large nutritive foramen is present on the dorsal surface of the femur (Fig. 4.12A). This foramen is located at the distal end of a 40 mm long, deep groove that shallows proximally. The distal intercondylar sulcus is a very deep groove between the large lateral condyle and small medial condyle. It is dorsoventrally oriented, and straight with the dorsal half curving anteriorly (Fig 4.14). The sulcus is wide and deep distally, but narrows and tapers proximally. The sulcus is

prevented from extending onto the ventral surface of the femur, by a raised ridge passing between the two condyles (Fig. 4.12B, 4.14A, C). Proximal to this ridge, on the ventral surface of the femur, the popliteal fossa depression is distinct but shallow, and measures 30 mm x 20 mm.

A ridge on the dorsal side of the right femur, just above the medial condyle, has been attributed to deformation or crushing, as it is not present on the undamaged left femur (Fig. 4.12A) (Broom 1903).

Distally, the lateral condyle is much larger than the medial condyle. It is important to note that the lateral condyle extends only 30 mm further distally (right femur) and 40 mm further distally (left femur) than the medial condyle. Both condyles have flat to slightly convex distal articular facets which articulate with the tibia (4.14A, C). These facets are dorsoventrally elongated and face ventrally, the lateral distal facet faces slightly anteriorly and the medial distal facet posteriorly.

In cross section both facets are “kidney-shaped” (double-lobed) with the lateral condylar facet being longer. On the right femur, a large, wide section of the facet of the medial condyle is sheared-off (Fig. 4.14A). Although weathered, the left medial condylar facet is complete (Fig. 4.14C).

Tibia (Figs. 4.1, 4.15; Table 4.6)

Both tibiae of SAM-PK-8034 are well preserved. Haughton and Boonstra (1930b) orient the tibia and fibula as vertical parallel bones, which is the orientation used in this description.

The tibia is dumbbell shaped, more deeply concave on the lateral side than medially (Fig. 4.15). Both ends of the tibia are greatly expanded, with the proximal end the widest. The shaft of the tibia in *Embrithosaurus* is very constricted (only 45mm mediolaterally wide) which is the narrowest of all the middle Permian pareiasaurs, and much narrower than *Nochelesaurus* (70-72 mm) or *Bradysaurus* (75mm).

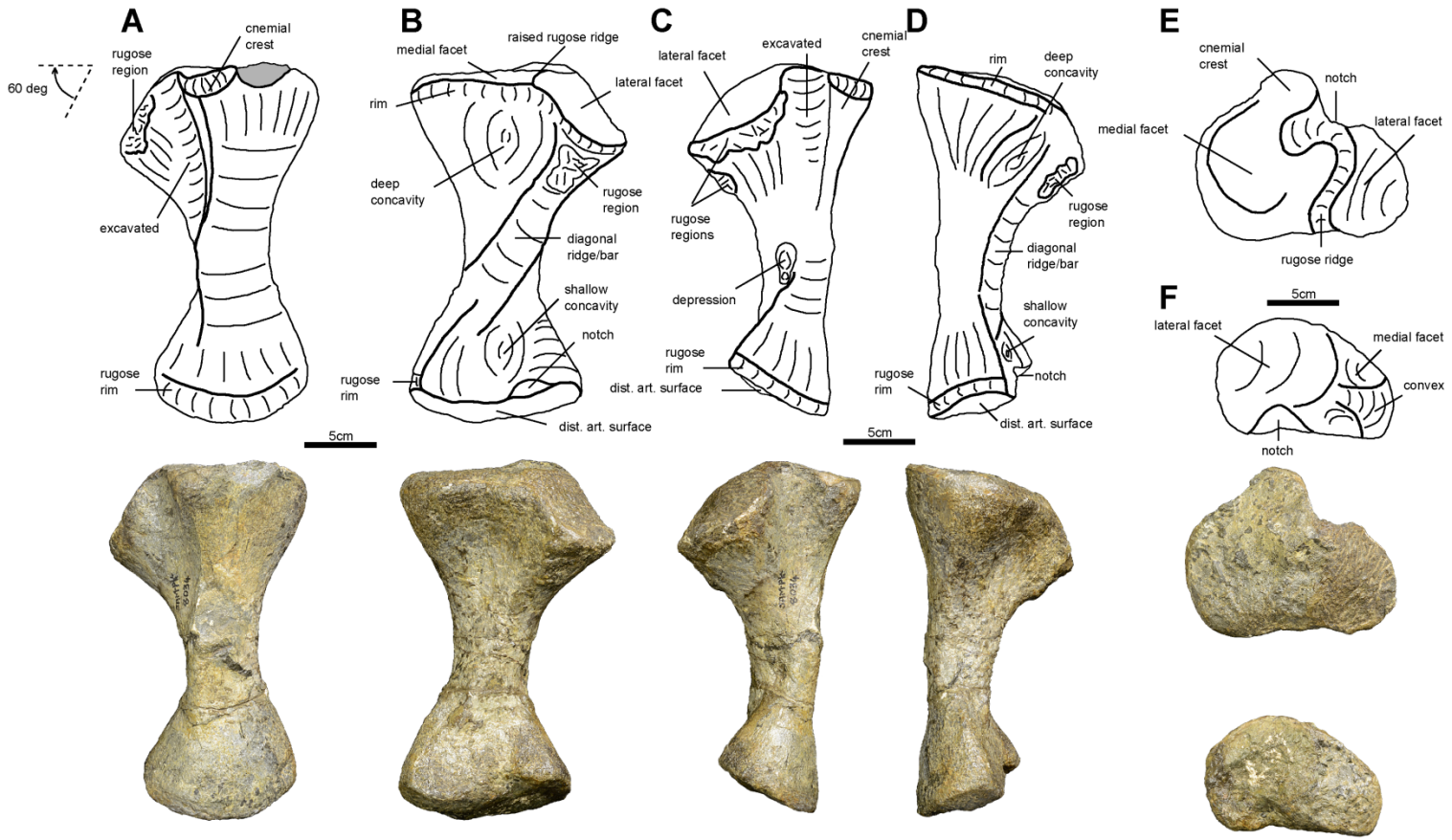


Figure 4.15: Photographs and interpretive drawings of the right tibia of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in anterior view, (B), in posterior view, (C), in lateral view, (D), in medial view, (E), in dorsal view, (F), in ventral view. Proximal to the top of the page in (A), (B), (C) and (D). Anterior to the top of the page in (E) and (F).

On the posterior side of the tibia, are two wide depressions located proximally and distally (Fig. 4.15B). The proximal depression is widest and deepest. A diagonal ridge extends between the proximal and distal regions, forming the lateral border of the proximal depression and the medial border of the distal one. A rugose region is present on the lateral border of the proximal depression.

Both the proximal and distal articulation surfaces of the tibia are rugose and the tibia is "twisted" so that the planes of the proximal and dorsal expansions are about 30^0 apart.

The proximal articulation surface of the tibia is elongated in cross section, dominated by the anterior projection of the cnemial crest and a very deep and distinct anterior notch, lateral to the cnemial crest, for reception of the fibula (Fig. 4.15E). The articulation surface comprises two flat facets for reception with the distal femur, separated by a median, curved ridge which fits in the intercondylar sulcus groove of the femur. The ridge is thicker anteriorly and thins posteriorly. The medial facet is largest, flat to slightly convex, faces primarily dorsally and slightly posteriorly and has sharp angled margins anteriorly and medially and rounded margins posteriorly. The lateral facet is much smaller, faces primarily dorsolaterally and slightly posteriorly. Interestingly, the medial and lateral facets are not on the same plane, and are instead separated by a large (60^0) angle, which is larger than the angle of about 40^0 of *Nochelesurus* and *Bradysaurus baini*.

The anterior cnemial crest is well-developed and is best preserved on the left tibia, being thickest proximally and tapering distally (Turner *et al.* 2015 character 126). A deep, concave, longitudinal excavation for the reception of the fibula is positioned laterally.

The distal articulation surface is roughly ovoid in cross section, with a curved anterior margin but flat posteriorly where a small, shallow notch is present (Fig. 4.15F). The majority of the surface is covered by a round lateral facet, slightly concave and articulates with the tarsus. The medial facet is smaller, consisting of

a slightly convex, raised portion posteriorly and a shallow, depressed, concave portion anteriorly. A small notch is present on the posterior margin of the distal articulation surface, between the lateral and medial facets.

Fibula (Figs. 4.1, 4.16; Table 4.7)

The right fibula is complete, but only the distal portion of the left one remains. The fibula of SAM-PK-8034 is gracile, long and slender, and slightly longer (261 mm) than the tibia (250 mm). The shaft is straight, narrow and cyclindrical midway, and the ends expanded with the distal end wider than the proximal end. The planes of the distal and proximal expansions are offset by 30^0 from each other, as is the situation with the tibia. The medial fibula carries two large, rugose, tubercles, one proximally and one distally. The distal articular surface is four-sided (diamond-shaped) in cross section and devotes two-thirds to a flat, large facet for articulation with the tarsus.

It must be noted that specimen CGP CBT 112 has a much thicker and more robust fibula than the holotype, although not much longer, and also has a thin, raised, elongated ridge for muscle attachment on the anterior side of the shaft of the fibula, comprising four to five small, rugose, projecting knobs (which are also present in *Nochelesaurus* specimen SAM-PK-6238).

Tarsus (Figs. 4.1, 4.16)

In pareiasaurs, a single proximal tarsal element is distinct and consists of a fused astragalocalcaneum, comprising the astragalus and the calcaneum (Tsuji 2013) or the fibulare and intermedium (Boonstra 1929b).

Broom (1903) briefly described and figured (Plate XV: Fig 23 & 24 and here Fig. 4.16G, H) a single large tarsal element which he considered as probably the united tibiale, intermedium and fibulare. This element is no longer present and appears to have been lost. Broom (1903) described a large foramen near the middle of the front of the bone in SAM-PK-8034 which Boonstra (1929b) considered to indicate the line of fusion on the tarsals of all pareiasaurs.

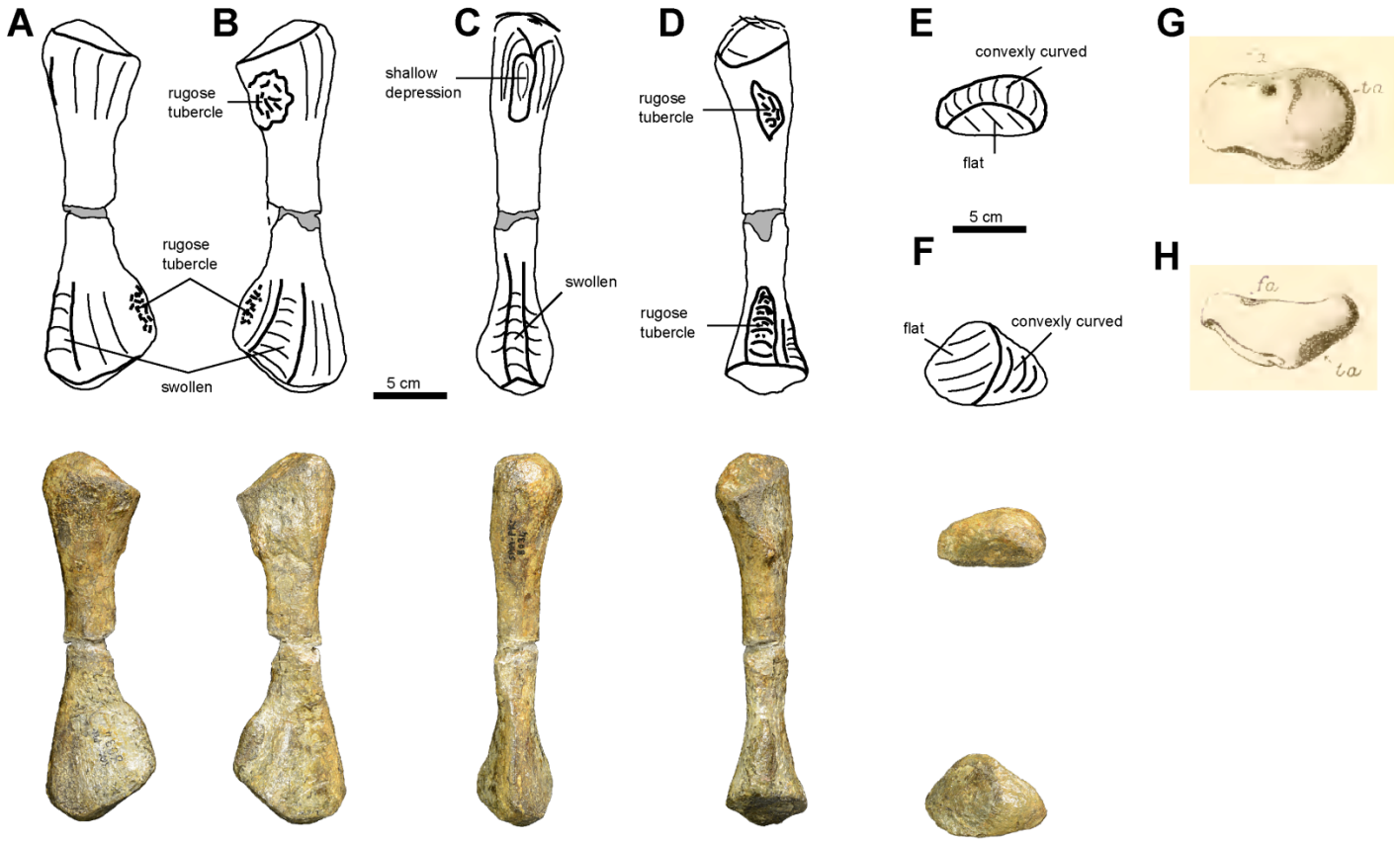


Figure 4.16: Photographs and interpretive drawings of the right fibula of the holotype of Embrithosaurus schwarzi (SAM-PK-8034), (A), in anterior view, (B), in posterior view, (C), in lateral view, (D), in medial view, (E), in dorsal view, (F), in ventral view. Proximal to the top of the page in (A), (B), (C) and (D). Anterior to the top of the page in (E) and (F). Interpretive drawings of the astragalocalcaneum of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034) by Broom (1903), (G), in dorsal view, (H), in anterior view, f.a articulation for fibula, t.a, articulation for tibia. Anterior to the top of the page in (G). This astragalocalcaneum is now missing.

Boonstra (1929b), in his paper on the pareiasaurian pes, published a photograph (Plate X) of the astragalocalcaneum of the holotype of *Embrithosaurus* (SAM-PK-8034) in articulation with the tibia and fibula.

Using Broom's (1903, here Fig. 4.16G, H) and Boonstra's (1929b) figures, the bone resembles a flattened triangle. The ventral surface is flat and rectangular, outlined by a raised rim. The dorsal surface is dominated by a raised central ridge that extends the length of the bone. Either side of the apex of the ridge, are the facets for articulation with the fibula and tibia (Fig. 4.16).

Pes (Figs. 4.1, 4.27)

Broom, in his fully body restoration (Plate XVI, and here Fig. 4.1), illustrated two of the hind digits of the holotype of *Embrithosaurus* and he (Broom 1903:124) documented that the second and third toes of the left foot were preserved. Boonstra (1929b) assigned a phalangeal hind foot formula of 2, 3, 3, 4, 3 for the holotype of *Embrithosaurus*, although it is difficult to determine the count from Broom's figure.

The holotype of *Embrithosaurus* preserves two partial digits articulated to the ventral surface of the vertebral block containing the 14th to 16th vertebrae. One of the digits comprises 3 phalanges and a terminal claw (Fig. 4.27). Although it is not possible to determine to which digits they belong, they are typical pareiasaurian: robust, short and wide and both digits end with thick, short recurved claws that are pointed.

4.4.4 Pelvic girdle

The pelvic girdle of pareiasaurs comprises a paired ilium, ischium and pubis, strongly fused along the midline to form two innominate bones (Haughton and Boonstra 1930b). For this description the innominates of SAM-PK-8034, FMNH UR 2443, FMNH UR 2486 and CGP CBT 112 were studied. In SAM-PK-8034, the pelvis is nearly complete, except for distal sections of both iliac blades, and small pieces of the left pubis and the right ischium. The sutures between the ilium,

ischium and pubis are strongly fused and not discernible. As pointed out by Haughton and Boonstra (1930b) the pelvis of SAM-PK-8034 is remarkably high and narrow (in anterior or posterior view) with a very narrow pelvic floor.

Ilium (Figs. 4.1, 4.17, 4.18, 4.19, 4. 20; Table 4.8)

The ilium forms the entire iliac blade dorsally, the shaft below the blade, and the dorsal portion of the acetabulum ventrally.

The large iliac blade, is a thin and slightly anteriorly directed elongated plate, consisting of a long and elongated anterior process, and a shorter posterior process. The right iliac blade is almost complete and preserves the entire anterior process, but the posterior process is mostly missing. The anterior and dorsal margins of the right anterior process are 15-20 mm wide and flat to slightly concave, sharp edged, with slightly raised rims. The ventral margins are thinner, more pointed, and convexly rounded where the iliac blade merges ventrally into the shaft of the ilium. The left iliac blade is very poorly preserved and deeply eroded, consisting of only a remnant internal core of bone.

There are three main differences in the size of the iliac blades, between specimens of *Embrithosaurus* and *Bradysaurus baini*. (See Table 4.8): 1) the mediolateral width of the blades, anteriorly and dorsally, is narrower in *Embrithosaurus* (15-20 mm) and wider in *Bradysaurus baini* (25-30 mm); 2) the total anteroposterior length of the dorsal sacral blade (anterior and posterior process) is shorter in *Embrithosaurus* (estimated 260-290 mm) and longer in *Bradysaurus baini* (290-310 mm) (Turner *et al.* 2015 character 112); 3) the anteroposterior length of the anterior process (measured from the anterior tip of the anterior process, to the anterior shaft border) is shorter in *Embrithosaurus* (60-90 mm) and longer in *Bradysaurus baini* (130 mm) (Turner *et al.* 2015 character 110).

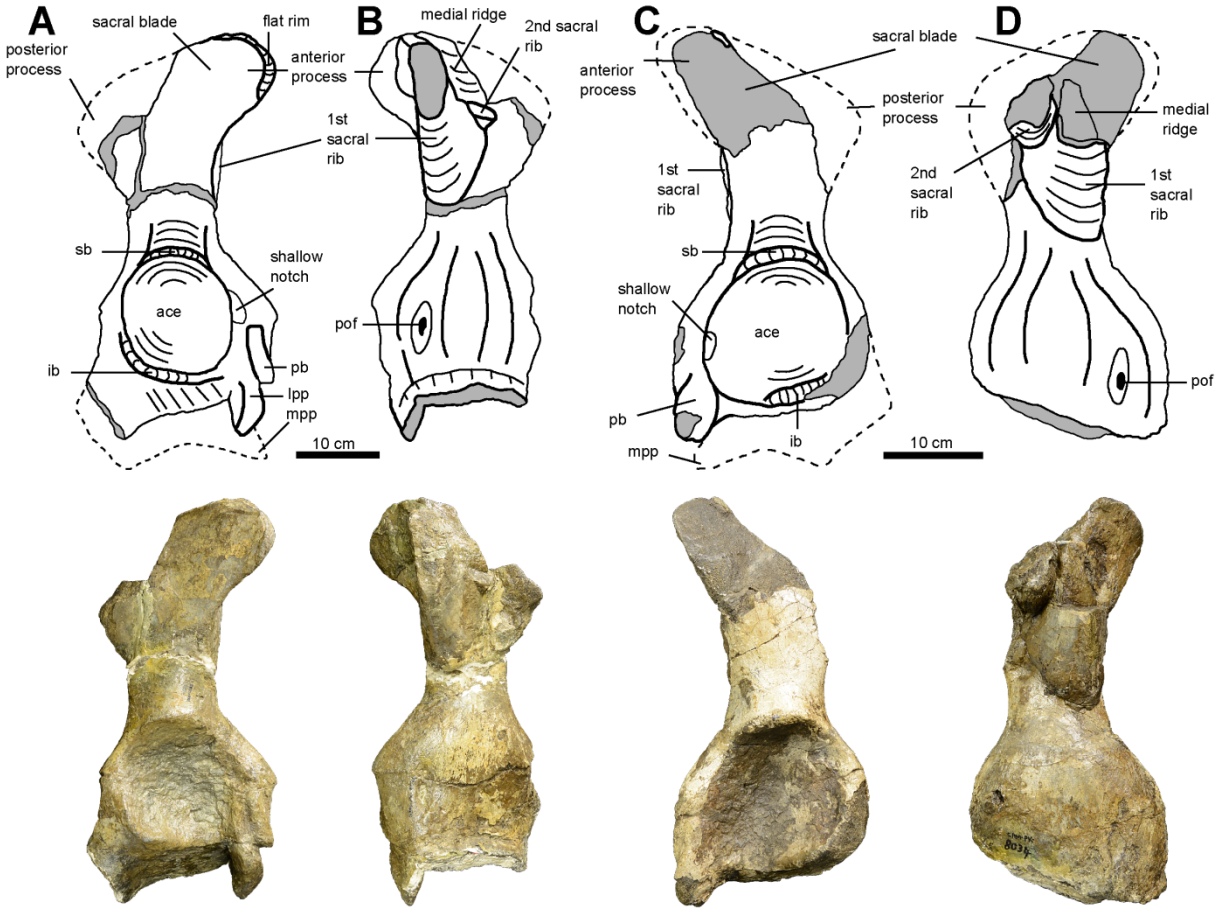


Figure 4.17: Photographs and interpretive drawings of the pelvis of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in right lateral view, (B), in right medial view. (C), in left lateral view, and (D), in left medial view. Dorsal to the top of the page.

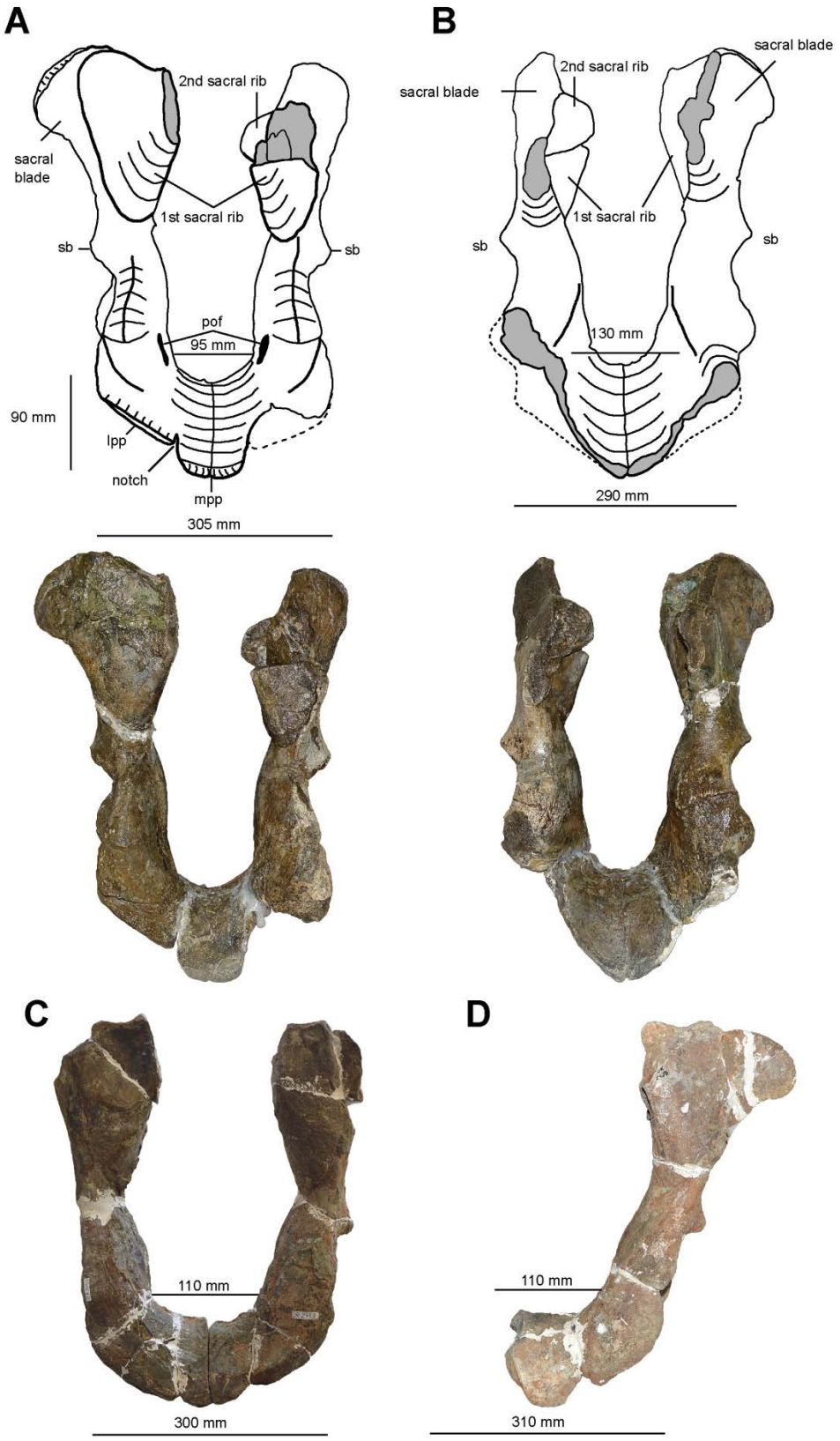


Figure 4.18: Photographs and interpretive drawings of the pelvis of *Embrithosaurus schwarzi*. The holotype (SAM-PK-8034) in (A), anterior view, and (B) posterior view. (C), FMNH UR 2443 in anterior view, and (D), FMNH UR 2486 in anterior view. Dorsal to the top of the page.

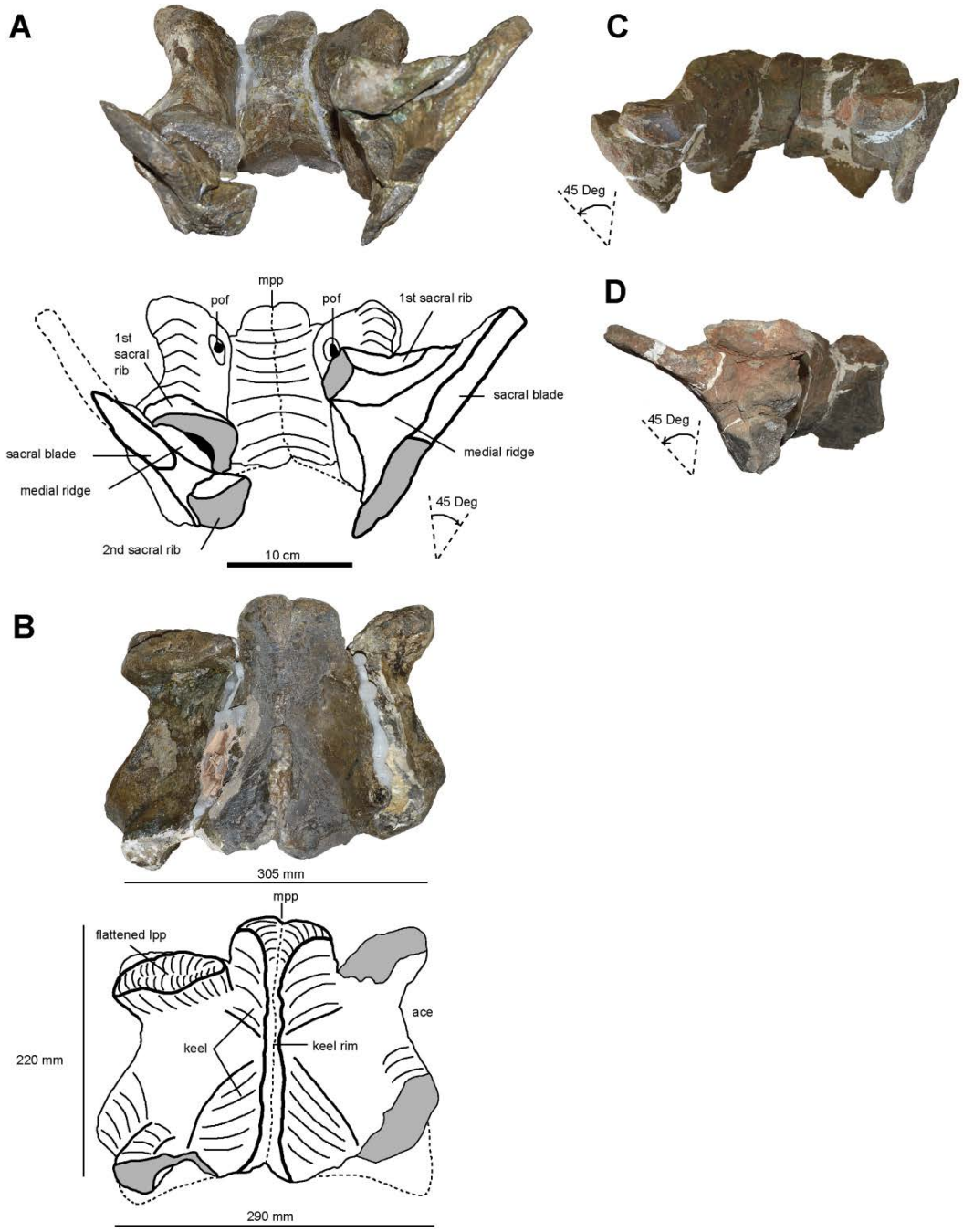


Figure 4.19: Photographs and interpretive drawings of the pelvis of *Embrithosaurus schwarzi*. The holotype (SAM-PK-8034) in (A), dorsal view, and (B), ventral view. (C), FMNH UR 2443, in dorsal view, and (D), FMNH UR 2486, in dorsal view. Anterior to the top of the page.

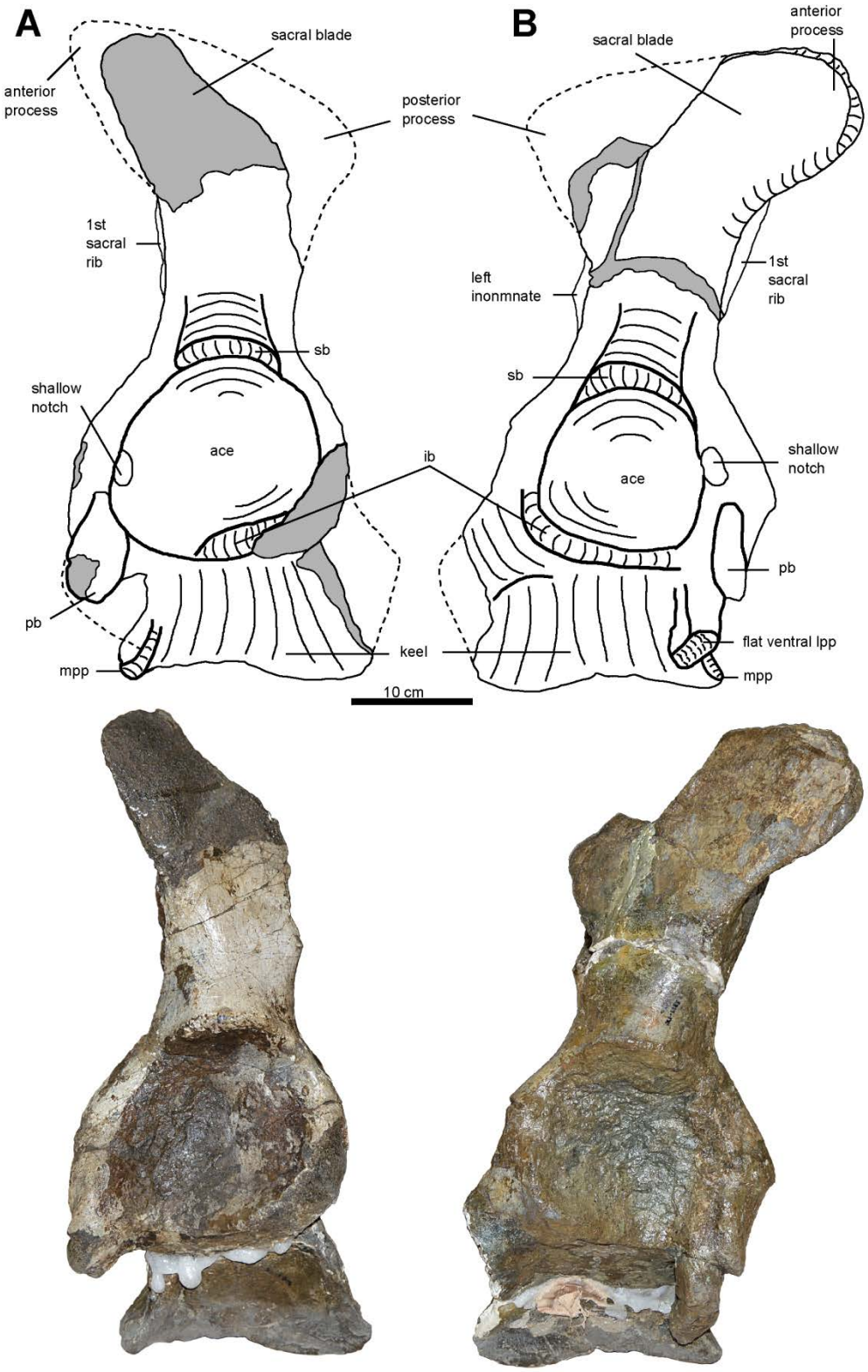


Figure 4.20: Photographs and interpretive drawings of the innominates of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), left innominate in lateral view, and (B), right innominate in lateral view. Dorsal to the top of the page.

Lee (1994, 1997a) recognised three autapomorphies in the shape and orientation of the iliac blades of *Embrithosaurus*, thus it is prudent to fully investigate these autapomorphies. There are a number of differences in the shape and orientation of the iliac blades between specimens of *Embrithosaurus* and *Bradysaurus baini*.

The morphology of the iliac blades of *Embrithosaurus* is simple (Fig. 4.19): 1) the entire blade is almost perfectly flat and straight (SAM-PK-8034, FMNH UR 2443), and on some specimens the blade is laterally slightly and evenly concave (FMNH UR 2486, CGP CBT 112), and 2) in living position, the entire blade is oriented almost perfectly dorsoventrally (vertically), except for the anteroventral margin or tip of the anterior process, which is very slightly curved (or everted) upwards and laterally outwards, extending only 10 mm laterally outwards from a vertical plane, and curved less than 10^0 upwards (Turner *et al.* 2015 character 111).

In contrast, *Bradysaurus baini* specimens show complex iliac blades: anteriorly they are severely laterally concave and everted upwards; posteriorly they are vertical and posterodorsally they curved medially inwards.

In dorsal view, the thin iliac blades of the holotype of *Embrithosaurus* are not parallel, and instead diverge anteriorly, being oriented 45^0 off the sagittal midline plane (Fig. 4.19). Specimens FMNH UR 2443 and FMNH UR 2486 show a similar degree of anterior diverging (Fig. 4.19) and CGP CBT 112 shows an extreme 60^0 divergence. In contrast, in *Bradysaurus baini,* the iliac blades are oriented parallel posteriorly, and only the anterior third of the blade diverges at 45^0 off the sagittal plane (Fig. 6.11A).

The shaft of the ilium of *Embrithosaurus* is more vertically oriented than that of *Bradysaurus baini*. In *Embrithosaurus* the shaft is oriented anterodorsally, only 20-30^0 off the transverse vertical plane in all specimens. This contrasts with *Bradysaurus baini* specimens which have much more horizontally oriented shafts, only 20-30^0 above the horizontal plane (Turner *et al.* 2015 character 113). The shaft of *Embrithosaurus* is mediolaterally compressed, oval in cross section,

measuring 110 x 70 mm at its narrowest point, just below the posterior process of the iliac blade.

The medial side of the iliac blade is not flat, but has a vertically oriented, elongated medial process or ridge which articulates with the first sacral rib. This process is medially convex, and thickens ventrally, forming a well fitting counterpart for articulation with the deeply concave lateral side of the first, large, sacral rib. The concave distal portion of the first left sacral rib is broken off and preserved attached to the convex articulation of the medial iliac process. Uncleared matrix fills a cavity between these two bones (Fig. 4.19A).

The acetabulum is almost perfectly round, wide and bowl-shaped with a rim that is thickened in three regions, each forming a ridge or buttress. The dorsal supra-acetabular buttress, under the shaft of the ilium, is the most prominent, forming a sharp edged overhanging dorsal lip to the acetabulum, with a ventrolaterally facing surface (Turner *et al.* 2015 character 114). The ischial buttress is located on the posteroventral corner of the acetabular rim, forming a slightly smaller sharp edged ridge, and faces anterodorsally. The pubic buttress is the least distinct of the three, being lower and flattened, and anteriorly widened. In CGP CBT 112 the acetabulum is higher than anteroposteriorly long. A shallow, indistinct notch is present (10 mm wide, 5 mm deep) on the anterior acetabular rim, just above the dorsal edge of the pubic buttress. This notch has also been reported in *Pareiasuchus peringueyi* and *Pareiasuchus nasicornis* by Lee (1997b) (Turner *et al.* 2015 character 115). In CGP CBT 112, there is a very distinct, large and deep notch on the posterior border of the acetabulum, just above the ischial buttress.

Pubis (Figs. 4.1, 4.17, 4.18, 4.19, 4. 20; Table 4.8)

The puboischiatic plate of the pelvis is mediolaterally very narrow. In the holotype it measures 305 mm between the anterolateral edges of the lateral pubic processes, and posteriorly 290 mm between the posterolateral edges of the puboischiatic plate (Figs. 4.18, 4.19B). This plate is not horizontally flat: the

dorsal surface is strongly and evenly concavely curved, rising steeply laterally to meet the ischium, and here, between the blades, the curved plate is narrow, measuring 95 mm wide anteriorly, and 130 mm wide posteriorly (Fig. 4.18).

The puboischiatic plate of SAM-PK-8034 is anteroposteriorly short (220 mm) (Fig. 4.19B) and dorsoventrally very thick through the pelvic symphysis (SAM-PK-8034, 90 mm; FMNH UR 2443, 106 mm; FMNH UR 2486, 110 mm; CGP CBT 112, 110 mm) midway between the anterior and posterior edges of the plate) (Fig. 4.18A) (Turner *et al.* 2015 characters 118 and 119). The dorsoventral thickness of the pelvic symphysis is the result of an elongated V-shaped, ventrally directed process, termed the keel or carina by Haughton and Boonstra (1930b) (Fig. 4.19B) which forms most of the ventral surface of the puboischiatic plate. From the sharp midline edge, the keel extends dorsolaterally upwards at a 50^0 angle above a horizontally flat plane (Fig. 4.18A). This is steeper than other middle Permian pareiasaurs.

The ventral surface of the puboischiatic plate does not form a straight plane, the posterior half of the plate is horizontally level, but the anterior half is oriented at a 25^0 angle below the horizontal plane (Fig. 4.20).

A small, anteroventrally projecting median pubic process (80 mm wide) is present on the anterior margin of the pubis of SAM-PK-8034. Laterally, a large and wide (120 mm) lateral pubic process is present either side (Turner *et al.* 2015 characters 116 and 117). The median pubic process extends far anteroventrally (50 mm anteriorly, 20 mm ventrally) to form a distinct “symphyseal tongue” (Haughton and Boonstra 1930b:327). It has rounded edges in comparison with the square edges in *Bradysaurus* and is directed anteroventrally compared to ventrally in *Bradysaurus*. It also extends further anteriorly than in *Bradysaurus* and has a notch either side. The lateral process is characterized by a rectangular, flattened to slightly convex, ventral surface (Fig. 4.19B).

The pubic/obturator foramen is large and distinct on the medial surface of the pubis and occupies the medial portion of a larger surrounding oval slit-like depression.

Ischium (Figs. 4.1, 4.17, 4.18, 4.19, 4. 20; Table 4.8)

The ischium forms the posterior portion of the puboischiatic plate and part of the acetabulum. The posterodorsal surface of the ischium on the midline forms a shallow concavity. The posterior edges of the ischium are less than 10 mm in width, but thicken at the posterior midline symphysis and dorsolaterally towards the acetabulum. Posteriorly, directly on the midline, the ischial symphysis is slightly notched and erosional damage has exaggerated the true size of the notch.

4.4.5 Vertebral column and ribs

The vertebral column of pareiasaurs comprises five distinct regions, each containing vertebra of similar morphology and distinct from other regions. The presacral region comprises: 1) the anterior cervicals (atlas and axis), 2) the posterior cervicals and the 3) dorsals. The 4) sacral vertebrae possess lateral ribs that articulate with the ilium of the pelvis and finally the 5) caudal vertebra occur posterior to the sacrum. The holotype of *Embrithosaurus* preserves the atlas, axis, posterior cervicals, dorsals, sacrals and six anterior caudal vertebrae. Compared to previous published accounts, extensive additional preparation of the vertebral column was performed for this study.

Broom (1903) noted 20 presacral vertebrae in holotype of *Embrithosaurus* However, Lee (1994, 1997a) recognised only 19 presacrals, which is the correct number.

Anterior cervical vertebrae (atlas and axis)

Proatlas

SAM-PK-8034 does not preserve a proatlas and Broom makes no mention of a proatlas in his (1903) description. Tsuji (2010, 2013) provisionally identified a shifted element in *Deltavatjia* as a proatlas and despite not finding a proatlas in any specimen, Boonstra contends its existence in pareiasaurs as "highly probable" in his lengthy pareiasaurian study of vertebrae and ribs (Boonstra 1934c:53).

Atlas (Figs. 4.21, 4.22)

The atlas and axis are preserved in articulation. The paired left and right neural arches of the atlas (atlantal arches) are no longer present, but were illustrated by Boonstra (1934c:53: Text-Fig. 2 and here Fig. 4.21) as curved, clasping bands covering the lateral aspects of the pleurocentrum, extending vertically from just below the ventral border of the pleurocentrum to just above the neural canal. The anterior side of the pleurocentrum of the atlas is strongly convex with a slightly raised central section for articulation with the concavity on the posterior side of the occipital condyle. Lateral to this raised region, shallow curved grooves are observed where the atlantal neural arches were once present, and indicate a loose articulation with the atlas (Fig. 4.22B). Lateral to each shallow groove is a deeper, thinner, vertical groove (Fig. 4.22A). The posterior border of the atlas forms a sharp edged rim laterally and ventrally. The dorsal surface of the atlas is excavated by the flattened neural canal. Currently missing, a very small, unpaired midline atlantal intercentrum was positioned ventrally between the atlas and axis, according to Broom (1903) and it was illustrated by Boonstra (1934c:53: Text-Fig. 2 and here Fig.4.21) (Turner *et al.* 2015 character 79). The atlas shows a process laterally, with a convex facet terminally, also present on the atlas of *Bradysaurus baini*.

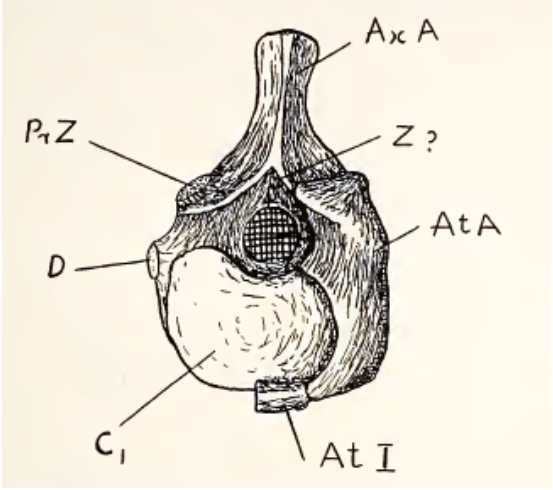


Figure 4.21: Anterior view of atlas and axis of *Embrithosaurus schwarzi* (SAM-PK-8034) taken from Boonstra (1934c:53: Text-Fig. 2). Boonstra figured only the left half of the atlantal arch, **At.A**, (omitting the right from the figure) and the left half of the unpaired atlantal intercentrum, **At.I**, (omitting the right) from the sketch. **At.A,** Atlantal arch; **At.I**, Atlantal intercentruml; **Ax.A**, axial arch; **C1**, atlantal pleurocentrum (odontoid); **D**, diapophyses on atlantal and axial arch; **Pr.Z**, axial prezygapophysis; **Z?**, an undeveloped zygosphene?

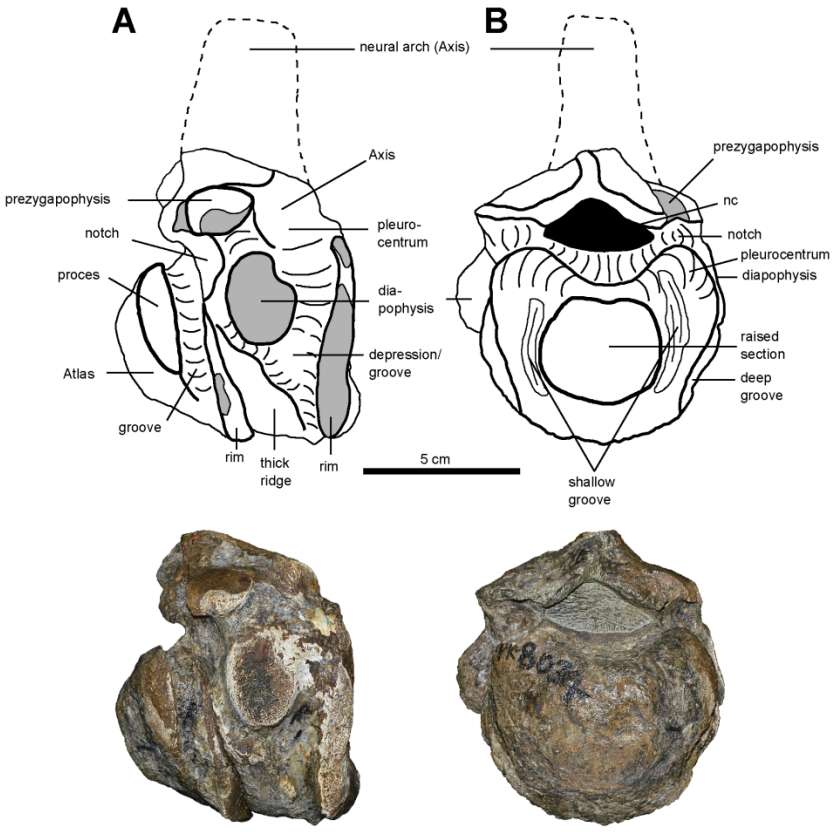


Figure 4.22: Photographs and interpretive drawings of the atlas and axis of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in left lateral view, and (B), in anterior view. Dorsal to the top of the page.

Axis (Figs. 4.1, 4.21, 4.22)

The dorsal portion of the neural arch of the axis is no longer present, and only a cross sectional triangular break, anteriorly tapering, with concave sides remains. Boonstra's illustration (1934c:53: Text-Fig. 2 and here Fig. 4.21) shows the complete arch as tall and narrow, with a mediolaterally expanded dorsal end (though much narrower than the base of the arch) and with a very sharp vertical anterior edge. The base of the arch is strongly fused to the pleurocentrum and laterally this ventral section of the preserved arch has the laterally facing diapophysial process, eroded on the left, for articulation with the head of the ribs (Fig. 4.22). The diapophysis is positioned in the anterior half of the lateral pleurocentrum.

The preserved axial pleurocentrum forms an anteroposteriorly flattened dumbbell, ventrally tapering and has a gently concave posterior surface. Laterally there are ventrally tapering deep grooves below the diapophysis which dissipate ventrally. As with the atlas, the posterior border of the axis forms a sharp edged rim laterally and ventrally, which is thicker than the corresponding region in the atlas.

Anterodorsal to the diapophysis, an upwardly directed process bears the prezygapophysis which is an oval, gently convex, anterodorsally facing facet for articulation with the no longer preserved atlantal neural arches. Both postzygapophyses are damaged. Broom (1903) noted the presence of a large, vertically elongated, curved axial intercentrum, between the axis (vertebra 2) and the 3rd cervical vertebra, that is no longer preserved. On the posterior side of the axis, the neural canal is ovoid and slightly dorsoventrally flattened.

Posterior cervical vertebrae (3rd, 4th and 5th vertebrae) (Figs. 4.1, 4.23)

The 3rd, 4th and 5th cervical vertebrae are preserved in articulation and are very similar to each other. The anterior and posterior sides of each centrum are concave (amphicoelous), and the anterior side more greatly so. The centra are

generally square to round, but the ventral portions of each centrum are anteroposteriorly expanded (Fig. 4.23). In overall aspect, these vertebrae are mediolaterally narrow and much taller than wide, with tall, slender neural spines and small zygopophyses that do not extend far laterally. The neural canal is large, ovoid in cross section and slightly dorsoventrally flattened. The centra of the 4th and 5th vertebra are of similar size and much larger than the pleurocentra of the axis and the 3rd vertebra.

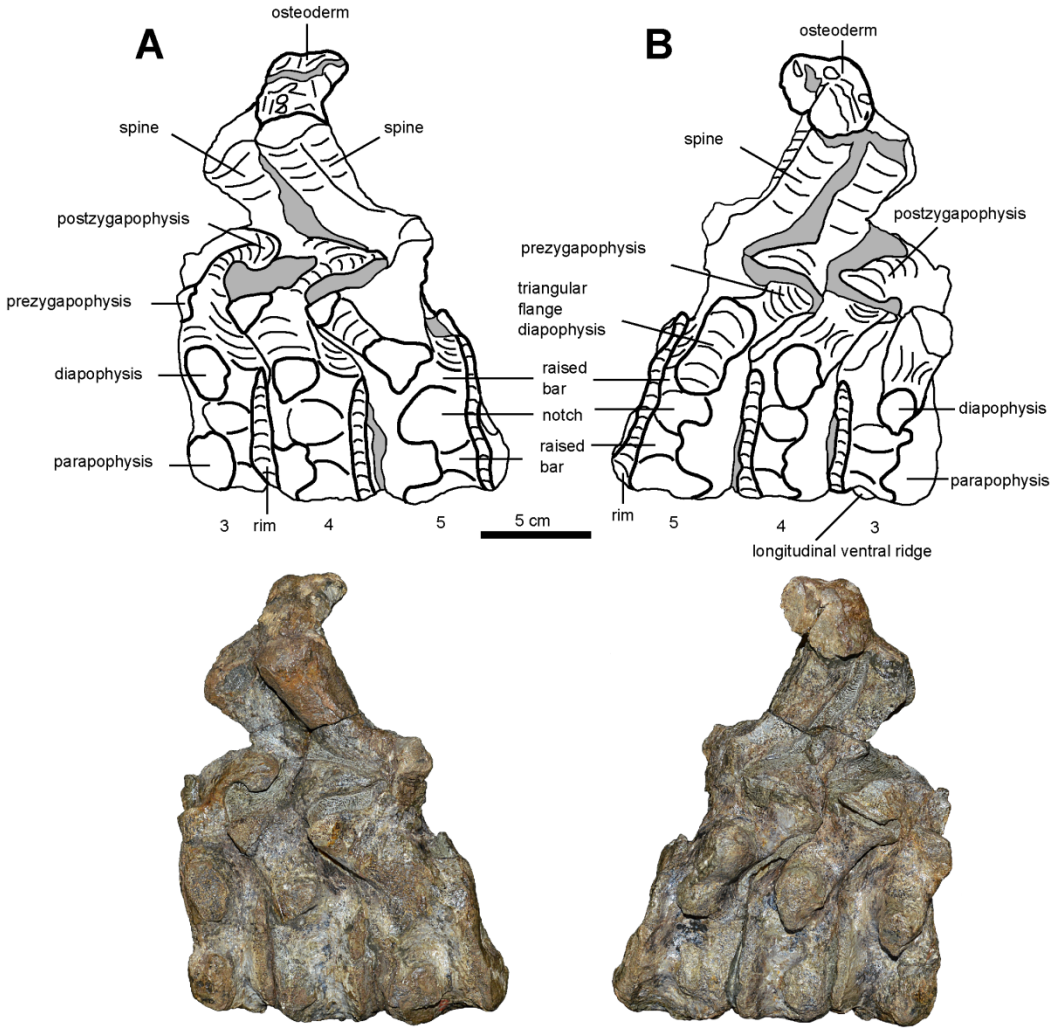


Figure 4.23: Photographs and interpretive drawings of the 3rd-5th vertebrae of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in left lateral view, and (B), in right lateral view. Dorsal to the top of the page.

Laterally there are two distinct processes with articulation facets for the heads of the ribs. The lower process, positioned on the anterior border of each centrum, is short and stubby and has a kidney-shaped parapophysial facet for articulation with the ventral part of the head of the rib. The posterolaterally projecting higher process is situated more posteriorly. It is longer, slightly curved, and has an oval diapophysis which articulates with the dorsal part of the head of the rib. The left diapophyses on the 3rd, 4th and 5th vertebra, are partially sheared-off. The anterior rim of the centra are thickened into a thin, vertical ridge, that joins the two processes. A deep notch behind the ridge, creates a wide and clear separation between the two processes and behind the notch each centrum is mediolaterally constricted. It is noteworthy that the 5th cervical diapophysis is much larger than the preceding two, and extends laterally and dorsally to form a distinct triangular flange.

The posterior border of each centrum forms a thin, sharp edged rim laterally and ventrally. The anteroventral border of each centrum, has a wide and flat rim with a posteriorly directed ledge, tapering posteriorly, to form a longitudinal midline ridge reaching the posterior rim.

The prezygapophysial processes are small, short and anterodorsally directed from the diapophysis, with dorsally and slightly anteriorly facing articulation facets for articulation with the postzygapophysis of the preceding vertebra. The small and short processes of the postzygapophyses form a posterolaterally and slightly ventrally directed arch, extending from the ventolateral corner of each spine, with flat, curved ventrally facing facets.

Two articulated osteoderms partially obscure the dorsal surface of the 4th and 5th neural spines. The neural spine of the 4th cervical is not preserved and only the posterior half of the 4th cervical neural spine is, but the complete 5th neural spine is slender and is slightly dorsoventrally shorter than the height of the centrum. It is diamond-shaped in cross section, and anteroposteriorly flattened, mediolaterally wide. The convex dorsal surface has a 10 mm deep, longitudinal

groove. As the spine extends dorsally it flares out mediolaterally, to nearly twice the width of its base. The spines on the 4th and 5th vertebra slant anteriorly. Benton (2016) reported similar forward leaning neural spines on the posterior cervical vertebrae of *Shihtienfenia* as "most unusual" (Benton 2016:20).

Dorsal vertebrae (6th to 19th vertebrae) (Figs. 4.1, 4.24, 4.25, 4.26, 4.27, 4.28, 4.29, 4.31)

The dorsal vertebrae are defined as those vertebrae that support the ribs that form a continuous cage over the length of the torso (Tsuji 2010, 2013) and in the holotype of *Embrithosaurus* they extend from the 6th to the 19th vertebrae. (Turner *et al.* 2015 character 80)

The 6th to 8th vertebrae are preserved in a single block (Fig. 4.24) and the 9th, 10th, 11th, 12th and 13th are single elements (Figs. 4.25, 4.26). The 14th to 16th (Fig. 4.27) and 17th to 21st (Figs. 4.28, 4.29) are preserved articulated, in two large separate blocks.

The entire dorsal vertebrae sequence of 14 vertebrae are very similar, differing only in the size and proportion of various features along the vertebral column. Broadly, the dorsal vertebral column can be considered as two regions in which the vertebrae are similarly sized and proportioned: anterior dorsal vertebrae extend from the 6th to 9th vertebrae, and the posterior dorsal vertebrae extend from the 10th to 19th vertebrae.

Dorsal vertebrae are larger and mediolaterally wider than the posterior cervicals and increase in size posteriorly. The significant mediolateral increase in size is largely due to the laterally projecting transverse processes, which form a vertical flange-like wall for articulation with the heads of the ribs (see below).

The dorsal vertebra are amphicoelous with the anterior articular facets concave and deep. In contrast the posterior articular facets have a concave dorsal half and a convex ventral half, producing a posteroventrally extended overhanging "lip-like" projection.

Anterior dorsal vertebrae have centra that are anteroposteriorly short, mediolaterally wide and dorsoventrally high. Posterior dorsal vertebrae have centra that are longer, such that the posterior-most dorsal vertebrae are as long as wide.

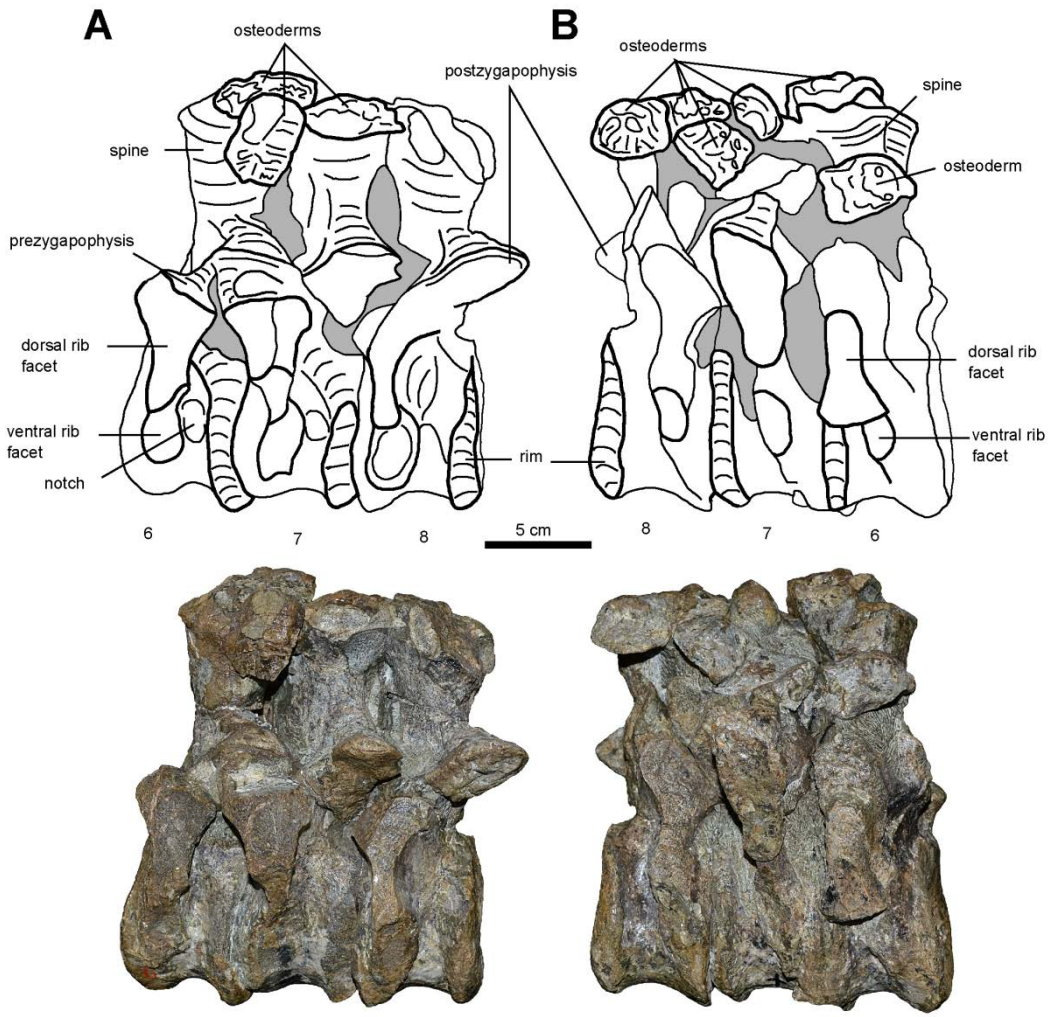


Figure 4.24: Photographs and interpretive drawings of the 6th-8th vertebrae of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in left lateral view, and (B), in right lateral view. Dorsal to the top of the page.

The centra of the dorsal vertebral are more mediolaterally constricted than the centra of the posterior cervicals, as a result of a deeper vertical groove on the lateral sides of each centrum. This constriction intensifies backwards on each subsequent vertebra, causing the anterior and posterior rims of each centrum to become more exaggerated and pronounced. From the 11th vertebrae backwards,

the mediolateral constriction is so severe that centra are “pinched in”, creating “hourglass” shaped centra, with a swollen cylindrical ventral bar. The posterior-most 18th and 19th vertebrae have a flat ventral surface with right angled square edges.

The sharp lateral rim on the posterior border of each dorsal centrum is thicker, and protrudes further than the anterior border rim. Ventrally, the anterior and posterior rims of the posterior dorsal centra are curved and extend towards each other. On all dorsal vertebrae, the ventral surface of the centra lack the longitudinal midline ridge of the posterior cervicals.

As noted by Broom (1903), from the 6th vertebrae backwards, the parapophysial and diapophysial articulations for the head of each rib are fused into a single vertical wall-like flange of the transverse process. Dorsally the flange is fused to the end of a short, posteriorly curved arc-like process, which extends ventrally behind and below the articulation surface of the prezygapophysis. The dorsal portion of the flange extends further laterally than the ventral portion.

The morphology and proportions of the transverse flange changes along the vertebral sequence. Anteriorly, on vertebrae 6-9 (best seen on the right side of the 7th vertebra, Fig. 4.24B) the flange is dorsoventrally longest (extending ventrally to almost reach the ventral surface of the centrum). This long lateral facing facet comprises two regions: a dominant flat, roughly rectangular dorsal region that faces ventolaterally, and a small oval and gently concave ventral facet which faces posterolaterally. The flange is vertically and slightly posterodorsally oriented.

From the 10th vertebra backwards (Fig. 4.25) the flange changes in proportions: the ventral facet on the lateral surface migrates upwards and merges with the more laterally projecting dorsal facet. This decreases the dorsoventral height of the lateral facet which gradually shortens in height on each subsequent posterior vertebrae (Fig. 4.27). The entire facet shifts significantly dorsally, so that the dorsal edge is at the same level as the articular surface of the prezygapophyses

and the ventral edge is several centimetres above the ventral edge of the centra. Finally, the almost vertical flange becomes more posterodorsally oriented over the dorsal vertebral sequence.

On the 18th dorsal vertebra, the lateral articular surface for the head of the rib is indistinct and on the 19th vertebrae only small dorsal and ventral facets remain (Fig. 4.28). Also, on these last two dorsal vertebrae, the ventral portion of the flange shifts lower and emerges smoothly with the anterior part of the dorsolateral edge of each centrum. The presence of these facets on the transverse processes suggest the 18th and 19th vertebrae may have born ribs, however, lumbar vertebrae are absent in all other pareiasaurs (Boonstra 1934c, Lee 1997b) and so these are probably not lumbar vertebrae here (Turner *et al.* 2015 character 81).

The processes bearing the prezygapophyses of the anterior dorsal vertebrae are small and extend only a short distance anterodorsally. They present a slightly convex surface that faces dorsomedially and slightly anteriorly. On the posterior dorsal vertebrae, the prezygapophysial processes increase in robustness but remain short. On the anterior dorsal vertebrae (vertebra 6-13), the prezygapophyses are mediolaterally narrow and laterally they do not reach the level of the articular surface of the flange. More posteriorly (vertebrae 14-19), the prezygapophyses are mediolaterally wider and extend laterally to just beyond the level of the articular surface of the flange.

In contrast the postzygapophysial processes greatly increase in lateral extent and overall robustness on each successive posterior vertebra. They are directed posterolaterally and extend slightly further laterally than the prezygapophyses with which they articulate, and reach far beyond the posterior border of each centrum.

The vertically oriented diamond-shaped neural spines are more robust on the anterior dorsal vertebrae (6–9) than those of the posterior cervical vertebra (3-5).

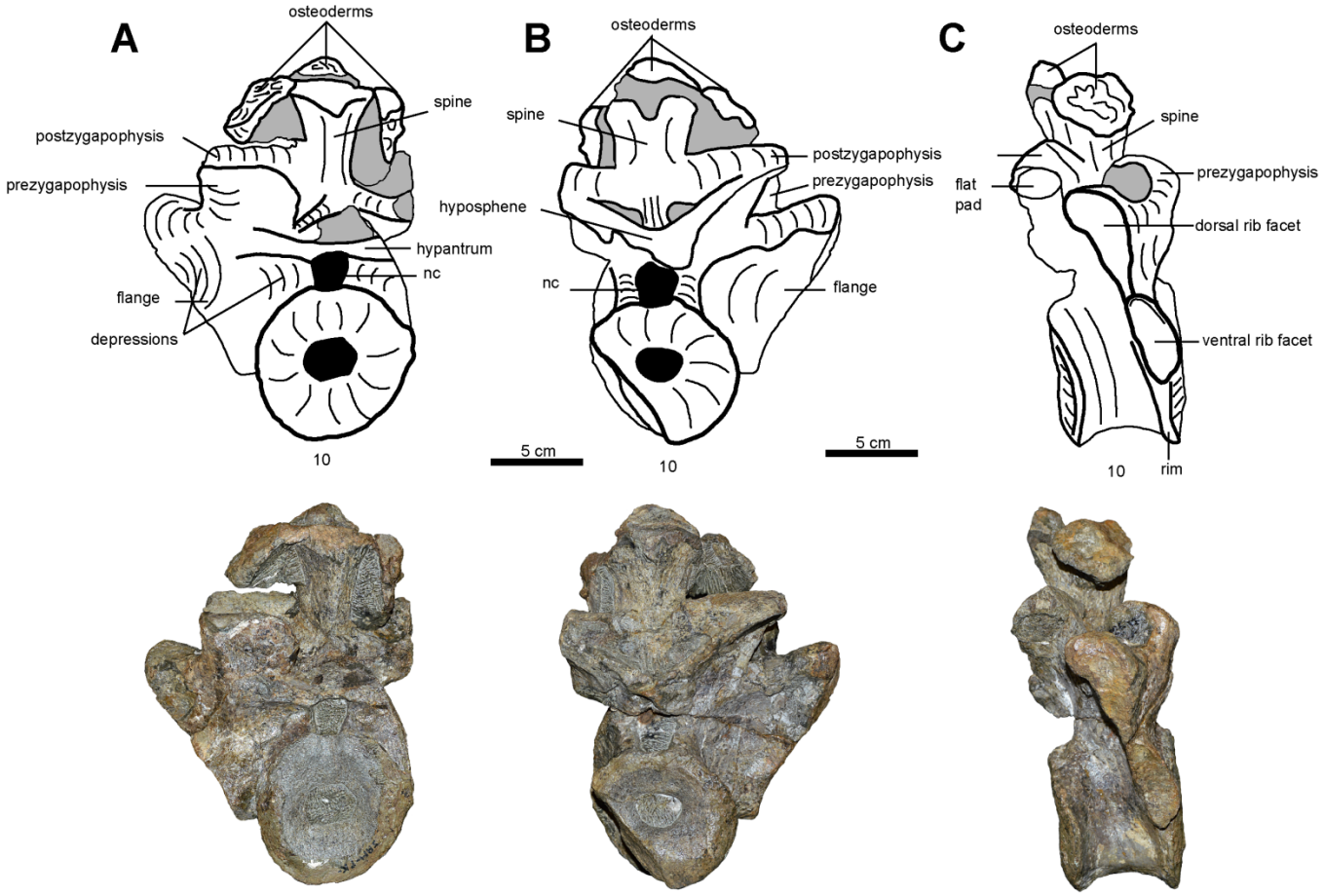


Figure 4.25: Photographs and interpretive drawings of the 10th vertebrae of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in anterior view, (B), in posterior view, and (C), in r lateral view. Dorsal to the top of the page.

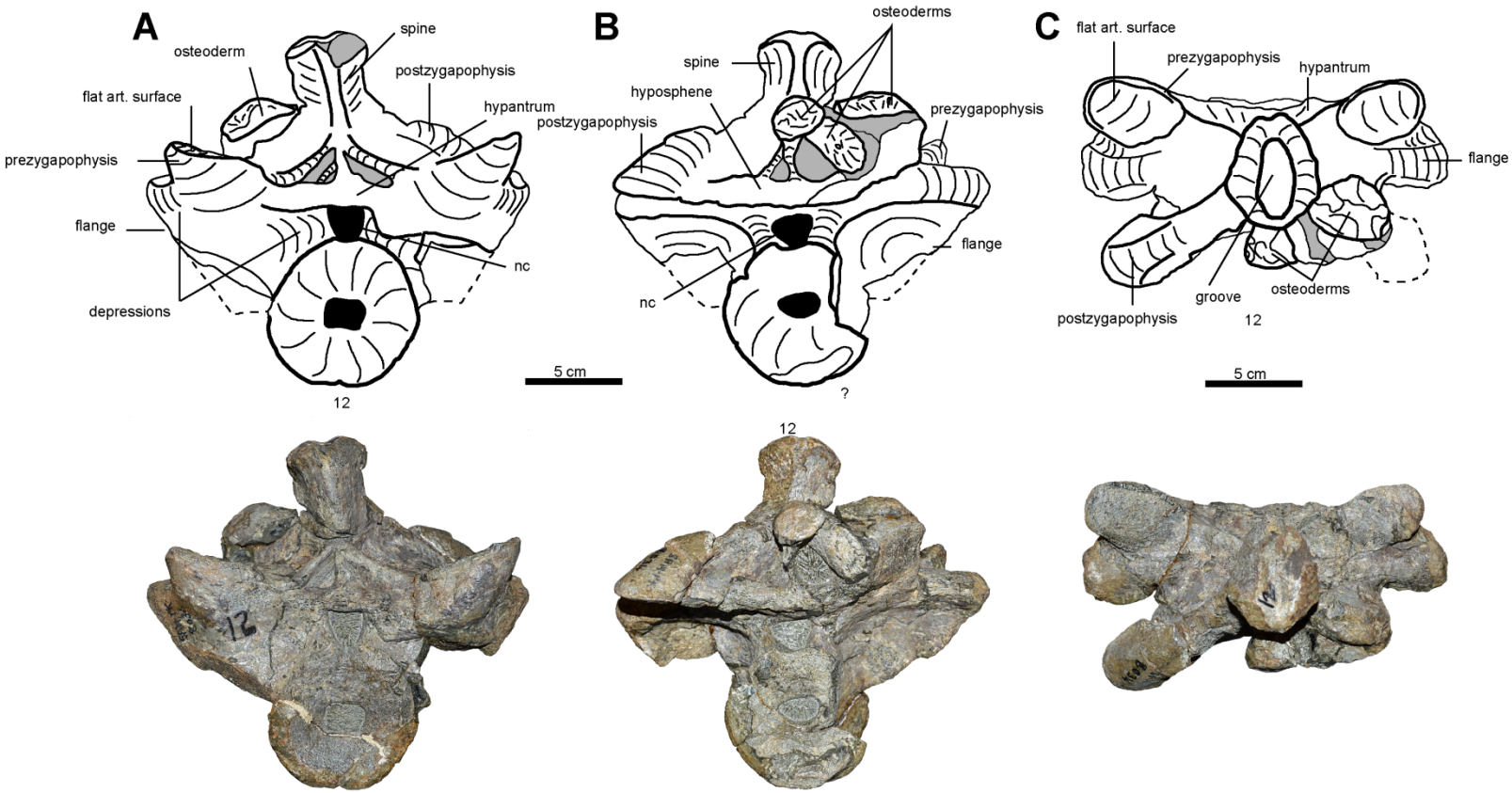


Figure 4.26: Photographs and interpretive drawings of the 12th vertebrae of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), (A), in anterior view, (B), in posterior view, and (C), in dorsal view. Dorsal to the top of the page.

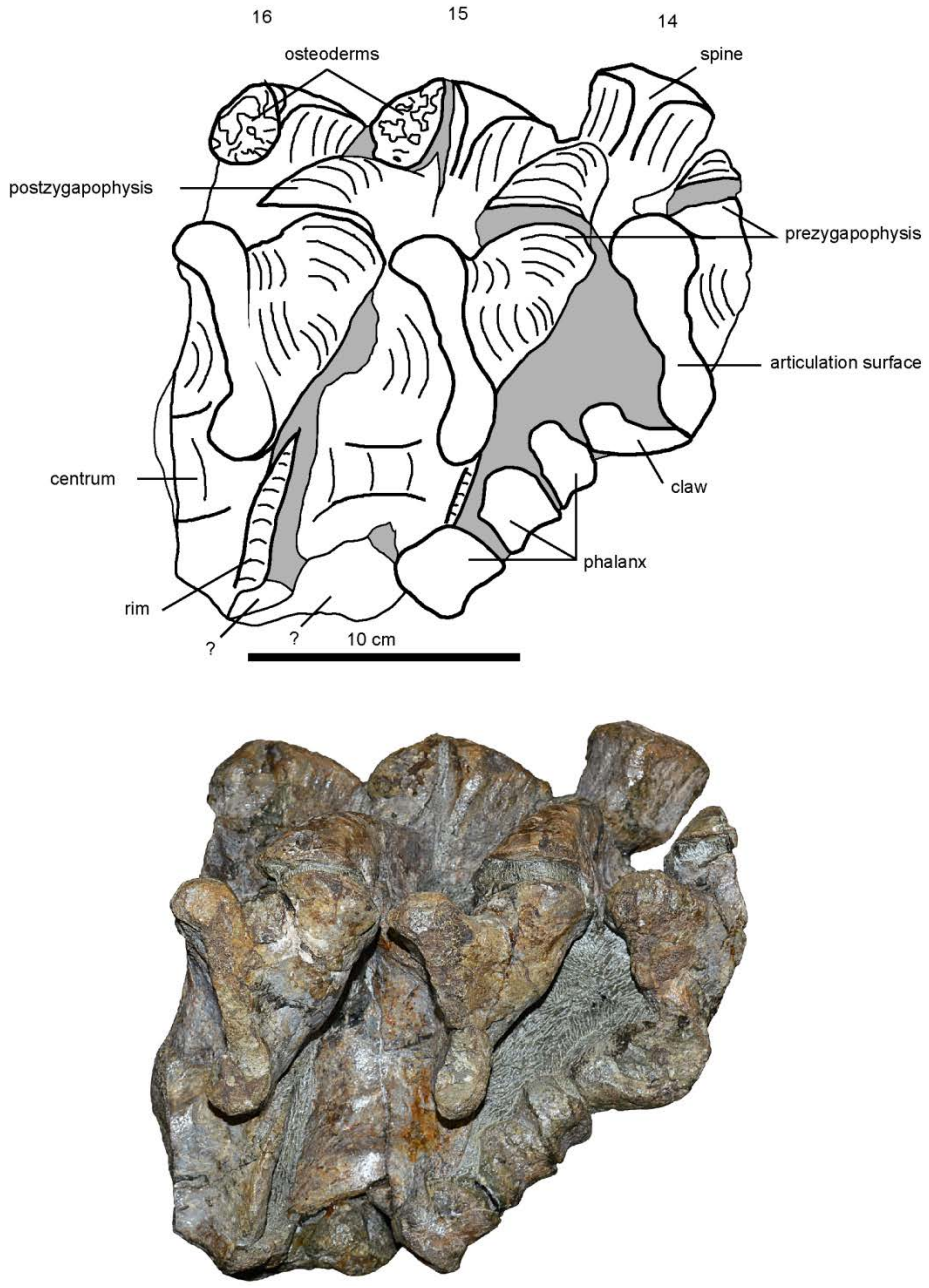


Figure 4.27: Photograph and interpretive drawing of the 14th-16th - vertebrae of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), in right lateral view. Dorsal to the top of the page.

The anterior side is rounded, the dorsal portion is more mediolaterally flared and the dorsal surface longitudinal groove is deeper and more distinct. However neural spines are slightly shorter than the height the centra. All the dorsal neural spines lean forward, similar to the spines on the cervical vertebrae. Interestingly, the neural spines are noticeably smaller on the 12th to 16th vertebrae, but larger on the 17th, 18th and 19th. A deep midline groove is present on the dorsal surface

of the spines of the 9th to 13th vertebrae of the holotype (Figs. 4.25, 4.26) and the single vertebrae of FMNH UR 2443. The 14th to 19th vertebrae present a rugose convex surface with small circular pitting and an indistinct, raised and rimmed, shallow midline groove (Fig. 4.29). Interestingly, these two very different morphologies of the dorsal surface of the neural spines of the dorsal vertebrae are also present in a specimen of *Nochelesaurus* (SAM-PK-6238) and in the holotype of *Bradysaurus baini*.

The neural canals of the anterior dorsal vertebrae have a greater diameter than those of the posterior cervical vertebrae, and the diameter of the canals decreases posteriorly on the posterior dorsal vertebrae. Below the neural spine is an upside down V-shaped cavity, formed laterally by the arms of the prezygapophysial processes that sweep down posteroventrally from the base of the neural spine (Figs. 4.25, 4.26). A vertical midline ridge divides the cavity in two equal halves. On the posterior side of the vertebra, the cavity is separated from the neural canal by a low horizontal bar-like process (the hyposphene) which articulates with the facet of the hypantrum on the anterior side of the adjacent vertebra.

Additional preparation has revealed that vertebrae 9-16 (and possibly more) have notochordal centra, as have also been reported for a juvenile specimen of *Deltavjatia* (Tsuji 2010, 2013).

Broom (1903:129) suggested that intercentra were “apparently” present between all the dorsal vertebrae. Boonstra (1934c) stated that small intercentra are found throughout the pareiasaurian dorsal vertebral series, except in the first five vertebrae. SAM-PK-8034 preserves no intercenta, but the holotype of *Bradysaurus baini* (NHMUK R1971) preserves several large, dorsoventrally flattened, midline intercentra, on the ventral surface between most of the nineteen dorsal vertebral centra and we can thus reasonably assume they were present in *Embrithosaurus*.

Sacral vertebrae (20th-23rd vertebrae) (Fig. 4.28, 4.29, 4.30)

There are four sacral vertebrae (20th to 23rd): the first two sacral vertebrae (20-21) are preserved on a large block containing the 17th to 21st vertebrae (Fig. 4.28, 4.29) and the last two sacral vertebrae (22nd and 23rd) are preserved articulated in a separate block (Fig. 4.30A) (Turner *et al.* 2015 character 82).

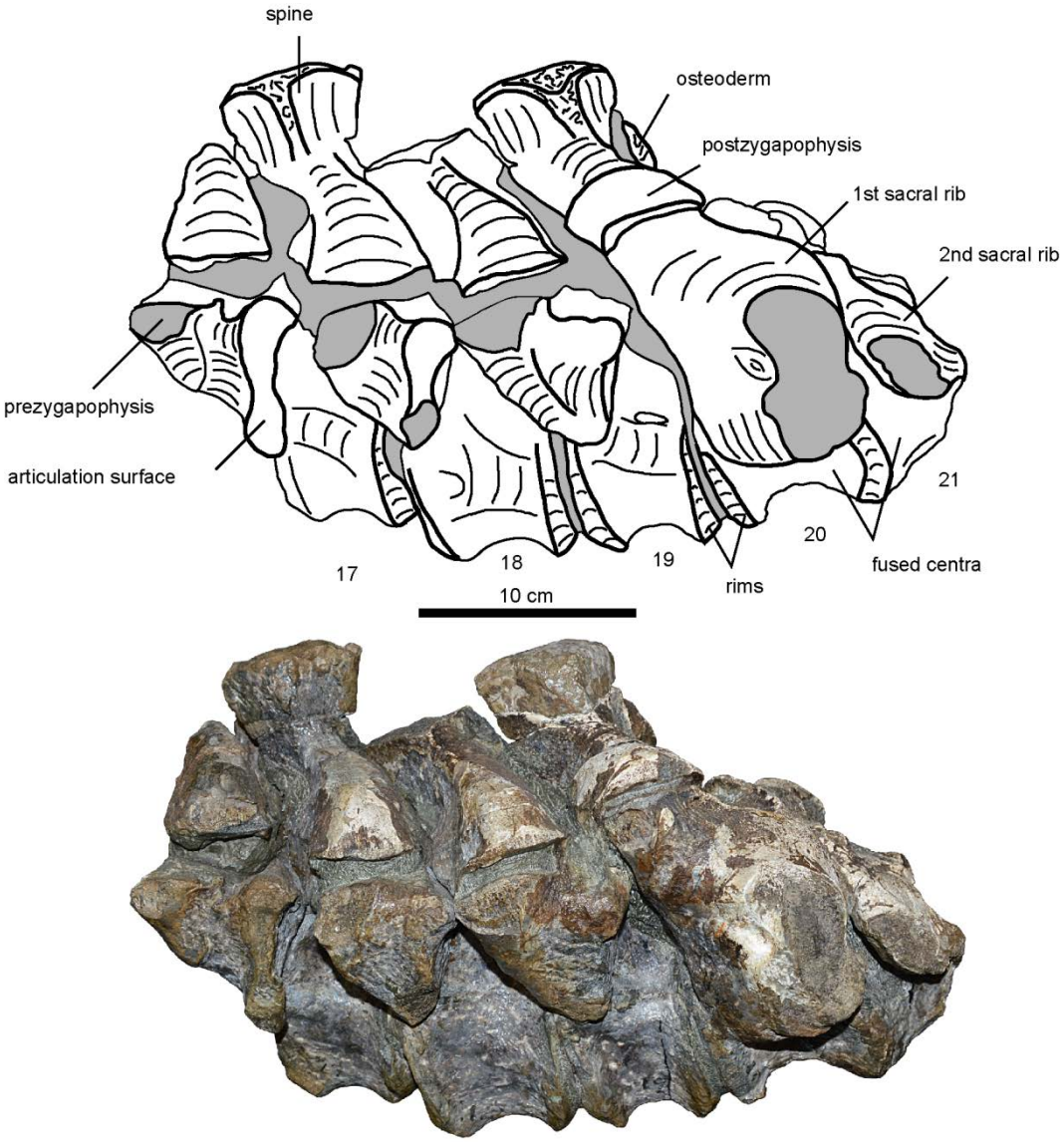


Figure 4.28: Photograph and interpretive drawing of the 17th-21st - vertebrae of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), in left lateral view.

Vertebrae 20-23 are badly damaged on the dorsal side, with the neural spines and processes of the postzygapophyses sheared-off. Judging from what is

preserved, these neural spines were more slender than the spines and arches of the preceding large 19th dorsal vertebrae, and decrease in size posteriorly along the vertebral column.

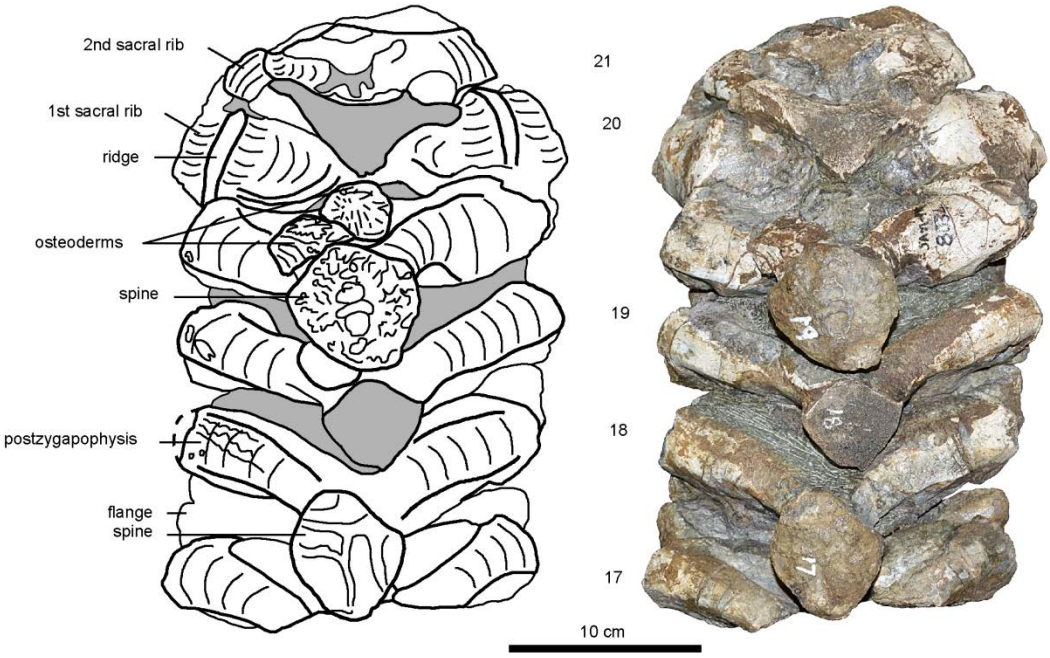


Figure 4.29: Photograph and interpretive drawing of the 17th-21st - vertebrae of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), in dorsal view. Posterior to the top of the page.

The first sacral vertebra (the 20th, Figs. 4.28, 4.29) is distinct from the last dorsal vertebra (19th) in the following ways: 1) dorsally, behind the prezygapophyses, the 20th vertebra is very robust and presents a wide, flattened, bowl shaped region, bordered laterally by a conspicuous, sharp and raised longitudinal ridge (Fig. 4.29); 2) the wide dorsal area behind the prezygapophyses supports the greatly expanded first sacral rib; 3) the processes of the prezygapophyses of the first sacral vertebra (20th) are the most robust and extend further anteroposteriorly, and 4) the breadth of the postzygopophyses is smaller/reduced compared to the breadth of the prezygopophyses.

Caudal vertebrae (24th vertebra backwards) (Figs. 4.1, 4.30)

Broom (1903:127) considered the caudal vertebrae as the 23rd vertebrae backwards and stated that there were "probably" 30 caudal vertebrae (Turner *et*

al. 2015 character 83). He reported that all vertebrae of the holotype from the atlas to the 28th, were present, after which a gap in the sequence occurs in which he estimated three missing caudal vertebra (29 - 31). Nine more caudal vertebrae (32 - 40) were preserved (Broom 1903) and are now lost. Lastly, Broom noted one very small isolated caudal vertebra (which he estimated to be the 47th) with a partial vertebra attached (the 48th).

Currently, a series of four (24th to 27th) articulated anterior caudal vertebrae are preserved (Fig. 4.30B) which represents the end of the first 28 vertebrae reported by Broom. Additionally, the 47th and a partial 48th vertebra are preserved (no figure).

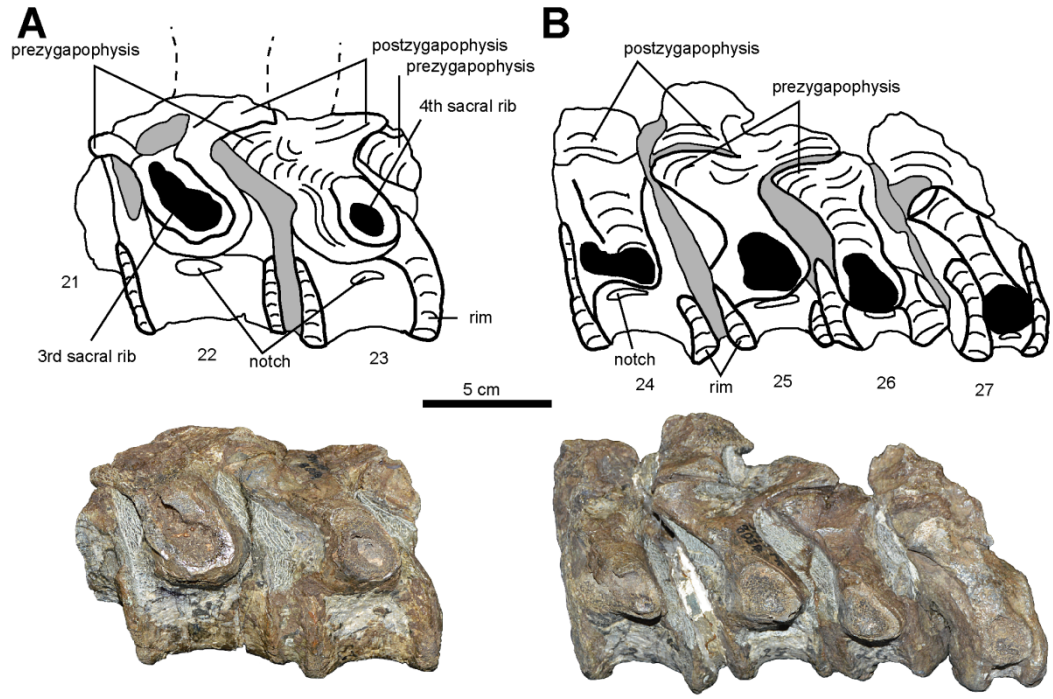


Figure 4.30: Photograph and interpretive drawing of the 22nd-27th - vertebrae of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), in left lateral view. Dorsal to the top of the page.

The four preserved articulated anterior caudal vertebrae (24-27) are smaller in than the posterior two sacral vertebrae (22-23) and decrease in size posteriorly, especially the processes of the postzygapophyses, which are remarkably short and almost non-existent. Each vertebrae is forward leaning. The neural spines are poorly preserved, partially sheared-off, and obscured by several displaced

osteoderm fragments, and are dorsoventrally very short and triangular (not diamond shaped) in cross section.

Short, lateral projections (transverse protuberances) are present on the lateral sides of each centrum. These have damaged tips and are slightly posteriorly directed, short, fused ribs. They cover the anteroposterior extent of the lateral centra and shift position ventrally and decrease in size in subsequent vertebrae. A distinct, deep, horizontal notch is present on the lateral surface of the centra, below the lateral projections.

Broom (1903) described and illustrated long chevrons on the (now missing) 32nd to 40th caudal vertebrae, stating that they developed from about the 5th (i.e. 27th or 28th) caudal vertebrae backwards and increase in length, and continue posteriorly at least to the preserved 47th isolated vertebrae. Chevrons (haemal arches) are not present on the 24th to 27th vertebrae. Boonstra (1934c) concluded that chevrons develop from the 4th caudal (postsacral) vertebrae backwards. The posteroventral rim of the 4th caudal vertebrae of *Embrithosaurus* (27th vertebra) appears to show short flattened facets either side of the midline, possibly for articulation of the missing paired chevrons, but poor preservation makes this conclusion tentative. The posteroventral rim of the centrum of the small isolated 47th vertebra, appears to show small notches either side of the midline for possible chevron articulation, but these notches may be the result of damage to the posterior rim.

Ribs

Broom (1903) did not describe the ribs of *Embrithosaurus*, but his skeletal restoration (Plate XVI; Fig. 4.1) shows that only three partial ribs were present, including the 12th rib as almost complete and preserving the head. Currently, only a single rib head is preserved (see Dorsal ribs below).

Cervical ribs (axis to 5th vertebrae)

Boonstra (1934c:59) stated that all pareiasaurian vertebrae, from the axis to the sacrum (excluding the atlas) bear a pair of ribs. This matches the condition in holotype of *Embrithosaurus* as all presacral vertebrae, except the atlas, possess facets for rib articulation.

The axis (2nd cervical vertebra) has only one clear rib articulation (the diapophysis) for the tuberculum of the head of the rib and the rest of the cervical vertebrae (3rd to 5th) show the additional parapophysial facet for the capitulum of the rib head. However, Boonstra (1934c:59) notes that the capitulum of the rib head would have articulated with a facet on the axial intercentrum (missing in *Embrithosaurus*). All the cervical ribs were therefore double headed.

Dorsal ribs (6th to 19th vertebrae) (Fig. 4.1)

The fused diapophysis and parapophysis of the 6th to 19th vertebrae, create a single, long, lateral facet and indicate that the rib articulations were single headed (holocephalus). The preserved (12th?) rib head has a sharp, hooked dorsal edge and the articular surface has a low concavity.

Sacral ribs (20th to 23rd vertebrae) (Figs. 4.17, 4.28, 4.29, 4.30)

The first and second sacral ribs are nearly complete but are broken and currenly articulated with other elements: the 20th and 21st vertebrae preserve the proximal (medial) portions of the first and second sacral ribs respectively, and the ilium preserves the distal (lateral) portions of the first and second sacral ribs.

On both lateral sides of the first sacral vertebrae are the fused medial portions of the very large, dorsoventrally elongated, first sacral rib, measuring 90 mm dorsoventrally and 70 mm in anteroposterior extent. Medially, the rib covers a large section of the dorsal portion of the lateral surface of the centrum and reaches ventrally 20 mm lower than the ventral border of the preceding transverse process. The right first sacral rib is complete, when the two separate

portions are brought together, and shows the thick swollen rib extending laterally to reach the ilium. Between the medial and lateral ends, the rib is constricted and the distal end of the rib is much more robust than the proximal end. Laterally, towards the articulation with the ilium, the rib swells and extends posteriorly very far, but anteriorly only a short distance. In anteroposterior length, the right lateral sacral rib articulation measures 230 mm and extends the length of the 20^{th} to 23^{rd} vertebrae. The first sacral rib slopes anteriorly and is oriented about 45^{0} above the horizontal plane.

As noted by Haughton and Boonstra (1930b) the sacral ribs of pareiasaurs are not equally developed. On the holotype of *Embrithosaurus*, the first sacral rib is massive and robust, oriented and elongated dorsoventrally, and covers a large central portion of the medial side of the iliac blade, occupying the entire dorsoventral height of the blade (Figs. 4.17, 4.18). This articulation stretches dorsally from a level just below the ventral margin of the posterior process of the ilium. The rib does not cover the anterior margin of the blade as the anterior edge of the rib articulates 40 mm posterior to the anterior margin of the right iliac blade. The right first sacral rib is more complete than the left and sutured strongly against the medial side of the iliac blade.

Ventrally, the anterior and posterior sides of the first sacral rib are convex. Dorsally, both sides are concave or excavated, but the posterior side much more so, in order to accommodate the adjacent second sacral rib.

The second sacral rib is much smaller than the first. The medial portions of the second sacral ribs are anterodorsally elongated (50 mm) and posterodorsally (20 mm) thick and the rib also slopes anteriorly, but is oriented more horizontally than the first sacral rib. The midway lateral constriction is less severe and the anterior and posterior extensions of the lateral ends of the rib project much less. The second left sacral rib is virtually complete, when the two separate portions are brought together, and show the ribs as relatively flat and sheet-like.

The medial articulation of the second rib against the ilium, is positioned high on the medial side of the iliac blade, above and behind the articulation of the first sacral rib. The medial portions of the second sacral ribs are much smaller than the first, extending only half the anteroposterior extent of the first and are positioned positioned dorsally, sutured against the posterior margin of the first rib.

Short medial portions of the third and fourth sacral ribs are preserved on the 22nd and 23rd vertebrae (Fig. 4.30). The third sacral rib is anteroposteriorly shorter than the second, but dorsoventrally thicker. It is anterodorsally oriented, more obliquely and less horizontally than the second sacral rib. The fourth sacral rib is the smallest of the series. Unlike the first three sacral ribs, the fourth rib is not flattened or plate-like, but is circular to slightly oval in cross section. Interestingly, internal to the cortical bone, the third and fourth sacral ribs show deep excavated internal cavities, whilst the first and second show spongy trabecular bone, which may indicate that the last two sacral ribs were not strongly fused to the ilium. Boonstra (1934c) notes that the fourth pareisaurian sacral rib does not reach the ilium, and was ligamentously attached to it.

Because the posterior dorsal portions of both iliac blades are not preserved, the lateral articulations of the third and fourth sacral ribs are not preserved.

Turner *et al.* (2015) reported a strange perpendicular flange of bone, just posterior to the first sacral rib in *Embrithosaurus* (CGP CBT 112), but this is in fact a piece of the first sacral rib which has broken off.

4.4.6 Osteoderms (Fig. 4.23, 4.25, 4.26, 4.31)

Twenty-three partial to complete osteoderms currently overlie the dorsal and lateral surfaces of several neural spines and the dorsal surfaces of several processes of the postzygapophyses along the vertebral column. A few osteoderms are also found between adjacent neural spines or postzygapophysial processes. The heaviest concentration preserves nine articulated scutes on the

block containing vertebrae 6-8 (Fig. 4.31) and these were described by Boonstra (1934b). The 11th, 13th and 16th vertebrae each preserve one scute, and the 12th, 15th and 19th vertebrae have two scutes each. The 10th vertebra preserves three scutes and small scute fragments occur on 24th to 27th vertebrae.

Broom (1903) in his restoration of *Embrithosaurus* (Plate XVI and here Fig. 4.1) purposefully omitted the dermal scutes from the figure, to allow the vertebrae to be more distinctly seen. He also did not describe the osteoderms.

Boonstra (1934b), in his detailed study of South African pareiasaurian armour, provided a detailed description of the armour of *Embrithosaurus*. In terms of scute arrangement, he noted a central row of the largest scutes, directly above the spinous processes, and two lateral rows of slightly smaller, but still large scutes, either side, resulting in five rows, extending probably along the whole length of the back.

There are two morphotypes of osteoderms: large, anterior dorsal osteoderms and small stud-like osteoderms.

On the 6th to 8th vertebrae (Fig. 4. 31, anterior dorsal vertebrae) are seven large osteoderms, 40-50 mm in diameter. They are roughly pentagonal in outline, with straight to concave edges. Most of these scutes are low (only 15-20 mm high), comprising very flat discs (5-7 mm high on their peripheries) with a small to medium sized distinct central boss (20-35 mm wide) which are very high (15 mm) accounting for most of the height of the osteoderm (Fig. 4.31).

This central raised boss is irregular (L-shaped or E-shaped) comprising one to more thickened rugose tab-like swellings or ridges. Lateral to the raised irregular central boss, the periphery of the largest osteoderms are flat and thin (5-7 mm high) and are covered with low, irregularly placed straight, radiating ridges which extend toward the edges from each central boss. These osteoderms appear as very thin, flat disks (not smoothly or evenly convex as seen in *Bradysaurs baini*) with distinct, irregularly outlined, raised central bosses. A minority of these

osteoderms are thicker, and more evenly convex, but they still have the distinct raised central boss, even if the periphery is thicker and not very disc-like.

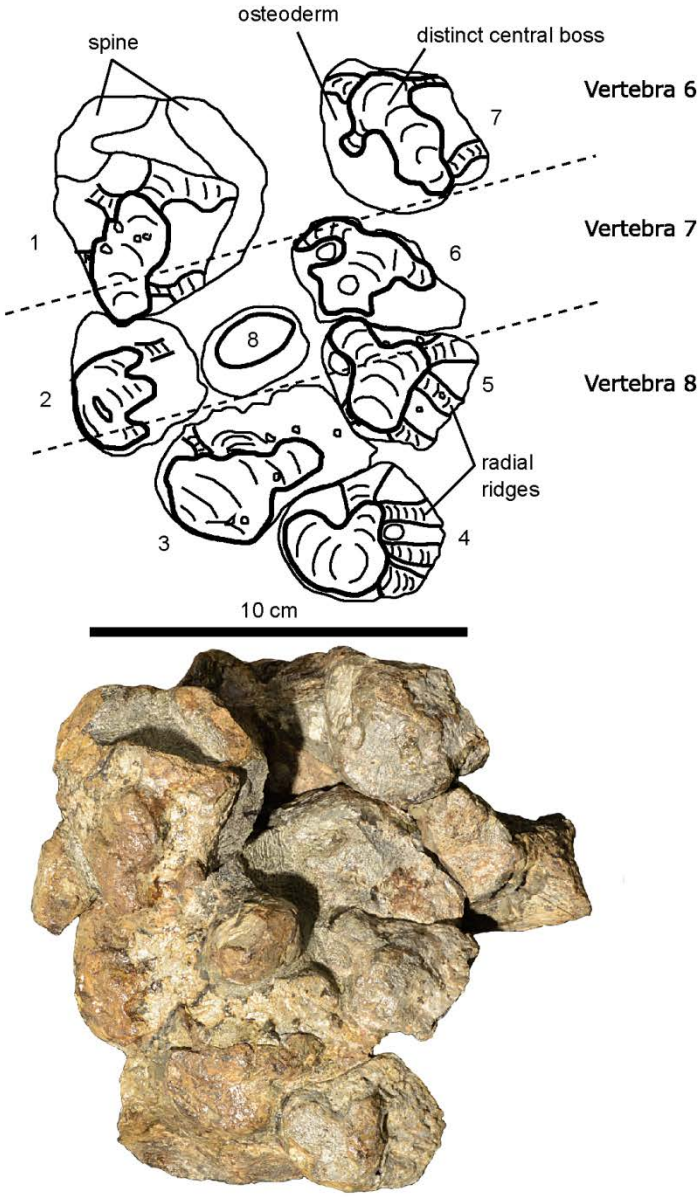


Figure 4.31: Photograph and interpretive drawing of the osteoderms on the 6th-8th - vertebrae of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034), in dorsal view. Anterior to the top of the page.

Large, wide, osteoderms are preserved closely associated with the neural spines of 5th (Fig. 4.23) and 10th vertebrae (Fig. 4.25) and the right postzygapophysial process of the 12th (Fig. 4.26) and show the same features, although on the 10th and 12th vertebrae they are slightly smaller (30-40 mm wide). The two

osteoderms on the 15th and 16th vertebrae are small (30-40 mm wide) and very low and disc-like with a thin periphery and an irregular tab-like distinct raised central boss.

One smaller osteoderm (30x23 mm) on the neural spine of the 7th vertebra (Fig. 3.31, boss no 8) is very different from the anterior dorsal osteoderms. It is oval in outline and stud-shaped as it is high and evenly convex, being smoothly curved or rounded without a pointed distal tip. It has no clearly delimited central boss. Boonstra (1934b) considered this unusual isolated, smaller scute to have been displaced from the flanks of the animal.

Scapulocoracoid													
#	Diagnostically Important	Measurement	*Embrithosaurus* SAM-PK-8034 left	*Embrithosaurus* CGP CBT 112 right	*Embrithosaurus* CGP CBT 112 left	*Nochelesaurus* SAM-PK-6239 right	*Nochelesaurus* SAM-PK-6239 left	*Nochelesaurus* SAM-PK-6238 right	*Nochelesaurus* SAM-PK-6238 left	*Bradysaurus* NHMUK R1971 right	*Bradysaurus* NHMUK R1971 left	*Bradysaurus* SAM-PK-5624 right	*Bradysaurus* SAM-PK-5624 left
1		Blade: proximal base (just above dorsal edge of acromion process), anteroposterior length	100	125	120	90	90	90	not presvd.	110	110	110	110
2		Blade: proximal base (just above dorsal edge of acromion process), mediolateral width	50	55	55	60	60	50	not presvd.	50	50	50	50
3	YES	Blade: mid point: just above medial side, swollen process: anteroposterior length	**150**	**140**	**140**		**115**	not presvd.	not presvd.	**130**	**140**	**140**	140
4		Blade: mid point: just above medial side, swollen process: mediolateral width	**20**	**30**	**30**		**30**	**35**	not presvd.	**35**	**35**	25	30
5	YES	Blade: dorsal end: anteroposterior length	**200 (Broom 1903)**	**220**	**215**	not presvd.	not presvd.	**not presvd.**	**171**	**200**	**200**	170	165
6		Blade: dorsal end: mediolateral width	not presvd.	43	48	not presvd.	not presvd.	not presvd.	45	40	40	37	36
7	YES	Blade: length (incl. accromion)	**425 mm (Broom 1903, Boonstra 1932c)**	**423**	**442**			**490**	**not presvd.**	**440**	**440**	330	340
8	YES	subscapular fossa: dorsoventral height	60	100	90	**50**		50?	not presvd.	damaged	80	not accessible	not accessible
9	YES	subscapular fossa: anteroposterior width	30	35	35	**15**		20?	not presvd.	damaged	20	not accessible	not accessible
10	YES	subscapular fossa: mediolateral depth	10	20	21	**5**		?	not presvd.	damaged	20	not accessible	not accessible
11		subscapular fossa: anteror margin of scapula to ant border of fossa	**45**	**45**	**45**	**40**		**40**		damaged	**55**	not accessible	not accessible
12		subscapular fossa: pos border of scapula to pos border of top of fossa	**70**	**75**	**60**	**90**		**90**	not presvd.	damaged	**110**	not accessible	not accessible
13		subscapular fossa: pos border of scapula to pos border of bottom of fossa	**130**	**150**	**145**	**130**		**135**	not presvd.	damaged	**175**	not accessible	not accessible
14	YES	glenoid fossa: max anteroposterior diameter	**210**	**215**	not presvd.	**150**		**190**	not presvd.	**200**	**180**	220	?
15		glenoid fossa: dorsoventral height	80	91	not presvd.	80		110	not presvd.	110	110	110	?
16		glenoid fossa: orientation above horizontal axis (oblique)	20 deg	20 deg	20 deg	30 deg		30 deg	not presvd.	25 deg	25 deg	?	?
17		coracoidal plate: anteroposterior length	350	390	not presvd.	n/a		290	not presvd.	290	310	made of plaster	made of plaster
18		coracoidal plate: depth	30	15	15	n/a		20	not presvd.	15-20	15-20	made of plaster	made of plaster
19		posterior coracoid: angle between dorsal edge and posterior scapula border	**120 deg**	**125 deg**	**125 deg**	not presvd.		**130-135 deg**	not presvd.	**125 deg**	**125 deg**	90 deg (slightly distorted?)	125 deg

Table 4.1: Scapulocoracoidal measurements of middle Permian pareiasaurs in millimetres.

Humerus													
#	Diagnostically Important	Measurement	*Embrithosaurus* SAM-PK-8034 right	*Embrithosaurus* FMNH UR 2443 left	*Embrithosaurus* CGP CBT 112 right	*Embrithosaurus* CGP CBT 112 left	*Nochelesaurus* SAM-PK-6239 left	*Nochelesaurus* SAM-PK-6238 right	*Nochelesaurus* SAM-PK-6238 left	*Bradysaurus* NHMUK R1971 right	*Bradysaurus* NHMUK R1971 left	*Bradysaurus* SAM-PK-5624 right	*Bradysaurus* SAM-PK-5624 left
1		Humerus: Length	420		**371**		430	430	430	425	425	410	450
2		entepicondyle and ectepicondyle (anteroposterior width)	**230**				**260**	**245**	**235**	**250 recstd.**	**290**	**230**	**235**
3	**YES**	Epicondyles: distal projections beyond the radial and ulnar articulation surfaces	**25**		**22**	**38**	**35**	**35**	**40**	**48**	**44**	**38**	**40**
4	**YES**	Proximal humerus, anteroposterior length, incl. delto-pect crest	250		251		?	275	284	**305**	300 recstd.	?	?
5		Proximal humerus, anteroposterior length of flat strip-like articualtiry surface	220				?	243	245	260	260 reconstd.	?	?
6	**YES**	Humerus: Torsion between proximal and distal ends	**70 -80 deg**	**60 deg**	20 deg (distortion)		**20 deg**	**30-40 deg**	**30-40 deg**	**10-20 deg (Recn.strucd)**	**10-20 deg (Recn.strucd)**	**70-80 deg**	**70-80 deg**
7		Humerus: Proximal Art Surface, max width	**90**				**60**	**92**	**93**	**89**	**93**	80 made of plaster	
8	**YES**	Intercondylar fossa depth: deepest proximal portion	**20**		**22**	**20**	**40**	**35**	**50**	**50**	**40**	**30**	**35**
9	**MAYBE**	Delto-pect crest: anteroposterior width	**57**				not presvd.	**90**	not presvd.	**90**	**90 reconsd.**		

Table 4.2: Humeral measurements of middle Permian pareiasaurs in millimetres.

Radius					
#	Diagnostically Important	Measurement	*Embrithosaurus* SAM-PK-8034 right	*Nochelesaurus* SAM-PK-6238 right	*Bradysaurus* NHMUK R1971 right
1		Radius: Length	231	250	245
2		Radius: Narrowest diamater	40x45	?	43x52
3		Radius: Torsion between proximal and distal ends	45 degrees	45 degrees	45 degrees
4		Radius: proximal end mediolateral width	110	110	125
5		Radius: distal end mediolateral width	100	120	113

Table 4.3: Radius measurements of middle Permian pareiasaurs in millimetres.

Ulna										
#	Diagnostically Important	Measurement	*Embrithosaurus* SAM-PK-8034 right	*Embrithosaurus* FMNH UR 2443 right	*Embrithosaurus* CGP CBT 112 right	*Nochelesaurus* SAM-PK-6238 right	*Bradysaurus* NHMUK R1971 right	*Bradysaurus* NHMUK R1971 left	*Bradysaurus* SAM-PK-5624 right	*Bradysaurus* SAM-PK-5624 left
1	YES	Ulna Length	295		345	370	370	380 reconsd.	369	368
2		Ulna Postaxial bar: oblique dorsoventral length below bend	110		110	120	110	120		
3	YES	Ulna Postaxial bar: oblique dorsoventral length above bend	30	90	85	90	90	90		
4	YES	Ulna Prox. Art. Surface: Perpendicular Dorsoventral length/height	90		95	130	130	130		
5	YES	Ulna Olecranon process (above Prox. Art. Surface)	NO	YES	YES	YES	YES	YES	YES	YES
6	YES	Ulna Olecranon process: dorsoventral height		40	22	20	45	15	33	36
7	YES	Ulna Posterodorsal Limiting ridge	NO	YES	YES	YES	YES	YES	YES	not presvd.
8	YES	Ulna Anterodorsal limiting ridge/lip/overhang (defines top of articular surface)	NO	YES	YES	NO	YES	YES	YES	YES
9	YES	Ulna: Anterodorsal corner: constriction: lateral, medial	NO	YES, Lat & Med	YES, Lat & Med	YES, Lat Only	YES, Lat & Med	YES, Lat & Med	YES, lateral, medial	YES, lateral, medial
10	YES	Ulna: Olecranon Crests	YES, prominent	NO	NO	YES, very low	NO	NO	NO	NO
11	YES	Ulna: Crests max height	20			5			no crests	no crests
12	YES	Ulna: Crest locations	ant/prox/post			ant			no crests	no crests

Table 4.4: Ulna measurements of middle Permian pareiasaurs in millimetres.

Femur											
#	Diagnostically Important	Measurement	*Embrithosaurus* SAM-PK-8034 right	*Embrithosaurus* CGP CBT 112 right	*Embrithosaurus* CGP CBT 112 left	*Nochelesaurus* SAM-PK-6239 right	*Bradysaurus* NHMUK R1971 right	*Bradysaurus* NHMUK R1971 left	*Bradysaurus* SAM-PK-5624 right	*Bradysaurus* SAM-PK-5624 left
1		Femur Length	410		425	420	415	445 Recondstd.	442	
2		Femur: Proximal end,anteropostero direct width	**225**		**220**		**255**	240 reconstrud.		
3		Femur: Shaft narrowest point anteroposteriorly	**110**		**120**	**120**	**135**	**130**		
4	**YES**	Femur: Distal condyles width anteroposteriorly	**170**		**200**	**155**	**190**	240 Reconstructd.		
5		Femur: Angle of femoral head to shaft	**40 deg**		**40 deg**	**40 deg**	**40 deg**	**40 deg Reconstud.**		
6		Femur: Proximal articulation surface: max width	95		85	80	75 (dor/vent crushed)	n/a reconstrudered		
7		Femur: Proximal articulation surface: length	190			160	200	n/a reconstrudered		
8	**YES**	Femur: Distal Lateral condyle, distal projection beyond medial condyle	**30Right, 40Left**		**45**	**70**	**20-30 estimated, erroded**	n/a reconstrudered	**50**	**40**
9		Femur: Major Trochanter: dorsoventral thickness	**35**	**40**	**30 erroded**	**35**	**35**	**35**		
10	**YES**	Femur: Major Trochanter: posterior projection from shaft level	**30**	**20**	**10 erroded**	**less than 5**	**10 est. as edge erroded**	**10**	**15**	
12	**YES**	Femur: Internal trochanter: Ventral extension (height) beyond adductor ridge	**20**		**15**	**5**	**30**	**30**		
13	**YES**	Femur: Internal trochanter: proximally straight or curved?	**gently curved**	**gently curved**	**gently curved**	**straight**	**very curved**	**very curved**	**not preserved= made of plaster**	**not preserved= made of plaster**
14	**YES**	Femur: Internal trochanter: proximally edge perpendicar or oblique to adductor ridge	**perpendicular**	?	?	**oblique**	**perpendicular**	**perpendicular**		

Table 4.5: Femur measurements of middle Permian pareiasaurs in millimetres.

Tibia							
#	Diagnostically Important	Measurement	*Embrithosaurus* SAM-PK-8034 right	*Nochelesaurus* SAM-PK-6239 right	*Nochelesaurus* SAM-PK-6238 right	*Bradysaurus* NHMUK R1971 right	*Bradysaurus* NHMUK R1971 left
1		Tibia: length	250	250	273	275	260 reconstd.
2	**YES**	Tibia: shaft narrowest point, max mediolateral width	**45**	**70**	**72**	**75**	**75**
3		Tibia: shaft narrowest point, min anteroposterior width	**55**	**50**	**48**	**45**	**50**
4	**YES**	Tibia: proximal end mediolateral width	150	**155**	**181**	180	180 reconstrud.
5	**YES**	Tibia: distal end mediolateral width	**120**	**130**	**140**	**135**	**135**
6	**YES**	Tibia: torsion between proximal and distal ends	**30 degrees**	**10 degrees**	**40 degrees**	**20 deg**	**30 deg reonstrud.**
7		Tibia: cneil crest height above excavation (anteriorly)	**45**	**33**	**48**	**45**	50 reconstrud.

Table 4.6: Tibia measurements of middle Permian pareiasaurs in millimetres.

Fibula							
#	Diagnostically Important	Measurement	*Embrithosaurus* SAM-PK-8034 right	*Embrithosaurus* CGP CBT 112 right	*Nochelesaurus* SAM-PK-6238 right	*Bradysaurus* NHMUK R1971 right	*Bradysaurus* NHMUK R1971 left
1		Fibula: length	261	297	300	not preserved.	n/a reconstructed
2		Fibula: proximal end width	70	77	73	64	n/a reconstructed
3		Fibula: distal end width	82	98	95	85	88
4		Fibula: scar	**No**	**Yes**	**Yes**	not preserved.	not preserved.
5		Fibula: Torion between proximal and distal ends	**30 deg**	**70 deg**	**45 deg**	not preserved.	n/a reconstructed

Table 4.7: Fibula measurements of middle Permian pareiasaurs in millimetres.

Pelvis											
#	Diagnostically Important	Measurement	*Embrithosaurus* SAM-PK-8034 right	*Embrithosaurus* CGP CBT 112 right	*Embrithosaurus* FMNH UR 2486 left	*Embrithosaurus* FMNH UR 2443 complete pelvis	*Bradysaurus* NHMUK R1971 right	*Bradysaurus* NHMUK R1971 left	*Bradysaurus* FMNH UC 1525 right	*Bradysaurus* FMNH UC 1533	*Bradysaurus* SAM-PK-5624 right
1	YES	ILLIAC BLADE: max width: anterior process: anterior and dorsal margins	20	20	15	20	25	25	30	25	?
2	YES	ILLIAC BLADE: total length, anteroposteriorly: Anterior process to posterior process	260	290	pos proces not preserved	pos proces not preserved	290	310	260 (ant proc broken off)	260	310
3	YES	ILLIAC BLADE: anterior process length: shaft border to anterior border of process	90	90	60	Ant. proces not preserved	130	130	not preserved	90	130
4		ILLIAC BLADE: posterior process length: shaft border to posterior border of process	30	30	pos proces not preserved	30	50	50	40?	not preserved	35
5	YES	ILLIAC BLADE: Orientation: VERTICAL EVERSION: Upwards angle of Anterior illiac blades, from the vertical	vertical, not everted	10 deg	10 deg	vertical, not everted	55-60 deg	55-60 deg	45 deg	30 Deg left, 50 deg right	45 deg
6	YES	ILLIAC BLADE: Orientation: Dorsal view: LATERAL BEND OUTWARDS outwards angle of Posterior illiac blades, from the midline	45 deg	60 deg	45 deg (average as blade is strongly curved)	45 deg on left, 40 deg on right side	10 deg	0 deg	10 deg (blade is very curved, pos part of blade 10 deg, ant part 45 Deg)	0 deg, (anterior process curved strongly outwards to 30 - 45 degres divering off the midline)	blade 10 deg, (anterior process curved strongly outwards to 30 - 40 degres divering off the midline)
7	YES	SHAFT ORIENTATION: Degrees above the horizontal flat pelvic plate	30 degrees off vertical	30 degrees off vertical	20 degrees off vertical, shaft is almost vertical!!!	10 degrees off vertical, basically straight up	30 deg above horizontal plane, very flat	30 deg, shaft is quite flat	30 deg above horizontal plane, very flat	50 deg (top of blades matches angles of verts, about 30 degrees below horizontal (bum)	40 deg
8	YES	ACETABULUM: diameter	155	150			180	180			180
9	YES	PUBIOISCHIATIC PLATE: width, anterior edge: (perpendicular measurement)	305	350	310	300	360		300 (estimated)	400	360
10	YES	PUBIOISCHIATIC PLATE: width, posterior edge: (perpendicular measurement)	290	350 estimate	310	260	360		320	350	310
11	YES	PUBIOISCHIATIC PLATE: width, BETWEEN THE BLADES (Ant & Pos)	95 Ant, 130 Post	130ant, 180Pos	110 Ant, 150 Pos	110 Ant, 150 Pos	210 Ant, 230 Post		190 Ant, 210 Post	180 Ant, 200 Post	?
12	YES	PUBIOISCHIATIC PLATE: length (midline)	220	280 estimated	250	245	325		270	210 (pos edge is damaged though, should be longer)	320
13	YES	PUBIOISCHIATIC PLATE: pelvic midline symphysis: anterior portion: dosoventral thickness, thickest anterior region	90	110	110	106	80		80 (estimated)	80 (estimated)	70
14	YES	KEEL: Anterior view: angle above horizontal	50 deg		55 deg	50 deg	50 deg		not accessible	30 Deg	?

Table 4.8: Pelvis measurements of middle Permian pareiasaurs in millimetres.

5. CHAPTER FIVE: POSTCRANIAL DESCRIPTION OF *NOCHELESAURUS ALEXANDERI*

5.1 Introduction

In a short addendum at the end of a pareiasaurian cranial paper describing a weathered juvenile skull, Broom (1924:507) briefly described and named a new species of pareiasaur (*Pareiasaurus strubeni*) based on a lower jaw with 'considerably large' teeth. To accommodate Broom's (1924) new large-toothed specimen into their new taxonomic classification, Haughton and Boonstra (1929a) erected the genus *Nochelesaurus*, including *N. strubeni*, and also created the new species *N. alexanderi*. Their very brief genus and species diagnoses were based entirely on a few cranial features. Boonstra (1934a) greatly expanded the diagnoses of the genus and the two species, but still based his analysis solely on crania.

The postcranium of *Nochelesaurus* was first described in the series of pareiasaurian papers produced by Haughton and Boonstra between 1929-1934, covering all South African pareiasaur taxa and a few foreign taxa, with each paper focusing on a different postcranial anatomical region (i.e. manus, Boonstra 1929a; pes, Boonstra 1929b; hind limbs, Haughton & Boonstra 1930b; fore limbs, Boonstra 1932b; dermal armour, Boonstra 1934b; and vertebrae and ribs, Boonstra 1934c).

Lee (1994, 1997a), noting the type species of *Nochelesaurus* (*N. strubeni*) as based on indeterminate material in the Broom Collection of the AMNH (New York), Lee declared the type species as *nomina vana* and so formally removed *N. strubeni*. He also synonymised *Dolichopareia angusta* and *Brachypareia watsoni* with *Nochelesaurus alexanderi* and published a brief description of the postcranium, importantly including three explicit postcranial autapomorphies. However, a detailed anatomical description of the postcranial elements was not produced by Lee. The cranium of the holotype of *Nochelesaurus alexanderi* is re-

described in detail in chapter 2 of this PhD project. However, this species will not be completely understood until the postcranium is described in detail.

This chapter aims to describe the postcranial elements of *Nochelesaurus alexanderi* using the holotype and referred specimens. Particular emphasis is placed on describing distinguishing features of the species, compared to the anatomically similar co-occurring species, and on describing and discussing the three autapomorphic postcranial features proposed by Lee (1994, 1997a). Particular attention is given to postcranial anatomical features which influence pareiasaurian phylogenetic characters and scoring.

5.2 Material

5.2.1 Holotype

Refer to Chapter Two, Material and methods

5.2.2 Referred material

Refer to Appendix A for a list of referred specimens of *Nochelesaurus alexanderi*.

5.2.3 Comparative material

Refer to Chapter Two, Material and methods.

5.2.4 Literature consulted

Refer to Chapter Two, Material and methods.

5.2.5 Preservation and preparation

Refer to Chapter Two, Material and methods.

5.2.6 Holotype horizon and locality

Refer to Chapter Two, Material and methods.

5.3 Systematic Palaeontology

REPTILIA Laurenti, 1768

PARAREPTILIA Olsen, 1947

PAREIASAURIA Seeley, 1888

PAREIASAURIDAE Cope, 1896

NOCHELESAURUS Haughton and Boonstra, 1929

Nochelesaurus alexanderi Haughton and Boonstra, 1929

Note: The genus *Nochelesaurus* is no longer valid, but following Lee (1997a:248) I have not erected a new genus yet, as the name is entrenched in the literature.

5.4 Postcranial description

This description is based on the holotype (SAM-PK-6239) and referred specimen (SAM-PK-6238, Lee 1994, 1997a; Van den Brandt 2016). The holotypes of *Nochelesaurus alexanderi* (SAM-PK-6239) and *Bradysaurus baini* (NHMUK R1971) are large adult specimens of similar size. The holotype of *Embrithosaurus schwarzi* (SAM-PK-8034) is slightly smaller and more gracile and may be a sub-adult.

5.4.1 Shoulder girdle

The shoulder girdle of *Nochelesaurus*, as in all pareiasaurs, comprises paired scapulocoracoids, clavicles and cleithra, and the single interclavicle.

The holotype of *Nochelesaurus* preserves a partial right scapulocoracoid, with the articulated distal end of the right clavicle (Fig. 5.1). Most of the interclavicle is preserved, with articulated proximal portions of the left and right clavicles (Fig. 5.3). An isolated long section of the left scapula blade with a partial left cleithrum is also preserved (Fig. 5.1).

SAM-PK-6238 preserves most of the right scapulocoracoid, including the scapula blade (Fig. 5.2), and the isolated dorsal end of the left scapula blade.

Scapulocoracoid (Figs. 5.1, 5.2)

Surrounding the glenoid fossa, the coracoid plate of the holotype is severely damaged with the distal-most 40mm (estimated) of the anterior, ventral and posteroventral portions of the plate not preserved (Fig 5.1). Only the posterodorsal portion of the plate, containing the glenoid fossa, is intact. Referred specimen SAM-PK-6238 preserves more of the coracoid plate, but is also missing large anterior sections (Fig. 5.2). SAM-PK-6238 shows that ventral to the glenoid fossa, the lateral surface of the corocoid pate is not smooth, but is rugose and irregular with three to four indistinct, raised regions and depressed regions in between. Three or four similar raised regions, with depressions between are also present on the well preserved holotypes of *Bradysaurus baini* and *Embrithosaurus schwarzi* and are therefore typical of this group.

On the medial surface of the isolated left scapula blade fragment of the holotype (Fig. 5.1), the scapula blade has a swollen, low process (50 mm anteroposteriorly wide, projecting medially 20 mm high), covering the anterior half of the medial blade, just above the depression caused by the distal articulation of the clavicle. This medial swelling is also seen on the scapula of SAM-PK-6238 (Fig. 5.2). This medial process is common to all large co-occurring pareiasaurian taxa as the holotypes of *Embrithosaurus* and *Bradysaurus baini* show similar swellings, but the process is much lower in *Embrithosaurus* and *Bradysaurus* (only 10 mm high in each).

The base of the scapula blade, just above the dorsal edge of the acromion process (the right and left scapula blades of the holotype and of SAM-PK-6238) is oval in cross section, anteroposteriorly elongated (90 mm) and mediolaterally narrow (50-60 mm). Both *Embrithosaurus* (100 mm x 50 mm) and *Bradysaurus* (110 mm x 50 mm) are slightly larger in these two measurements than *Nochelesaurus*. The mid scapula blade of *Nochelesaurus* flares significantly less

anteroposteriorly than the other taxa and is very narrow. At the level just above the swollen process of the medial surface, the isolated left scapula blade fragment of the holotype, measures only 115 mm anteroposteriorly, which is much narrower than *Embrithosaurus* (150 mm) and *Bradysaurus baini* (130-140 mm) at the same level. On the right scapula of SAM-PK-6238, the entire anterior border of the blade is deeply eroded and it is not possible to confirm the anteroposterior width of any part of the blade besides for the base just above the acromion process.

Distally, only the left scapula blade of SAM-PK-6238 is anteroposteriorly complete (Fig. 5.2C) as the distal right scapula blade of SAM-PK-6238 is eroded and missing (Fig. 5.2A, B). The complete left blade is only slightly flared and the preaxial and postaxial margins are straight and not very curved (Turner *et al*. 2015 character 88) and it measures anteroposteriorly only 171 mm, which is narrower than the wide and flared distal end of the scapula's of *Embrithosaurus* (estimated at 200 mm) and *Bradysaurus* (200 mm).

The right scapula blade of only SAM-PK-6238 is dorsoventrally complete and it is very long (490 mm, including the acromion process) compared to *Embrithosaurus* (estimated to 425 mm long) and *Bradysaurus* (440 mm). The length of the scapula blade is thus two and a half times the anteroposterior diameter of the glenoid fossa (190 mmm) (Turner *et al*. 2015 character 87). Boonstra (1932c: 469) also noted the "very tall" right scapula blade of SAM-PK-6238. Interestingly the glenoid of the right holotype measures a very narrow 150 mm anteroposteriorly across.

The right scapula blade of SAM-PK-6238 is slightly convex over its dorsoventral length. Distally however, the lateral surface of the right and left blades is flat to shallowly concave and the medial side strongly convex. Both the lateral and medial surfaces of the scapula blades of SAM-PK-6238 are covered with vertical striations and ridges: highly rugose, densely packed, thin, long, dorsoventral

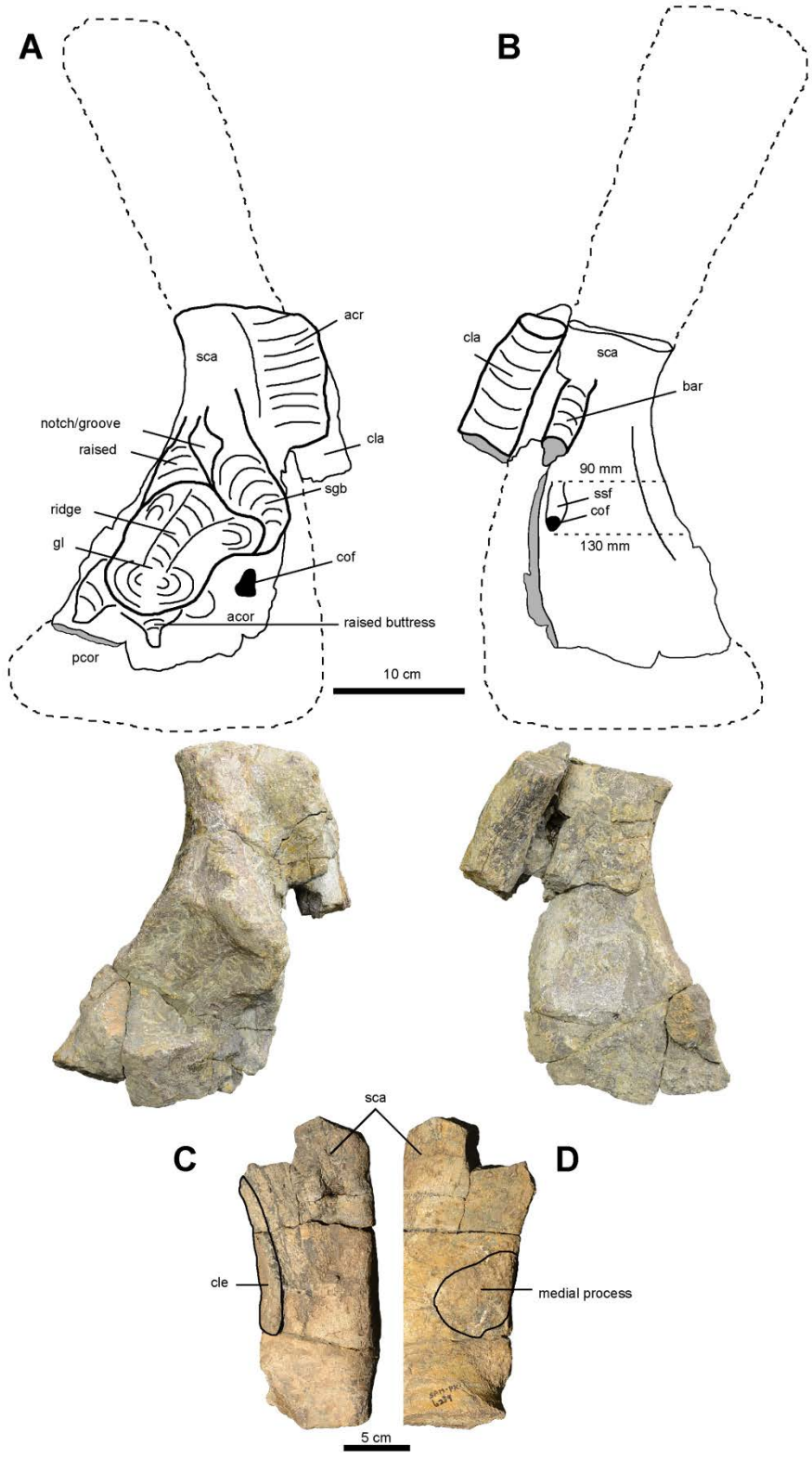


Figure 5.1: Photographs and interpretive drawings of the scapulocoracoid of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), (A), right scapulocoracoid, in lateral view, and (B), in medial view. Base of the left scapula blade in (C), lateral view, and (D), medial view. Dorsal to the top of the page.

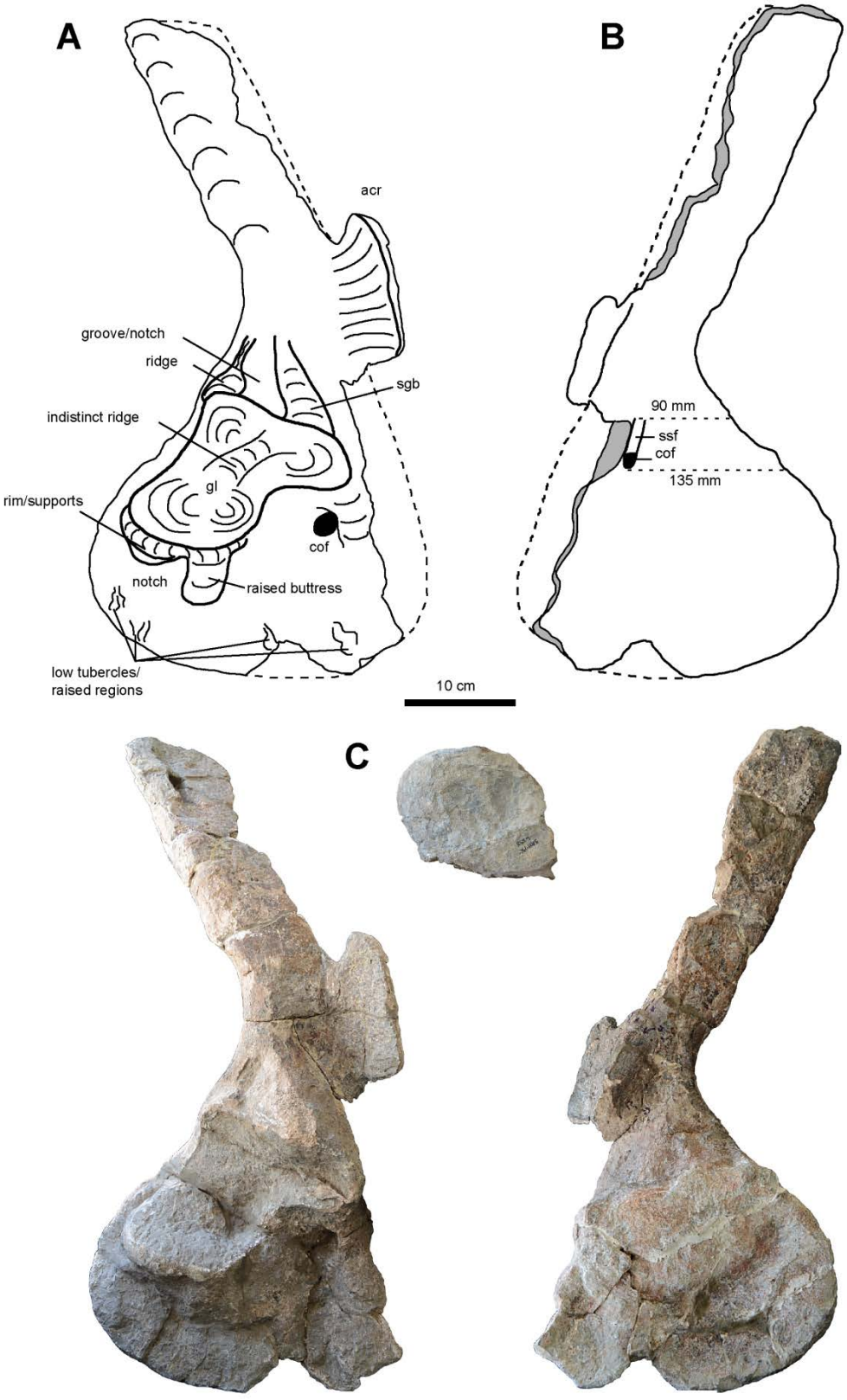


Figure 5.2: Photographs and interpretive drawings of the scapulocoracoid of SAM-PK-6238, (A), right scapulocoracoid in lateral view, (B), right scapulocoracoid in medial view, and (C), dorsal end of the left scapula blade in lateral view. Dorsal to the top of the page.

striations and ridges on the lateral surface of the left blade fragment, and two deep, wide grooves on the medial surface.

The inner (medial) surface of the right scapulocoracoid of the holotype was prepared to reveal the complete dorsoventral groove of the subscapular fossa. The groove is similar in size, although slightly smaller in all dimensions, than in *Embrithosaurus* and much smaller than in *Bradysaurus* (see Table 4.1). The medial surface of right scapulocoracoid of SAM-PK-6238 is damaged but the subscapular fossa also appears small (see Table 4.1).

On the medial surface of the holotype's right scapula, the oval coracoid foramen is positioned on the ventral-most portion of the subscapular fossa. The foramen is passes through the coracoid plate almost directly vertically and slightly laterally as revealed by preparation, as the lateral exit of the foramen is present 35mm below the ventral rim of the anterior facet of the glenoid fossa. Laterally, the foramen forms a vertically elongated tear-drop, with a wide dorsal margin tapering ventrally to a point. In SAM-PK-6238 the lateral coracoid foramen in the same location is large and rounded.

The acromion process is situated above the supraglenoid buttress. As in all large basal South African pareiasaurs, the acromion process is large, forming a wide rectangular, plate-like flange. It is 120 mm (holotype) to 125 mm (SAM-PK-6238) in dorsoventral length, projecting 40 mm above the anterior border of the scapula, and 15 mm mediolaterally wide. The long, thin, anterior margin is flat and convex at the anterodorsal corner. The short, dorsal margin is notched, but the short, ventral margin emerges from anterior border of the scapula at a right angle and is straight. The flat plate-like acromion is gently convex laterally and concave medially (Turner *et al*. 2015 character 89).

The sigmoidal glenoid fossa is anteroposteriorly elongated (150 mm long, 80 mm high in the holotype; 190 mm long and 110 mm high in SAM-PK-6238) and oriented about 30^0 obliquely anterodorsally above the horizontal ventral border of the corocoid plate. In the holotype, the glenoid fossa is significantly

anteroposteriorly shorter than *Embrithosaurus*, but it is almost as long in SAM-PK-6238. In both specimens of *Nochelesaurus*, it is oriented at a slightly higher angle above the horizontal plane (30^0) compared to *Embrithosaurus* (20^0).

The border of the glenoid is thickened, especially the anterodorsal supraglenoid buttress which is curved and rounded, all other margins have sharper edges, with flatter sides. The holotype and SAM-PK-6238 have a large supraglenoid buttress which tapers dorsally into the base of the scapula blade. Behind this tapering is a groove (20 mm wide, 50 mm high) on the lateral surface of the scapula, bordered posteriorly by a raised ridge emanating dorsally from the posterodorsal rim of the glenoid fossa.

The posterior facet of the bipartite glenoid fossa is generally horizontally flat, with its posterior portion facing dorsally and its anterior portion facing slightly anterodorsally and very deep. In SAM-PK-6238, the posterior facet is supported by a particularly robust, thickened, shelf-like projection, almost as large as the supraglenoid buttress, which tapers ventrally into the flat lateral surface of the corocoid plate. In the holotype, the anterior facet of the glenoid fossa faces posteroventrally and is located anterior to a low, oblique ridge (25mm wide, 70 mm long, 10 mm high) that does not cover the flat posterior facet. This ridge is also seen in *Bradysaurus* and is probably also present in *Embrithosaurus* but cannot be confirmed due to obscuring bone. Overall, the glenoid faces primarily laterally, and slightly posteroventrally due to the larger anterior facet.

In the holotype of *Nochelesaurus* the posterior coracoid is only partially preserved posterior and ventral to the glenoid fossa and the scapula blade above the acromion process is not preserved. Determining the angle between the dorsal border of the coracoid and the posterior edge of the scapula blade is not possible. In SAM-PK-6238, the dorsal border of the posterior coracoid is nearly horizontal and forms an angle of $130\text{-}135^0$ with the posterior border of the scapula blade (Turner *et al*. 2015 character 90). This is very similar to *Embrithosaurus* and *Bradysaurus*.

Cleithrum (Fig. 5.1)

The distal half of the degenerate cleithrum is partially fused to the left scapula blade fragment of the holotype (SAM-PK-6239) and is long, thin, and flat (Turner *et al*. 2015 character 91).

Interclavicle (Figs. 5.3, 5.4)

Most of the interclavicle of SAM-PK-6239 is preserved, apart from the posterior-most portion of the median stem. The interclavicle of SAM-PK-6238 preserves the entire median stem, and most of the right lateral arm (apart from a small piece at the distal tip).

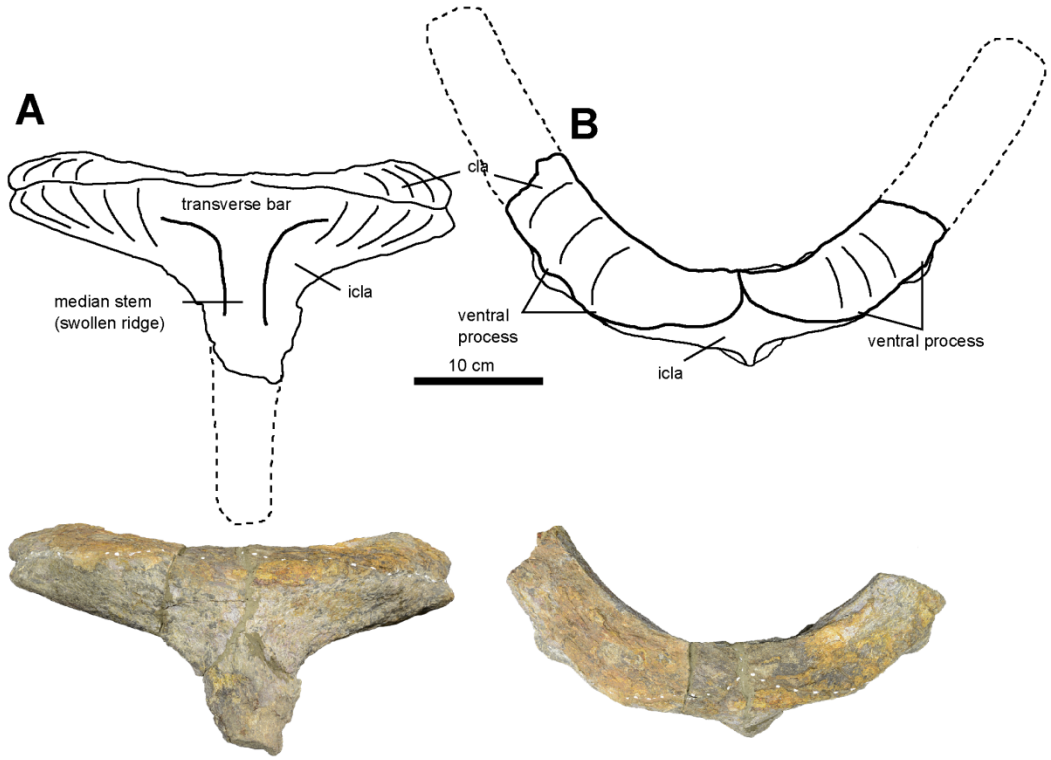


Figure 5.3: Photographs and interpretive drawings of the partial interclavicle, and partial right and left clavicles of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), (A), in ventral view, and (B), in anterior view. Anterior to the top of the page in (A), dorsal to the top of the page in (B).

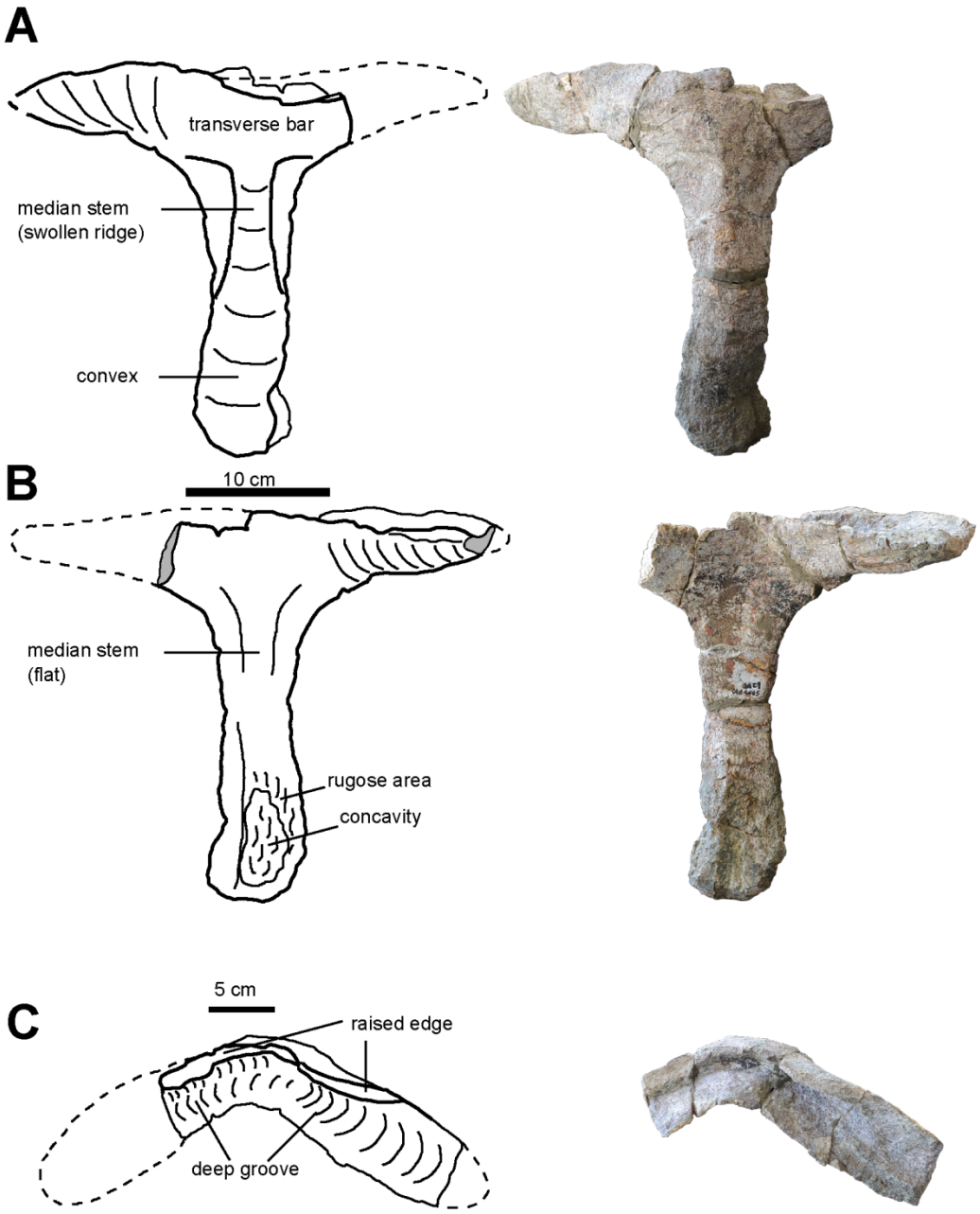


Figure 5.4: Photographs and interpretive drawings of the interclavicle of SAM-PK-6238, (A), in ventral view, (B), in dorsal view, and (C), in anterior view. Anterior to the top of the page in (A) and (B), ventral to the top of the page in (C).

The median stem of SAM-PK-6238 is generally thin and flat. It is slightly dumbbell shaped as anteriorly it is mediolaterally 80 mm wide, narrowing posteriorly to 50 mm midway width, before widening to 70 mm wide at the posterior end of the bone. The anterior half of the bone is triangular in cross section, with a flat dorsal side and a ridged ventral side that comprises two ventrolateral faces either side

of the swollen central ridge of the bone. Posteriorly, the ventral side is gentle convex and the dorsal side develops a midline concavity and rugosity.

The transverse bar of the interclavicle is robust and the anterior surface is deeply grooved (as in *Embrithosaurus* and *Bradysaurus*) for the articulation with the sharp posterior process of the clavicles. There is a raised ridge on the anterior surface, above the groove. Laterally, the lateral extensions of the interclavicle flatten anteroposteriorly: the deep groove on the anterior surface dissipates, and the convex posterior surface flattens to the distal ends of the lateral extensions.

Clavicles (Figs. 5.1, 5.3, 5.4, 5.5)

The holotype preserves only the medial halves of each clavicle, tightly articulated to the interclavicle (Fig. 5.3). The complete right clavicle of SAM-PK-6238 is beautifully preserved as a separate element (Fig. 5.5). The bone is 520 mm long, gently curved and anteroposteriorly flat and oriented as a thin, flat, vertical wall.

The anterior surface of the clavicles of the holotype are badly eroded. The well preserved right clavicle of SAM-PK-6238 (Fig. 5.5) shows that medially the generally flat bone narrows dorsoventrally and becomes triangular in cross section as a sharp posterior process emerges for articulation with the anterior groove of the interclavicle. This morphology is identical to that of the clavicle of *Embrithosaurus* and the anterior surface of the clavicle here develops a shallow groove.

On the ventral margin of the right clavicle of SAM-PK-6238 and on the holotype, the ventral process is wide (90 mm) but low, projecting only 10 mm posteroventrally. The ventral process is slightly damaged in SAM-PK-6238. *Nochelesaurus alexanderi* and *Bradysaurus baini*, lack the distinct, deep notch just medial to the ventral process seen in *Embrithosaurus*.

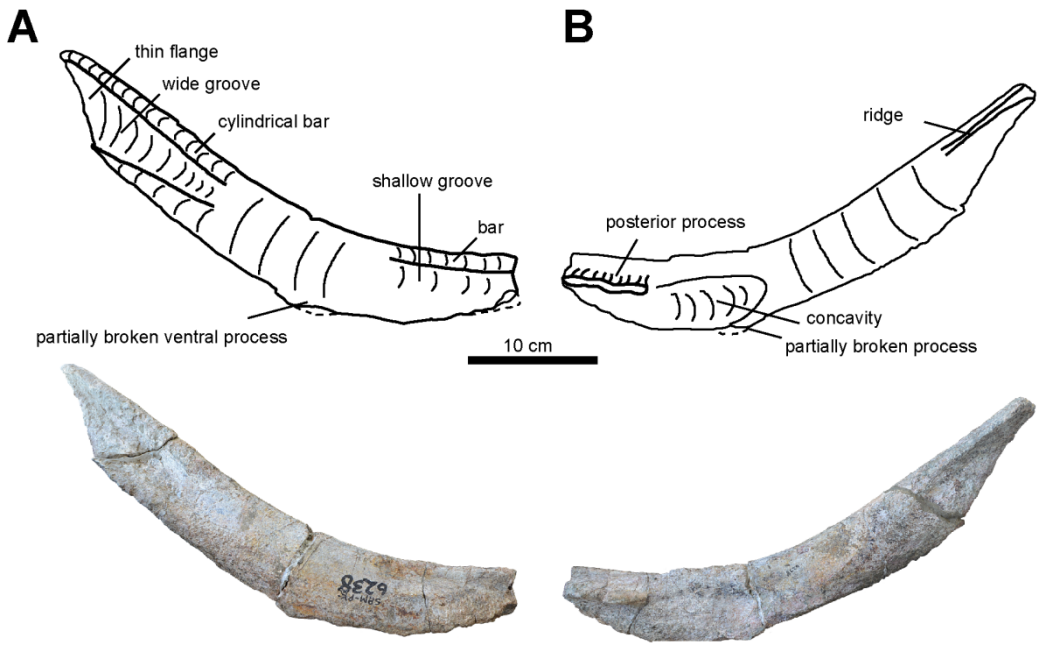


Figure 5.5: Photographs and interpretive drawings of the right clavicle of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in anterior view, and (B), in posterior view. Dorsal to the top of the page.

On the posterior border of the clavicle, a shallow depression is present for reception of the anterior side of the distal or lateral ends of the extension arms of the interclavicle.

Laterally, the right clavicle of SAM-PK-6238 (Fig. 5.5) has a wide, deeply grooved anterior surface and a convex posterior surface. The clavicle extension arm tapers drastically over the last 110 mm distally, where the dorsal border is swollen to form a cylindrical bar distally, and the ventral side of the clavicle forms a flat, thin, flange of bone. At the distal lateral tip the clavicle is triangular in cross section due to a sharp ridge on the posterior side.

5.4.2 Forelimbs

Humerus (Figs. 5.6, 5.7, 5.8, 5.9, 5.10, 5.11)

The in-life horizontally oriented (Boonstra 1932c, Lee 1997a) left humerus of the holotype of *Nochelesaurus* (SAM-PK-6239) is missing a large section of the preaxial side of the expanded proximal blade and a section of the distal end of

the postaxial entepicondyle or ulnar condyle (Figs. 5.6, 5.7, 5.8). The right humerus of SAM-PK-6238 is well preserved and complete, apart from a large section of the ectepicondyle and part of the postaxial flange of the entepicondyle (Figs. 5.9, 5.10, 5.11). The left humerus is less well preserved, with severely weathered condyles and a sheared-off deltopectoral crest

The torsion between the proximal and distal expansions of the humerus of the holotype is only 20^0 (Fig. 5.7), also noted by Boonstra (1932c:466), resulting in the distal and proximal expansions appearing nearly on the same plane. Referred specimen SAM-PK-6238 shows slightly more twisting in both humeri of $30\text{-}40^0$ (Turner *et al.* 2015 character 92).The range is therefore $20\text{-}40^0$ for *Nochelesaurus*. This is still much less than the torsion in *Embrithosaurus* ($60\text{ - }80^0$). Lee (1997a) noted the torsion as 45^0 for *Nochelesaurus*.

Measured across the ect- and entepicondyles, the humerus of the holotype of *Nochelesaurus* is 260 mm anteroposteriorly, which is 30 mm wider than the holotype of *Embrithosaurus* (230 mm), but those of SAM-PK-6238 are only 5 mm (left humerus) and 15 mm (right humerus) wider than *Embrithosaurus*.

As in all large middle Permian South African pareiasaurs, the ectepicondyle is very robust, and large and dorsoventrally more than twice as thick as the entepicondyle (Figs. 5.8B, 5.11B). Turner *et al.* 2015 character 99).

On the preaxial border, the ectepicondyle forms a thin, but expanded and wide flange, very similar in morphology to that of *Embrithosaurus* and *Bradysaurus* (Turner *et al.* 2015 character 93). The flange houses the small ectepicondylar foramen, only visible in distal dorsal view on the holotype and on SAM-PK-6238 (Figs. 5.6A, 5.7A, 5.9B, 5.10A) at a level slightly proximal to the sharp pointed proximal edge of the intercondylar fossa (Turner *et al.* 2015 character 94). The ectepicondylar foramen is present in all pareiasaurs according to Lee (1997b:237).

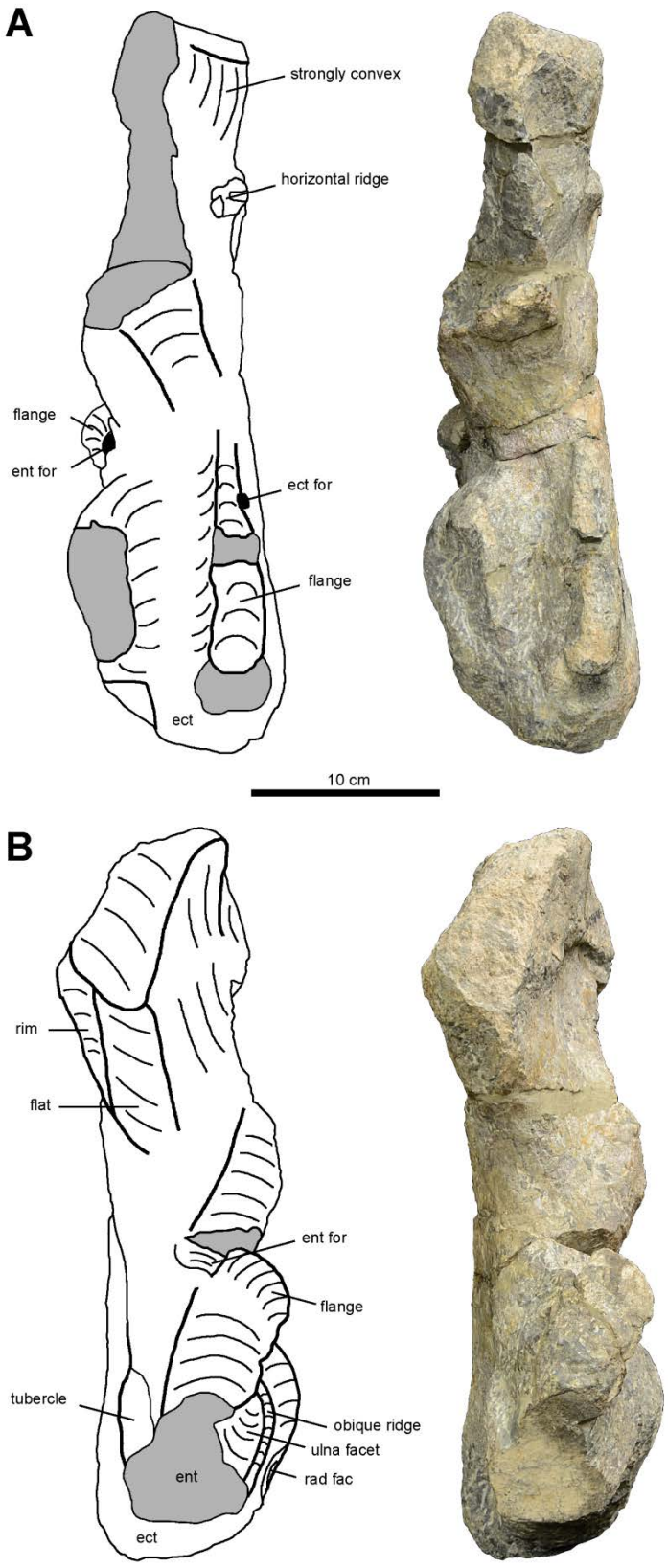


Figure 5.6: Photographs and interpretive drawings of the left humerus of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), (A), in anterior view, and (B), in posterior view. Medial to the top of the page.

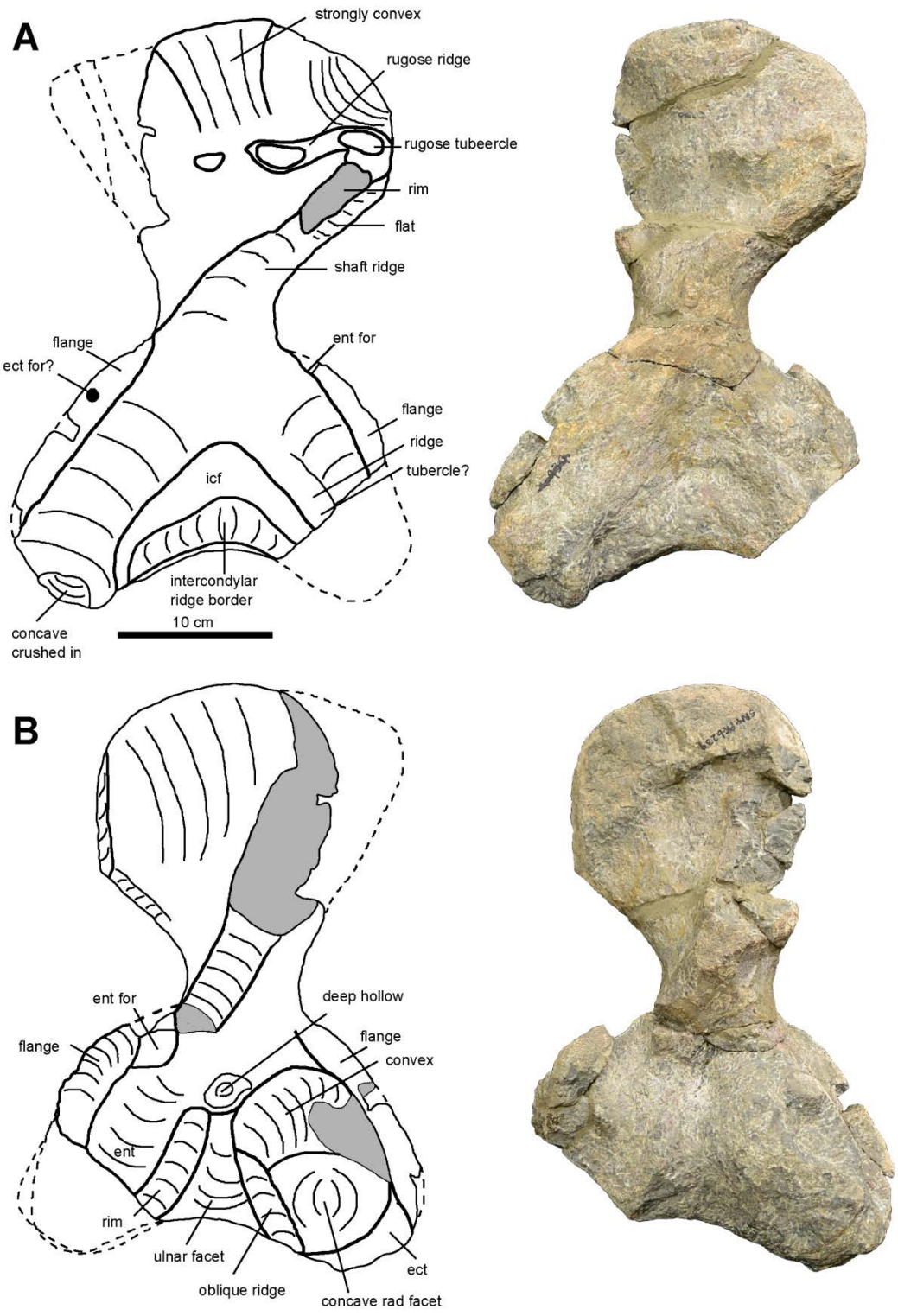


Figure 5.7: Photographs and interpretive drawings of the left humerus of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), (A), in dorsal view, and (B), in ventral view. Medial to the top of the page.

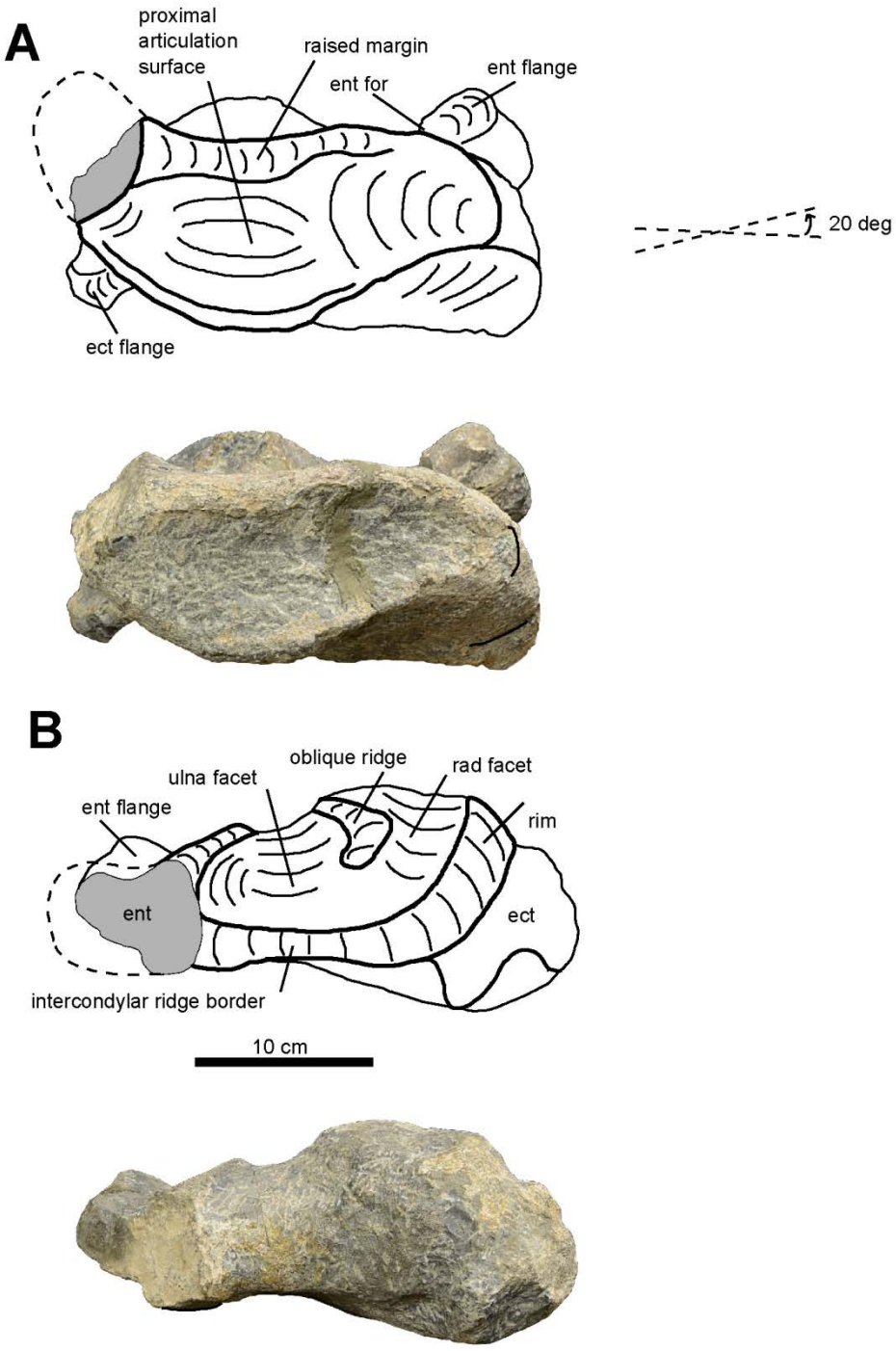


Figure 5.8: Photographs and interpretive drawings of the left humerus of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), (A) and (C), in proximal view, and (B), in distal view. (C) illustrates the angle between the proximal and distal expansions as 20^0. Ventral to the top of the page.

The smaller postaxial entepicondyle of the holotype carries a wider, thicker, slightly curled over, more square-edged flange with to a sharp, right-angled edge on the proximal corner, very similar to the wide, square-edged flange of *Embrithosaurus* (Turner *et al.* 2015 character 95). The holotype preserves the large, elongated entepicondylar foramen, presumably completely enclosed, as most of its ventromedial 'bridge-like' margin is not preserved (Figs. 5.6, 5.7) (Turner *et al.* 2015 character 96). The foramen has similar dimensions as that of the holotype of *Embrithosaurus* and like in *Embrithosaurus*, the entepicondylar foramen is positioned so that it is visible (completely open and can been seen right through) when the distal expansion of the humerus is viewed dorsally (Figs. 5.7A, 5.10A) (Turner *et al.* 2015 character 97).

The two epicondyles of the holotype of *Nochelesaurus* project distally 35 mm beyond the radial and ulnar articulation surfaces. In SAM-PK-6238, they project distally between 35 mm (right humerus) and 40 mm (left humerus) to the distal ends of the ectepicondyles (Turner *et al.* 2015 character 98).

The intercondylar fossa (olecranon fossa) is large, wide and deep in *Nochelesaurus*, with an irregular, not very smooth, surface. The fossa is deeper than that of *Embrithosaurus*, which is 20 mm deep, proximally reaching 40 mm deep in the holotype left humerus and in SAM-PK-6238 it is 35 mm deep on the right humerus and 50 mm deep on the left. This generally deep fossa suggests a prominent, large olecranon process of the ulna, which is indeed the case (see Ulna) (Turner *et al.* 2015 character 103). On the dorsal surface, the preaxial and postaxial margins of the fossa are straight, swollen ridges and the dorsal distal margin is formed by a gently concavely curved, wide and low transverse ridge (intercondylar ridge border), which does not reach round onto the distal side of the humerus, and which separates the intercondylar fossa from the radial facet and the ulnar facet (Turner *et al.* 2015 character 102). The intercondylar fossa is much wider than the width of the proximal ulna (olecranon process) (Turner *et al.*2015 character 104).

A large, distinct tubercle is present midway along the swollen, straight, postaxial margin of the intercondylar fossa of the right humerus of SAM-PK-6238 (Figs. 5.9, 5.10). The anterior and posterior margins of the tubercle are sharp edged and 35 mm apart, but the proximal and distal margins show rising sides and are slightly further apart (45 mm). The dorsal surface of the tubercle is slightly convex. The tubercle has a small notch on its distal margin. Confirmation of the tubercle on the left humerus of SAM-PK-6238 is hampered as the entire dorsal surface of the entepicondyle is deeply weathered. However, it does appear that the low, eroded remnants of a round, similarly sized tubercle is present in the corresponding position.

The left humerus of the holotype of *Nochelesaurus* is missing several centimetres at the distal end of the entepicondyle (Fig. 5.7). Proximal to the missing section, the straight, swollen postaxial border of the intercondylar fossa forms a raised ridge (25 mm wide, 50 mm long). A crushed region on the posterior side of the ridge exacerbates the distinctiveness and height of the ridge. One can interpret this as the preserved proximal part of a tubercle, but it is possible that this feature is merely the swollen, ridge-like postaxial border of the intercondylar fossa, which is often seen in specimens of large South African middle Permian pareiasaurs (e.g. *Embrithosaurus* holotype). Referred *Nochelesaurus* specimens FMNH UR 2436 and FMNH UP 2480 also appear to show the humeral tubercle.

The radial facet/condyle (Lee 1997a) or capitellum (Boonstra 1932c) of the holotype and SAM-PK-6238 is very large, round to ovoid, and bulbous. In the holotype, the facet is variously damaged but in SAM-PK-6238 the facet is well preserved and distinctly demarcated with sharp edges. It is strongly convex proximally and shallowly concave distally, a morphology also seen in the holotype and *Embrithosaurus* and *Bradysaurus*. An oblique ridge separates the radial facet from the adjacent ulnar facet on the ventral surface of the humerus.

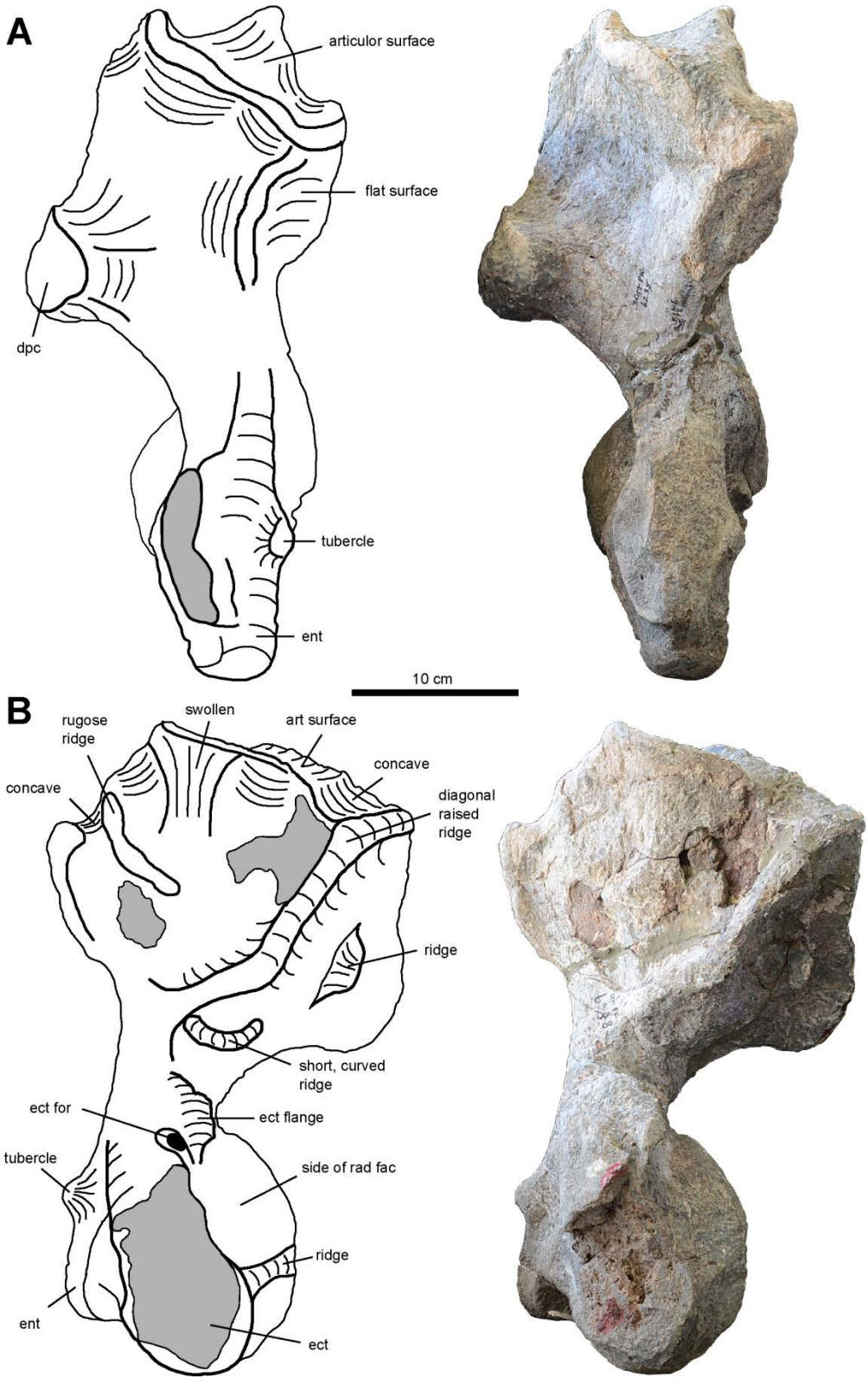


Figure 5.9: Photographs and interpretive drawings of the right humerus of the SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in anterior view, and (B), in posterior view. Medial to the top of the page.

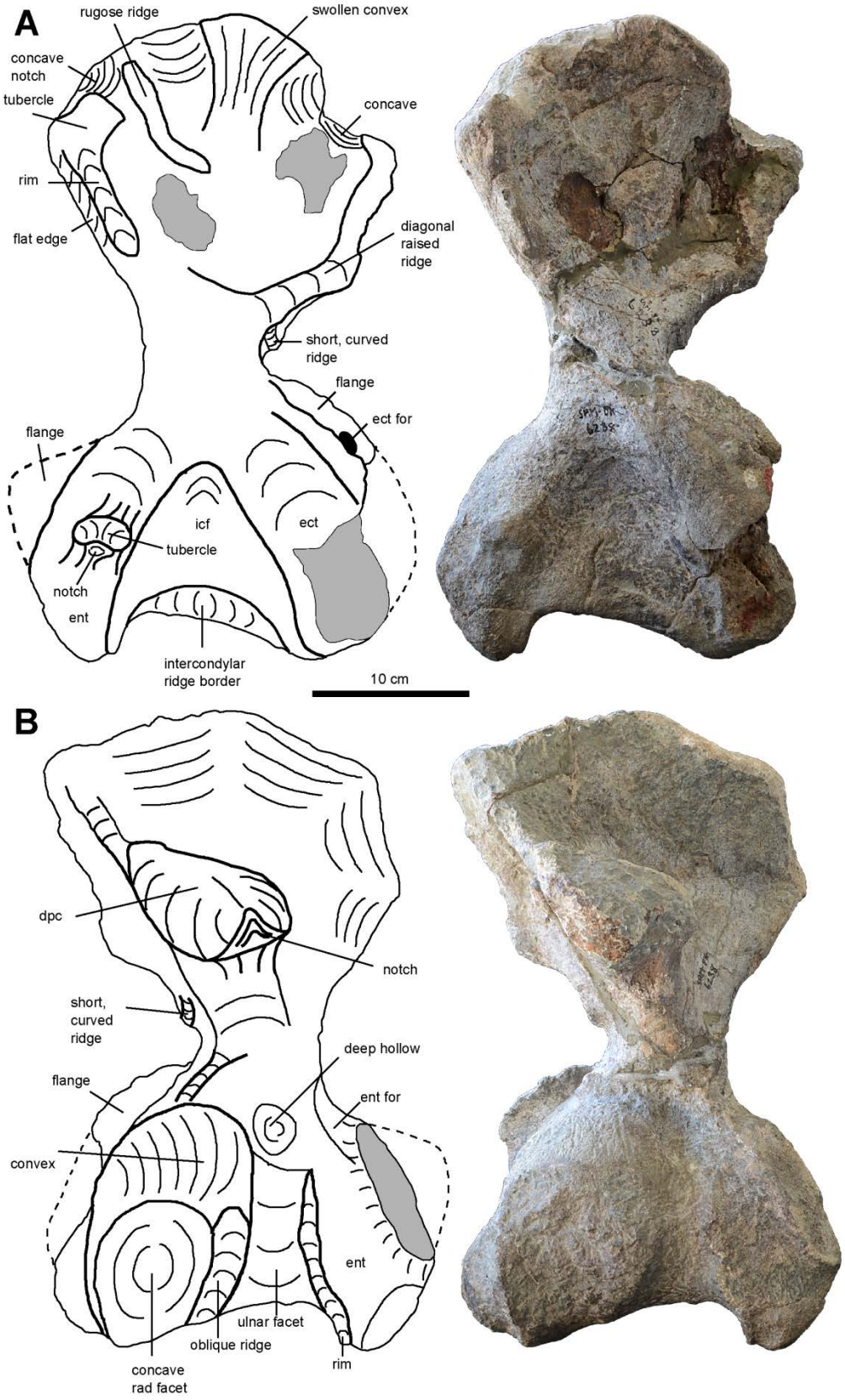


Figure 5.10: Photographs and interpretive drawings of the right humerus of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in dorsal view, and (B), in ventral view. Medial to the top of the page.

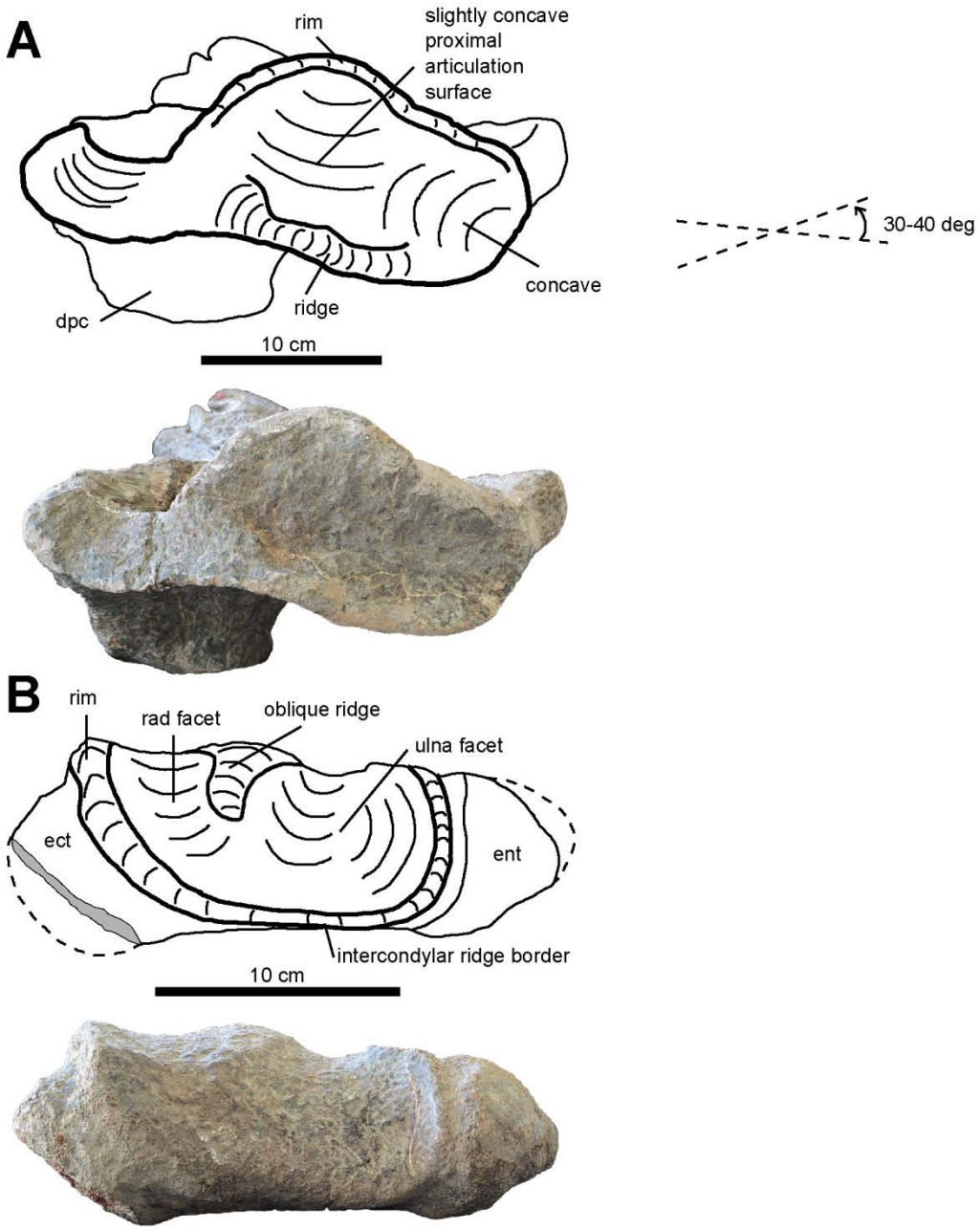


Figure 5.11: Photographs and interpretive drawings of the right humerus of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in proximal view, and (B), in distal view. Ventral to the top of the page.

The ulnar facet (trochlear ulnar groove, ulnar articulation surface) is a proximally tapering, elongated triangular depression and is much deeper than the radial facet, with the postaxial (posterior) margin formed by a distinct, raised, sharp-tipped pointed rim (Turner *et al.* 2015 character 101). Both the radial facet and the ulnar facet of the ventral surface of the humerus, are prevented from

reaching onto the distal side of the humerus by the transverse curved intercondylar ridge border at the distal-dorsal edge of the humerus (Figs.5.8B, 5.11B) (Turner *et al.* 2015 character 100).

Only the postaxial portion of the proximal half of the humerus of the holotype is preserved. As in all large middle Permian South African pareiasaurs, the dorsal side of the blade is gently convex and the ventral side deeply concave. The postaxial delto-pectoral crest is not preserved on the holotype, but SAM-PK-6238 shows a massive, robust delto-pectoral crest (Fig. 5.10) and the proximal humerus measures 275 mm (right humerus) and 284 mm (left humerus), including the delto-pectoral crest . Distally it is swollen to 90 mm in anteroposterior width, much wider than the narrower condition of *Embrithosaurus*. The ventral surface is roughened and irregular, and overall convex is “heart shaped” and has a notch on the ventrodistal corner. The ventral surface lacks the long, central, ventral groove of *Embrithosaurus*. Preaxially the crest is very curved and rounded compared to the straighter preaxial side of *Embrithosaurus*.

The dorsal side of the proximal blade of SAM-PK-6238 shows the typical prominent large, diagonally oblique, raised ridge, extending distally from the anterodorsal side of the proximal articular surface to the shaft, with expanded proximal and distal portions as seen in co-occurring middle Permian South African pareiasaurs (Fig. 5.10). A short (45 mm), crescent-shaped, ridged insertion point for muscle attachment is present on the humeral shaft, distal of the thick oblique ridge, and is also present on the holotype of *Bradysaurus baini*, but not in *Embrithosaurus*. A, short, thin, roughly straight ridge, also present in *Embrithosaurus* and *Bradysaurus baini*, is seen anterior to the dominant thick triangular ridge (Fig. 5.9).

The postaxial side of the proximal blade of SAM-PK-6238 is thickened, with raised rims, and presents a very flat and slightly concave postaxial surface, as in *Embrithosaurus* and *Bradysaurus baini* (Figs. 5.9, 5.10). A rugose, oblique ridge

extends from a prominent notch and tubercle on the proximal-postaxial corner of the blade, to reach the central region of the dorsal face of the blade (Fig. 5 .9, 5.10) also present in *Embrithosaurus* and *Bradysaurus baini.*

The proximal articulation surface of the head of the humerus forms a s-shaped surface, generally flat, but with a much deeper concavity medially towards it central portions (on the holotype) than seen in *Embrithosaurus* suggesting a larger cartilaginous cap. SAM-PK-6238 shows a very deep cavity with the central ventral margin projecting 30 mm above the concave surface. The proximal articulation surface of the holotype is much narrower than in *Embrithosaurus,* but in SAM-PK-6238 it is identical to *Embrithosaurus.*

Radius (Fig. 5.12)

The holotype preserves no radius. SAM-PK-6238 preserves the right radius in good condition, apart from a large, cleanly sheared off proximal lateral piece.

The right radius of SAM-PK-6238 is robust and stout**,** slightly larger and 30 mm longer (250 mm in total) than the radius of the holotype of *Embrithosaurus*, about the same length as the holotype of *Bradysaurus baini* (245mm). The radius is significantly shorter than the much longer ulna. The shaft is very narrow, roughly oval to rectangular in cross section. Interestingly, the radius of SAM-PK-6238 is non-symmetrical as the distal half off the right radius is ventrolaterally expanded. This morphology is not seen in *Embrithosaurus* or *Bradysaurus baini* (best observed in anterior or posterior view Fig. 5.12A, B). As a result, distally, the radius is mediolaterally wider (120 mm) than that of the holotypes of *Embrithosaurus* (100 mm) and *Bradysaurus baini* (113 mm).

The distal radius is wider (by 10 mm, measuring 120 mm), than the proximal end (110 mm), which contrasts with the condition in *Embrithosaurus* and *Bradysaurus baini* where the radii are slightly wider proximally than distally.

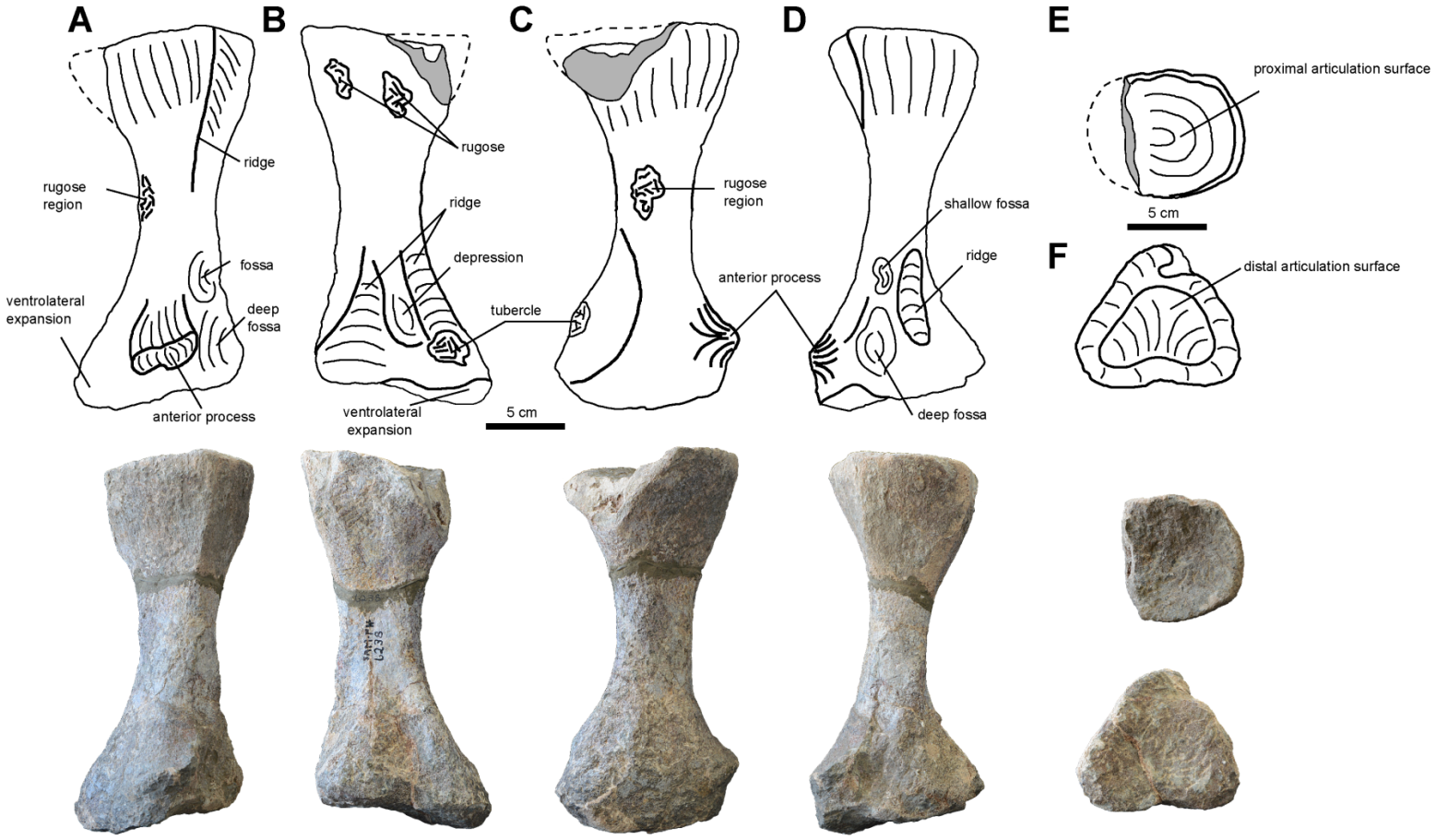


Figure 5.12: Photographs and interpretive drawings of the right radius of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in anterior view, (B), in posterior view, (C), in lateral view, (D), in medial view, (E), in dorsal view, (F), in ventral view. Dorsal to the top of the page in (A), (B), (C) and (D). Anterior to the top of the page in (E) and (F).

Assuming a horizontal proximal articulation surface, the distal articulation surface of the radius is oblique, and creates an angle of about 20^0 above a horizontal plane (Fig. 5.12D) similar to that of *Embrithosaurus* and *Bradysaurus baini*.

Posteriorly, the proximal portion of the radius is convex and has two rugose areas (Fig. 5.12B). The distal portion is shallowly concave between the lateral and medial borders of the radius, which form two vertical ridges, and there is a low, indistinct rugose tubercle near the distal edge of the lateral ridge (Figs. 5.12 B, C).

Along the medial side of the distal portion of the shaft is a distinct ridge, vertically and slightly posteriorly oriented, extending from near the base of the radius (tapering dorsally) and extends midway up the shaft. The vertical ridge is damaged, and would have been larger in life (Fig. 5.12D). A deep, circular, fossa, 25 mm in diameter is present, low on the medial side of the radius, anterior to the ridge and a shallow, small fossa is present above. This ridge does not appear to be present in *Embrithosaurus* or *Bradysaurus baini*.

The proximal (dorsal) articulation surface of the radius is ovoid, and the concavity that articulates with the radial condyle of the humerus is typically deep with thin, raised borders (Fig. 5.12E).

Consistent with *Embrithosaurus*, the distal (ventral) articulation surface is flat, slightly concave, and forms a triangle in cross section (Fig. 5.12F). The anterior process of the radius, is larger and more distinct than that of *Embrithosaurus*. It measures 40 mm mediolaterally, 25 mm dorsoventrally and projects 10 mm anteriorly above the surface of the radius.

As in *Embrithosaurus*, the proximal and distal ends of the radius of SAM-PK-6238 are not in the same plane, but form an angle of about 45^0.

Ulna (Figs. 5.13, 5.14, 5.15)

The holotype of *Nochelesaurus* preserves no ulna. Referred specimen SAM-PK-6238 has a well preserved right ulna. As in all large pareiasaurs, the ulna is mediolaterally narrow, with a proximal half that is significantly mediolaterally thickened to support the large proximal articulation surface.

As in other middle Permian pareiasaurs, the straight postaxial border of the ulna is thickened and swollen to form a proximally widening cylindrical bar, covered by long, straight rugose ridges for muscular attachment (Boonstra 1932c) Deep, vertical, concave regions not present anterior to the bar, on both the medial and lateral surfaces of the ulna. In *Nochelesaurus*, the postaxial bar consists of two regions separated by a bend on the postaxial side: the distal portion of the bar is long, almost cylindrical, gently rugose, narrow, and gradually widens mediolaterally proximally. The proximal portion is flatter, with sharper more square-edged sides, massive rugose ridges. The ulna of SAM-PK-6238 measures 370 mm in dorsoventral length (as does the right ulna of the holotype of *Bradysaurus baini*), which is significantly longer than the right ulna of *Embrithosaurus* (295 mm). The proximal portion of the postaxial bar, above the postaxial bend, measured obliquely, is much longer, in SAM-PK-6238 (90 mm) and in the holotype of *Bradysaurus baini* (90 mm) than in the holotype of *Embrithosaurus* (30 mm). The proximal articulation surface is also longer in SAM-PK-6238 (130 mm) and in the holotype of *Bradysaurus baini* (130 mm) than in the holotype of *Embrithosaurus* (90 mm).

Distally, the small distal articular surface of the ulna is convex and elongated, and faces ventromedially.

The sigmoidal (radial) notch is 50–60 mm deep and its dorsal margins are formed by the lateral and medial and sigmoidal processes (Fig. 5.14A). The lateral sigmoidal process is covered with a large piece of uncleared matrix on the anterolateral side, below the proximal articular surface of the ulna.

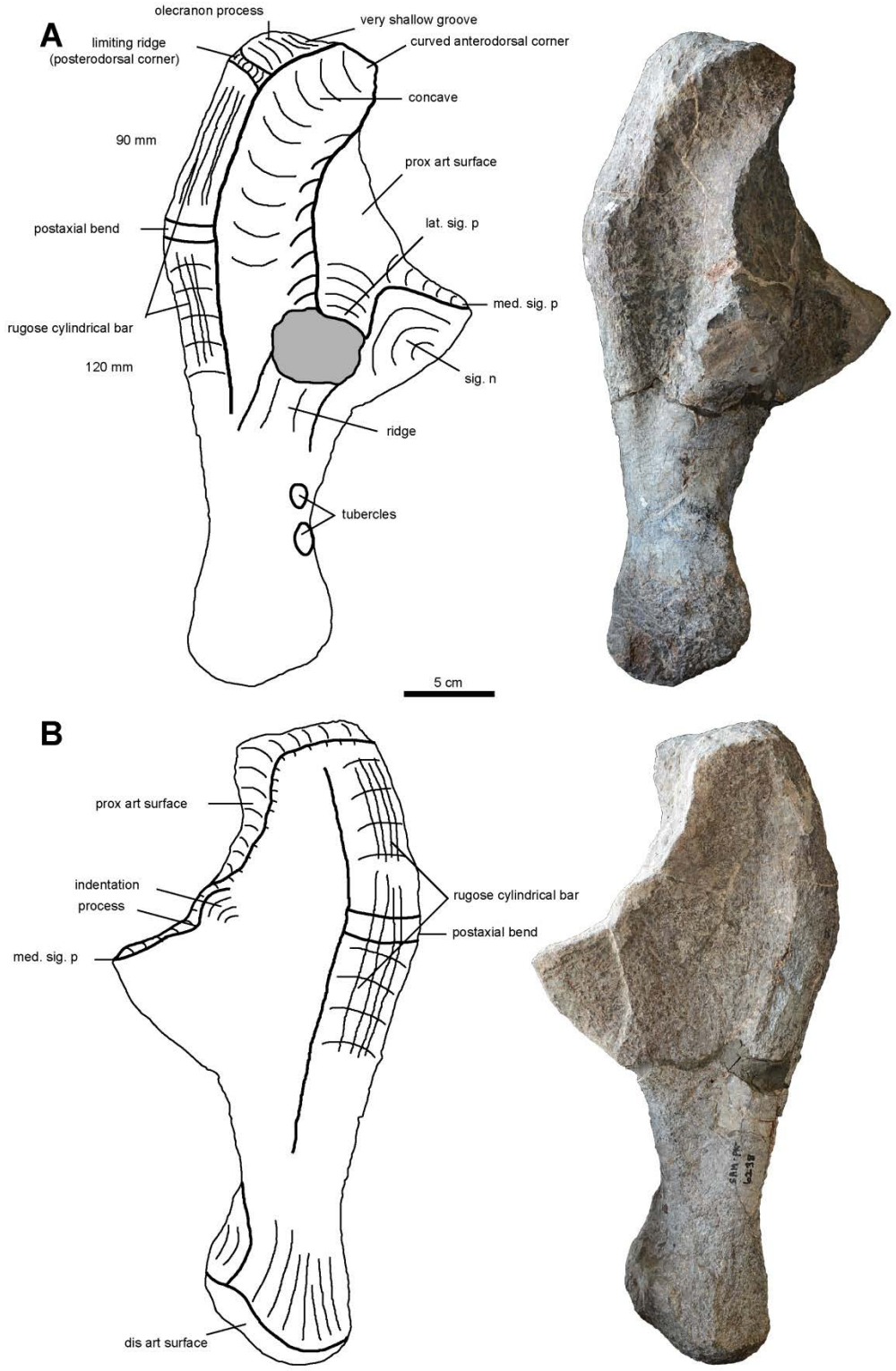


Figure 5.13: Photographs and interpretive drawings of the right ulna of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in lateral view, and (B), in medial view. Proximal to the top of the page.

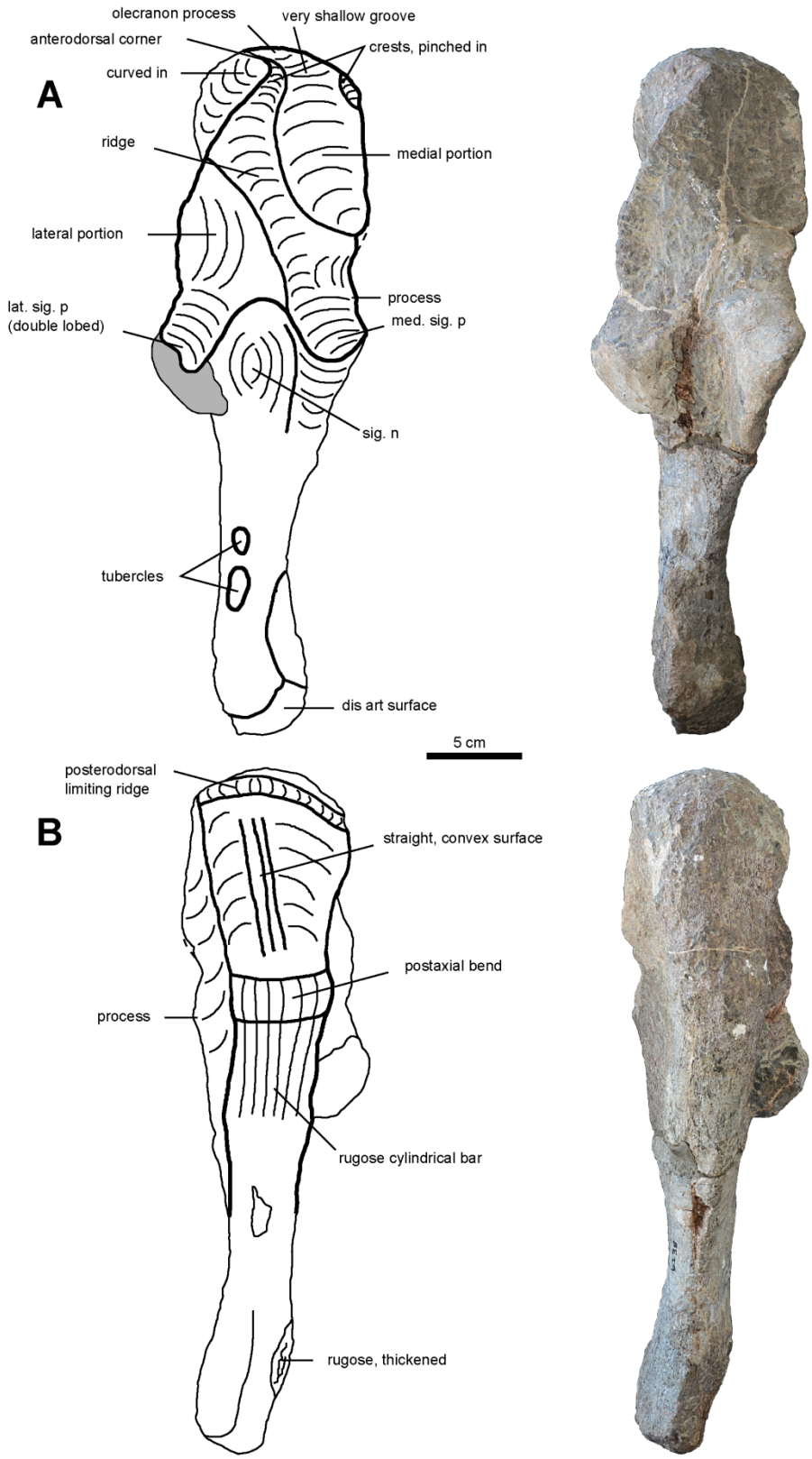


Figure 5.14: Photographs and interpretive drawings of the right ulna of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in anterior view, and (B), in posterior view. Proximal to the top of the page.

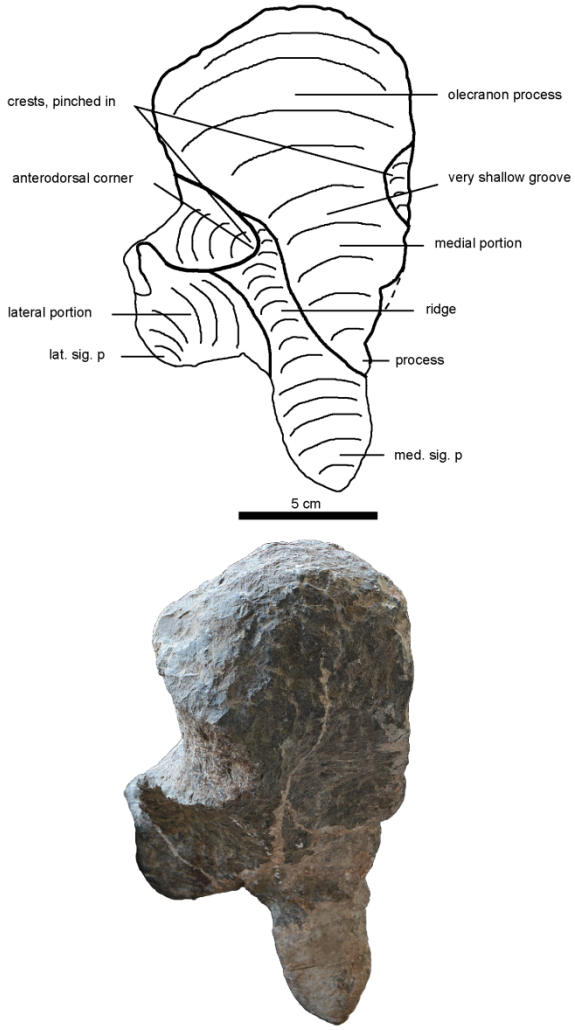


Figure 5.15: Photograph and interpretive drawing of the right ulna of SAM-PK-6238 (*Nochelesaurus alexanderi*), in proximal view. Posterior to the top of the page.

The medial process extends further preaxially from the base of the sigmoidal notch (60 mm) than the lateral process extends laterally (35 mm). The medial process is narrow (35 mm at its base) and forms a triangular projection, which tapers to end in a rounded tip. The lateral process is wider (45 mm at its base), tapers less than the medial process, and ends in a blunt 35 mm wide, double lobed projection, with a slight notch between the lobes. At the postaxial base of the medial sigmoidal process, on the medial rim of the proximal articular surface, is a small process, with an indention above it (Fig. 5.13B, 5.14A). This rim process is similar to the same structure present on the ulna of the holotype of *Embrithosaurus.*

The proximal articular surface of the ulna of SAM-PK-6238 is complex (Fig. 5.14A). A swollen, oblique, ridge (20 – 30 mm wide) divides the surface into equal-sized medial and lateral portions. This dividing ridge is not present in *Embrithosaurus* where the entire articular surface is gently convex. The lateral portion is gently, shallowly concave and faces anterolaterally. The medial portion forms a deeper concavity, is positioned more proximally, and faces directly anteriorly (preaxially) (Turner *et al.* 2015 character 105).

At the anterodorsal corner of the ulna, the proximal articulation surface is laterally constricted ('pinched in'), especially laterally, where the lateral surface of the ulna is concave and curves medially 20 mm, narrowing the articular surface. Here the lateral and medial rims of the proximal articulation surface are slightly raised (5 mm) and form small, short olecranon crests (similar to *Embrithosaurus,* but much lower) and the articular surface forms a very shallow, wide groove between the crests. The anterodorsal constriction evident in SAM-PK-6238 is not present in the holotype of *Embrithosaurus*. In SAM-PK-6238, the short (5 mm high) anterodorsal crests and shallow groove do not extend onto the proximally side of the ulna, whereas in the holotype of *Embrithosaurus*, they do extend proximally and over onto the postaxial (posterior) surface of the ulna.

Above the constriction point, on the proximal side of the ulna, is a bulbous, low (20 mm high) olecranon process, convex and smoothly curved, which terminates postaxially (posteriorly) at the posterodorsal corner of the ulna, which is square-edged and has a transverse limiting ridge (Figs. 5.13A, 5.14B). The limiting ridge separates the olecranon process from the rugose, proximal portion of the postaxial cylindrical bar.

Boonstra (1932c:472) declared that the ulna of SAM-PK-6238 has "hardly any olecranon process". The olecranon process is low (20 mm high) and convex on the proximal side of the ulna only and does not project anteriorly beyond the articulation surface (Turner *et al.* 2015 character 106).

The olecranon on the holotype of *Bradysaurus baini* is much larger and projects high proxmally and anteriorly.

Two small but distinct tubercles (<10 mm in diameter each) are present on the preaxial border of the shaft, 80 mm and 110 mm above the distal-most edge of the ulna. These are not present in the holotype of *Embrithosaurus*, although this could be the result of poor preservation or over preparation of the holotype specimen.

5.4.3 Hindlimbs

Femur (Figs. 5.16, 5.17, 5.18)

The right femur of SAM-PK-6239 is almost completely preserved and in good condition, except for a long, narrow piece of the postaxial flange and a portion of the articular facet of the medial condyle. I apply the "obliquely outwardly oriented" life position for the femur, ascribed to all large middle Permian South African pareiasaurs (Haughton & Boonstra 1930b: 303) as a result of the "permanently bent knee".

As in the holotype of *Embrithosaurus*, the femur of SAM-PK-6239 is dorsoventrally compressed (420 mm long) with an expanded proximal end (200 mm wide) oval shaft in cross section (120 mm anteroposteriorly, by 70 mm dorsoventrally) and two robust distal condyles (155 mm anteroposteriorly wide) which is slightly narrower than the holotype of *Embrithosaurus* (170 mm) and much narrower than the holotype of *Bradysaurus baini* (190 mm) The torsion of the planes between the proximal and distal articulations is 30^0, similar to the holotype of *Embrithosaurus* and within the range of *Bradysaurus baini* (10-30^0).

The proximal articulation surface of the head of the femur is anteroposteriorly flattened. Compared to *Embrithosaurus*, the surface has a much deeper concavity over the middle portion of its surface and its elongated "tear-drop" shape is much narrower. But since the proximal articulation surface was covered by a cartilage cap in life, this difference is probably not significant. The

articulation surface is well defined with raised, rimmed borders. Postaxially, the surface curves slightly distally and terminates before a very shallow notch (as in *Embrithosaurus* and *Bradysaurus*), after which the postaxial border curves much more strongly distally. Preaxially, the surface is gently convex and curves distally before terminating at a 90^0 sharp bend (Turner *et al.* 2015 character 120).

The femoral head juts anteriorly (preaxially) out of the shaft of the femur and creates an angle similar to that of *Embrithosaurus* and *Bradysaurus*, of about 40^0 from the plane of the femoral shaft. This relatively flat femoral head supports a more horizontal femur orientation and a sprawling limb posture.

The major (external) trochanter of SAM-PK-6239 is small (Turner *et al.* 2015 character 121). Posteriorly the major trochanter hardly protrudes beyond the postaxial (posterior) shaft of the femur (<5 mm), and projects much less than the condition seen in *Embrithosaurus* (which projects 30 mm posteriorly) even when taking into account that the posterior edge of the postaxial flange of SAM-PK-6239 is eroded over much of its length (Fig. 5.16) (Turner *et al.* 2015 character 122). Dorsoventrally it similarly swollen to 35 mm in width, comparable with that of the holotypes of *Embrithosaurus* and *Bradysaurus baini*. The notch on the proximal-postaxial corner of the femur is shallow, as in the holotypes of *Embrithosaurus*, and *Bradysaurus baini*. Distally, *Nochelesaurus*, as *Bradysaurus*, lacks the deep notch, and has no or only a very shallow notch on the on the postaxial flange separating the major trochanter from the postaxial shafts (the notch is deep only in *Embrithosaurus)*.

There is a prominent tubercle on the proximal-postaxial corner of the femur, immediately dorsal to the postaxial edge (slight) notch near the major trochanter. This tubercle is not seen in *Embrithosaurus or Bradysaurus baini*.

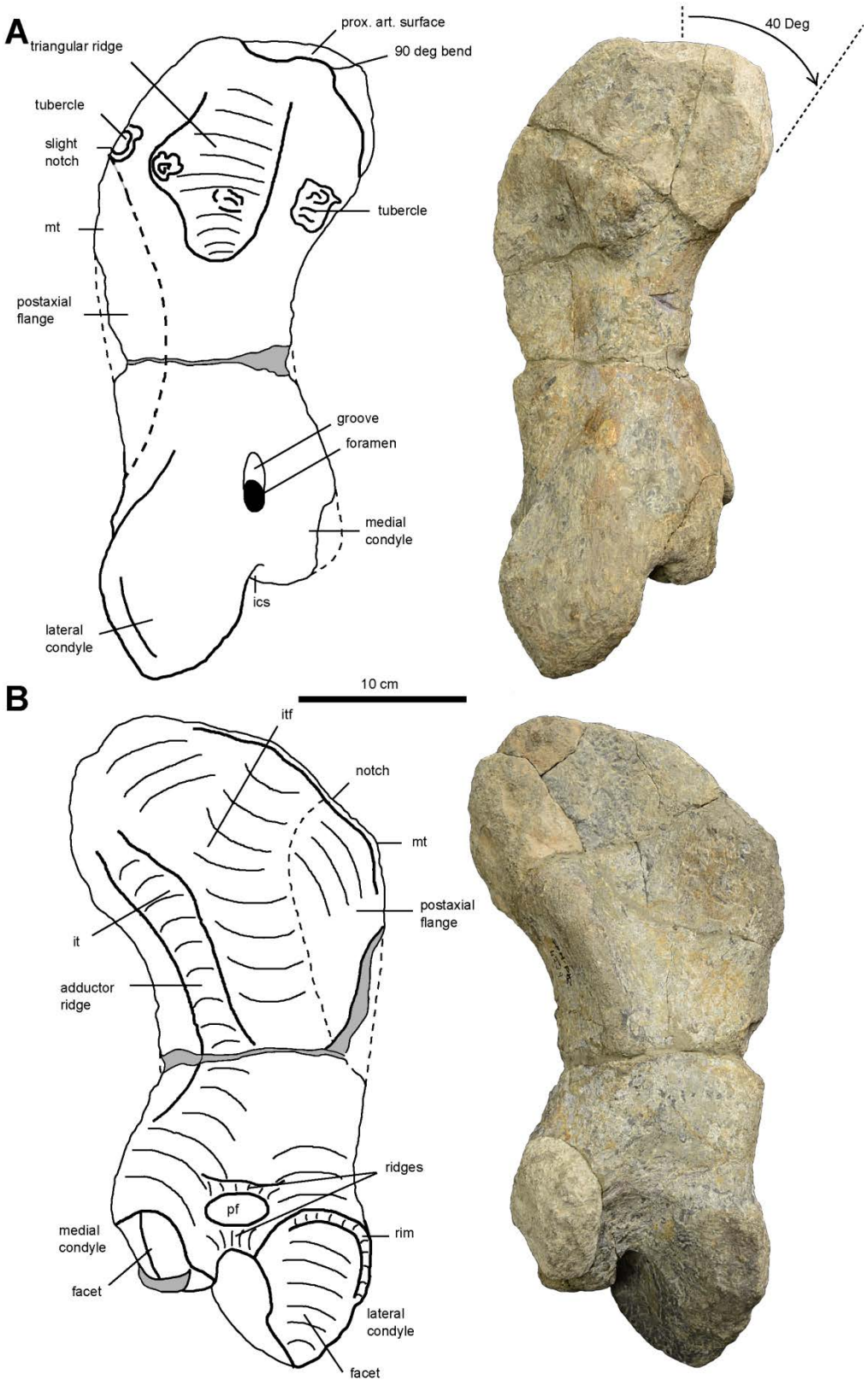


Figure 5.16: Photographs and interpretive drawings of the right femur of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), (A), in dorsal view, and (B), in ventral view. Proximal to the top of the page.

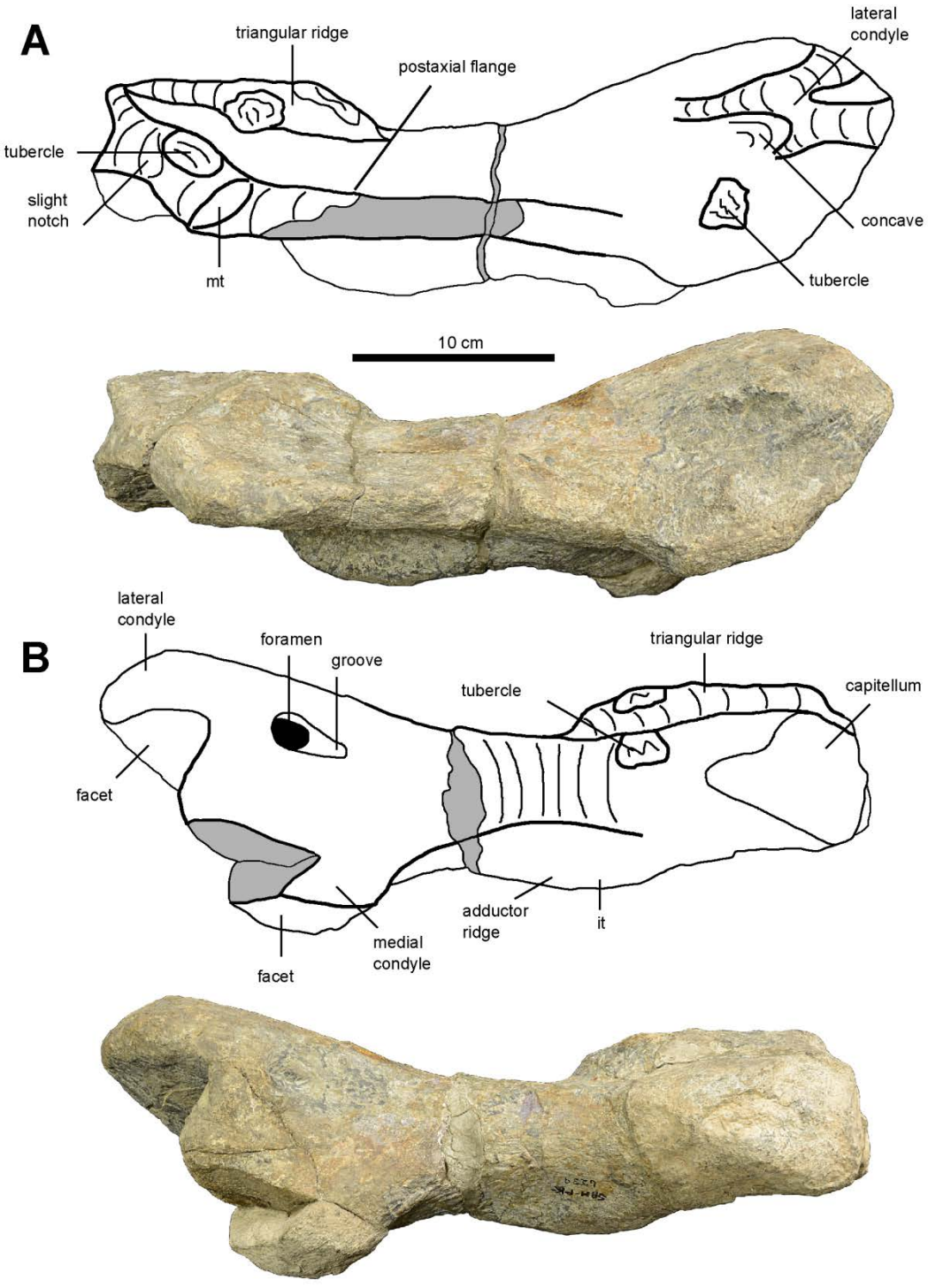


Figure 5.17: Photographs and interpretive drawings of the right femur of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), (A), in posterior view, and (B), in anterior view. Dorsal to the top of the page.

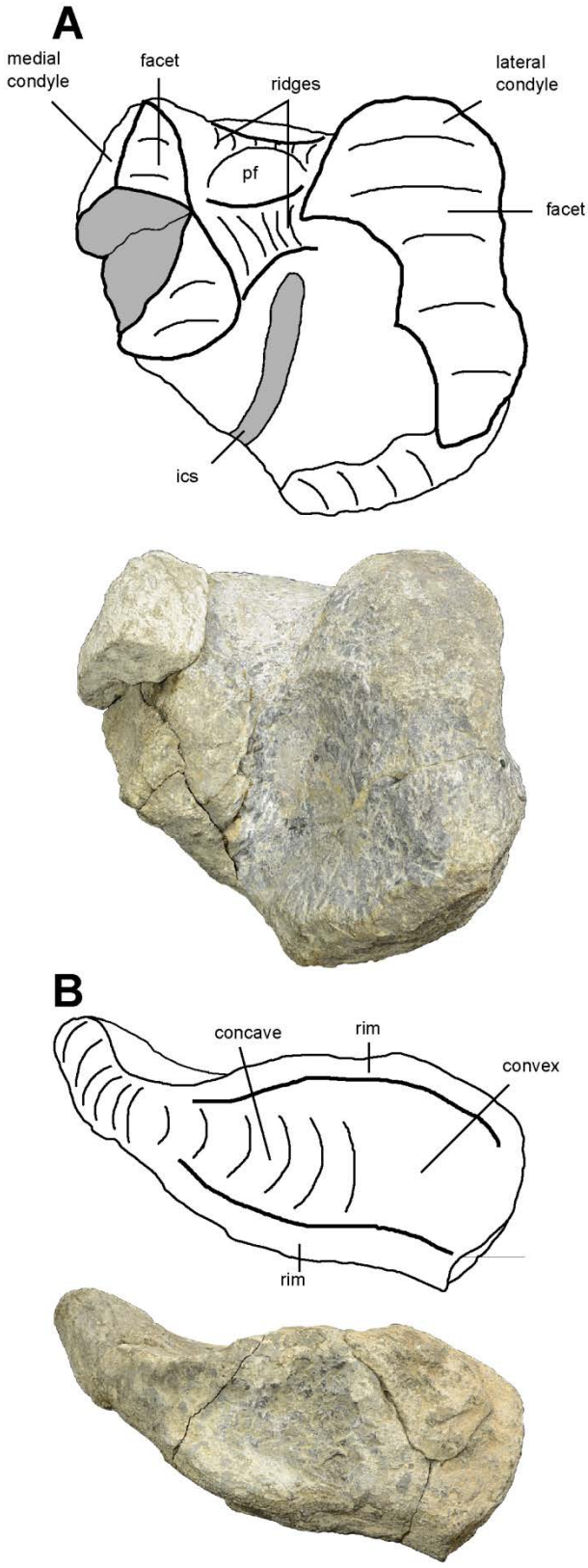


Figure 5.18: Photographs and interpretive drawings of the right femur of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), (A), in distal view, and (B), in proximal view. Ventral to the top of the page.

The morphology of the postaxial flange is indistinguishable from that of *Embrithosaurus*. The flange extends distally from the major trochanter to cover the entire length of the shaft of the femur (Turner *et al.* 2015 character 123). As in *Embrithosaurus*, the damaged postaxial edge of the flange appears to be straight (not concave) in both dorsal and ventral view, and the femur is consistently extremely wide over the length of the shaft (Turner *et al.* 2015 character 124).

The rugose, broad, low, triangular ridge for muscular attachment on the dorsal surface of the proximal portion of the femur between the major trochanter and the preaxial edge of the femur, is similar to *Embrithosaurus* (Fig. 5.16). As in *Embrithosaurus*, a small tubercle is present anterior to this ridge, on the preaxial border.

The internal (minor) trochanter near the preaxial edge of the femur is roughly straight, and very slightly curved over its entire length (Turner *et al.* 125). This straight morphology is very different from that of the internal trochanters of *Embrithosaurus* and *Bradysaurus baini* which have curved proximal regions that are concave anteriorly and convex posteriorly. The internal (minor) trochanter is also much lower and less ventrally protruding compared to the internal trochanters of *Embrithosaurus* and *Bradysaurus baini*, and extends only 10 mm from the shaft of the femur.

Distally, between the large lateral condyle and the small medial condyle, the intercondylar sulcus is deep. On the dorsal surface is a shallow groove that holds a large nutritive foramen. The popliteal fossa on the ventral surface is large and wide.

It is important to note that the large lateral condyle extends distally very far in *Nochelesaurus*. In the holotype of *Embrithosaurus* it extends 30 mm beyond the edge of the medial condyle, but in the holotype of *Nochelesaurus* it extends 70 mm. A large piece of the small medial condyle is not preserved. The distal articular surfaces are very similar to those of *Embrithosaurus*

Tibia (Figs. 5.19, 5.20)

The right tibia of both the holotype of *Nochelesaurus* and SAM-PK-6238 are preserved. As in all large middle Permian pareiasaurs, the tibia is dumbbell shaped, with a constricted shaft and greatly expanded proximal and distal ends, with the proximal end widest. The tibia is anteroposteriorly flattened.

In the holotype, the tibia is hardly twisted with the planes of the proximal and distal expansions in almost the same plane, only about 10^0 apart. However, in the referred SAM-PK-6238, the planes are about 40^0 apart, indicating a wide range of twisting in this taxon.

On the posterior side of the tibia, proximal and distal depressions are present and the diagonal ridge that extends between these depressions is relatively strongly developed in the referred *Nochelesaurus* (SAM-PK-6238), but is slightly less prominent in the holotype of *Nochelesaurus*. A rugose region is present in all tibia of *Nochelesaurus* on the proximal lateral border of the proximal depression. This rugose region is also present in *Embrithosaurus* and *Bradysaurus baini*.

As in *Embrithosaurus*, the proximal and distal articulation surfaces of the tibia of *Nochelesaurus* are especially rough, highly rugose and irregular, suggesting a thick cartilaginous covering was present. This has also been reported in *Honania* (Xu *et al.* 2015).

The cnemial crest of the holotype is anteriorly very low compared to that of the other middle Permian taxa, extending anteriorly only 33 mm beyond the floor of the lateral excavation, but this is probably due to anteroposterior compression or erosional damage to the anterior surface of the crest, since the right tibia of SAM-PK-6238 has a very prominent cnemial crest (48 mm), similar in height to the holotypes of both *Embrithosaurus* and *Bradysaurus* (45 mm) (Turner *et al.* 2015 character 126).

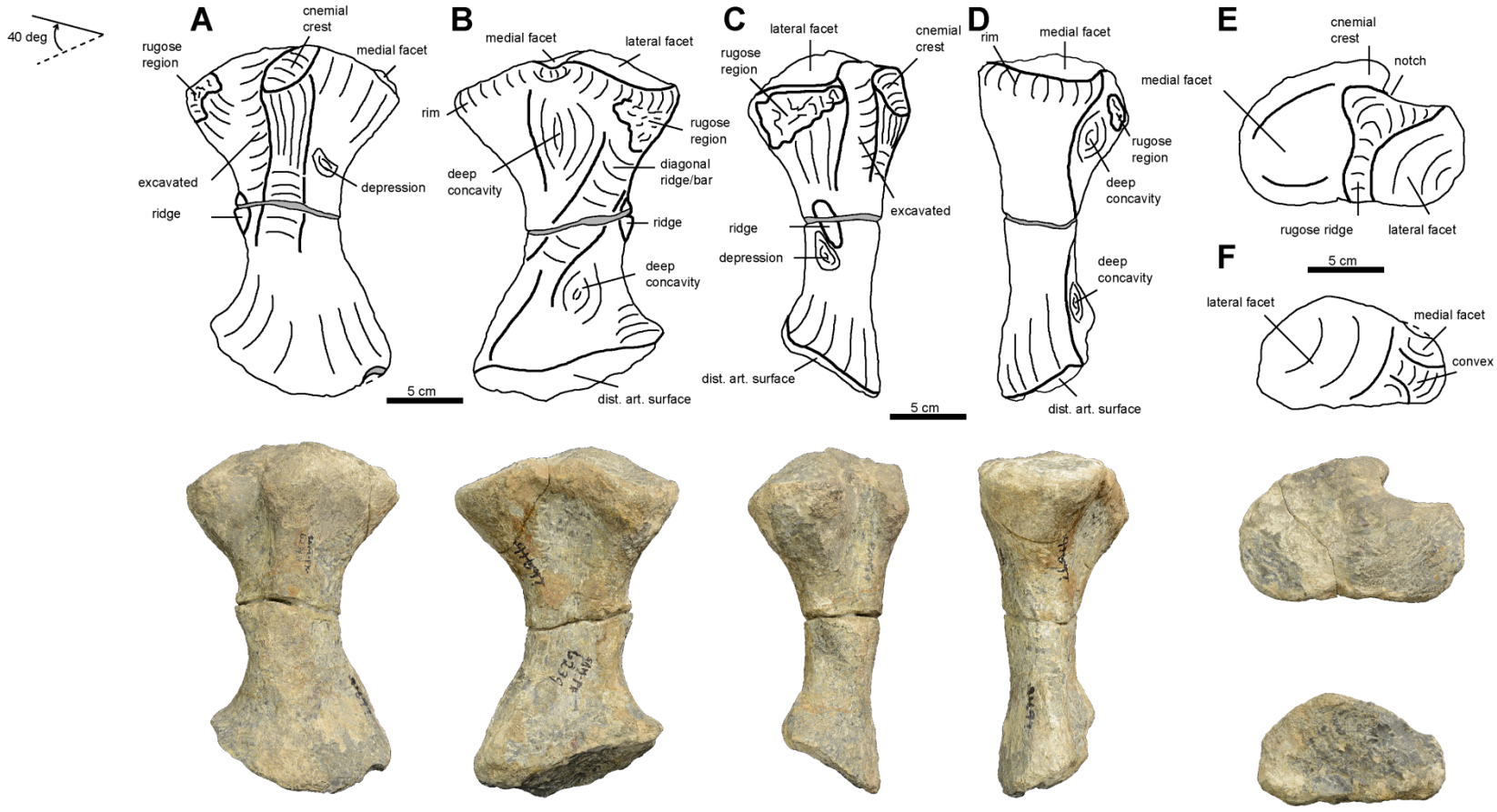


Figure 5.19: Photographs and interpretive drawings of the right tibia of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239) (A), in anterior view, (B), in posterior view, (C), in lateral view, (D), in medial view, (E), in dorsal view, (F), in ventral view. Proximal to the top of the page in (A), (B), (C) and (D). Anterior to the top of the page in (E) and (F).

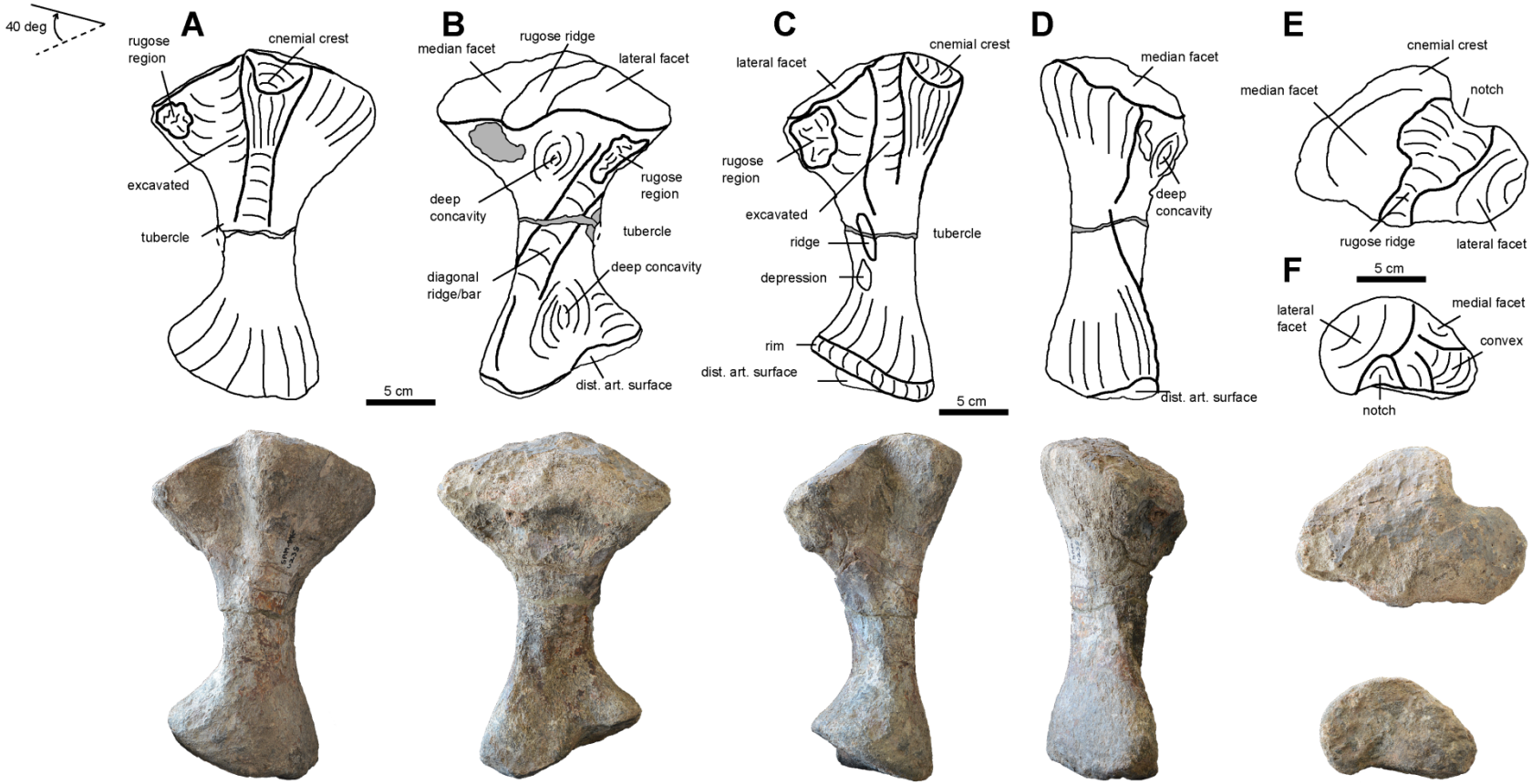


Figure 5.20: Photographs and interpretive drawings of the right tibia of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in anterior view, (B), in posterior view, (C), in lateral view, (D), in medial view, (E), in dorsal view, (F), in ventral view. Proximal to the top of the page in (A), (B), (C) and (D). Anterior to the top of the page in (E) and (F).

On the anterior face of the tibia of the holotype of *Nochelesaurus*, the cnemial crest twists and extends laterally to slightly overhang the deep vertical excavation that dominates the anterior tibia. This overhang is probably an artefact due to compression in the holotype, because it is absent in referred *Nochelesaurus* specimen SAM-PK-6238 (and all other middle Permian pareiasaurs).

The proximal tibia of the holotype is only 155 mm mediolaterally wide, whilst referred specimen SAM-PK-6238 is mediolaterally extremely wide (181 mm), confirming a wide range in *Nochelesaurus*.

Both *Nochelesaurus* tibial specimens show the proximal articulation surface carrying the oblique, curved, raised ridge which fits in the intercondylar sulcus groove of the femur, as very similar to that of *Embrithosaurus* and is wide, rugose and irregular. The surface is badly eroded in SAM-PK-6238. The large medial facet is slightly anteroposteriorly convex, faces primarily dorsally and slightly posteriorly. The smaller lateral facet is significantly bent and differently directed compared to the medial facet to face primarily dorsolaterally and slightly posteriorly and also slightly convex. The lateral and medial facets of the proximal articulation are therefore not on the same plane but are 40^0 apart.

The distal articulation surface of both specimens of *Nochelesaurus* is similar to that of all large middle Permian South African pareiasaurs. The lateral facet is large and flat to slightly concave, and the smaller medial facet comprises a convex, raised portion posteriorly and a very shallow, depressed, concave portion anteriorly. A small notch is present on the posterior margin of the distal articulation surface, between the lateral and medial facets.

Interestingly, only *Nochelesaurus* and *Bradysaurus baini* show the distal tibia as ventromedially expanded, with the ventrolateral side upturned or extended proximally, making the distal tibia mediolaterally wider than the condition seen in *Embrithosaurus.*

An elongated rugose ridge is present, just dorsal to a vertical depression, on the lateral edge of the shaft of the right tibia of SAM-PK-6239 and SAM-PK-6238. The ridge and depression are present in *Bradysaurus baini*, but only the depression is present in the holotype of *Embrithosaurus*.

Nochelesaurus, *Embrithosaurus* and *Bradysaurus baini* all show the proximal and distal articulation surfaces of the tibia to be strongly oblique and not horizontal.

Fibula (Fig. 5.21)

SAM-PK-6238 preserves the complete right fibula, which is gracile, long and slender, and is similar to the right fibula of the holotype of *Embrithosaurus* in morphology. The shaft is very narrow and triangular in cross section, with the distal end expanded much wider than the proximal end. The lateral side of the shaft is straight but the medial side is severely concave. As in *Embrithosaurus*, the medial side houses large rugose tubercles, both proximally and distally.

A thin, sharp, raised, elongated ridge for muscle attachment (10 mm wide, 80 mm long) is present on the anterior side of the shaft, comprising four to five small, rugose, projecting knobs. This ridge is not present on the fibula of the sub-adult sized holotype of *Embrithosaurus*, but is in the larger referred *Embrithosaurus* specimen CGP CBT 112, suggesting that it develops late in ontogeny.

The proximal articular surface forms a strongly convex arc in cross section. The distal articular surface forms an elongated four sided, roughly diamond-shape in cross section, with most of the surface forming a large, flat facet for articulation with the tarsus and the minority of the surface a raised, convex platform.The planes of the distal and proximal expansions are offset from each other by 45^{0}.

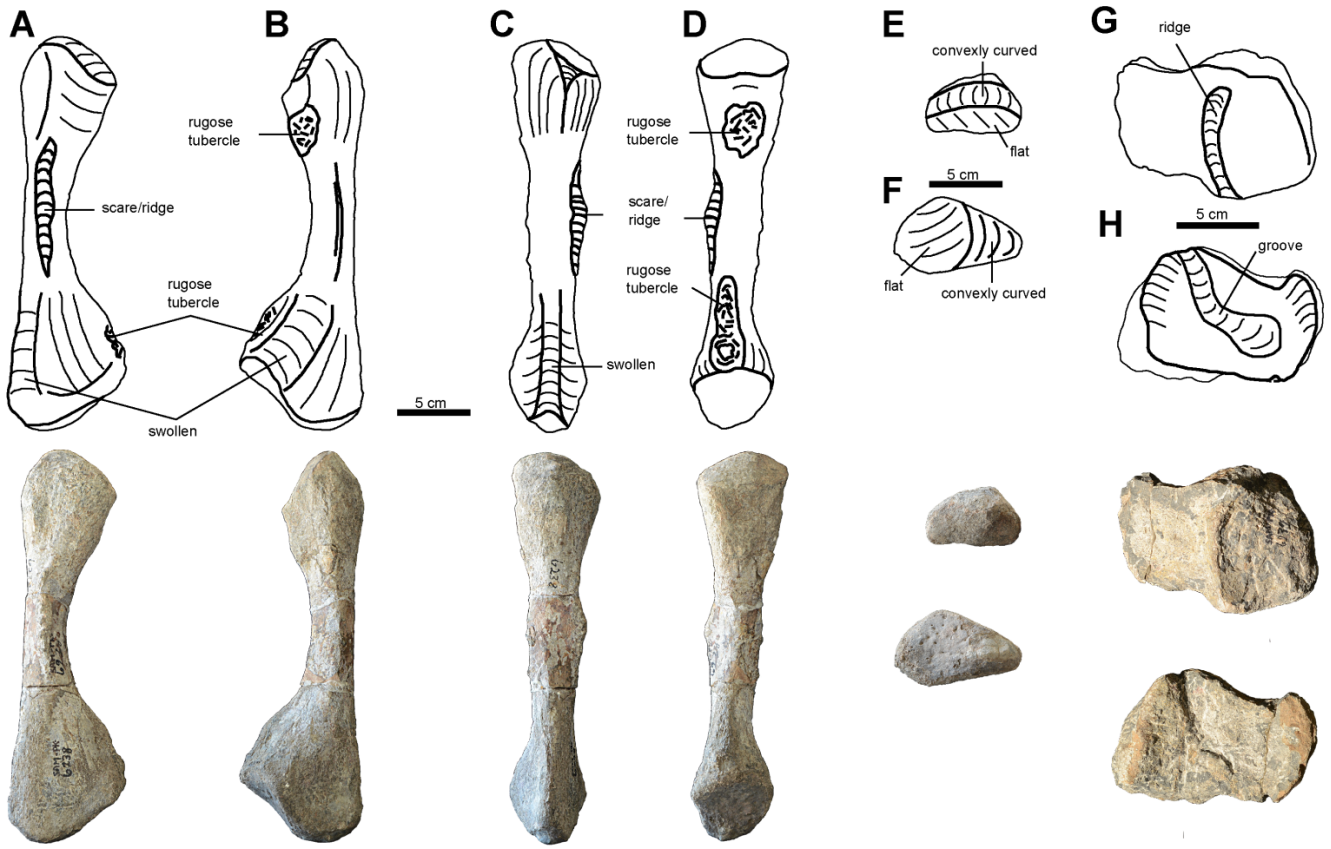


Figure 5.21: Photographs and interpretive drawings of the right fibula of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in anterior view, (B), in posterior view, (C), in lateral view, (D), in medial view, (E), in dorsal view, (F), in ventral view. Proximal to the top of the page in (A), (B), (C) and (D). Anterior to the top of the page in (E) and (F). Photographs and interpretive drawings of the astragalocalcaneum of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), (G), in dorsal view, (H), in ventral view. Anterior to the bottom of the page in (G) and (H).

Tarsus (Fig. 5.21)

The roughly rectangular astragalocalcaneum of the holotype of *Nochelesaurus* is similar to the astragalocalcania of both *Embrithosaurus* and *Bradysaurus baini*. Some damage and poor historic preparation hampers identification of the large foramen opening on both the dorsal and ventral surfaces, but a large foramen is always present in the astragalocalcaneum of this pareiasaurian group and was probably also present in *Nochelesaurus*.

The diagonal or oblique groove on the ventral surface is typical: open at one corner, shallow, extending and widening towards the centre of the bone. Unlike the condition in *Embrithosaurus* and *Bradysaurus baini*, the wide end near the centre of the bone is enclosed within well-defined edges. The dorsal articulation surface is dominated by a curved, 20 mm high, ridge, with tapering surfaces either side of the ridge.

5.4.4 Vertebral column and ribs

Lee (1994, 1997a) stated that the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239) included six caudal vertebrae. Despite a thorough search I was unable to find these, or any other vertebrae.

Referred *Nochelesaurus* specimen SAM-PK-6238 preserves presacral vertebrae comprising the anterior cervicals (axis, but no atlas), posterior cervicals (3rd to 5th vertebrae), and most of the dorsals (6th to 16th vertebra) in sequence. Four large, isolated neural spines are also preserved, however, they do not appear to fit onto any of the preserved first sixteen sequential vertebrae. In *Embrithosaurus* dorsal vertebrae comprise the sixth to nineteenth vertebrae. The vertebrae of SAM-PK-6238 are very poorly preserved, weathered and over prepared, especially the first seven in the sequence. All vertebrae are preserved as isolated separated elements, apart from the 11th to 13th vertebrae which are articulated.

Anterior cervical vertebrae (axis)

Axis (2nd vertebra) (Fig. 5.22) (labelled as "1" on the fossil)

The neural arch is sheared off at a very low level, leaving a posteriorly pointing, triangular bone break visible. The pleurocentrum of the axis is amphicoelous and disk-like, with deeply concave anterior and posterior surfaces and is possibly notochordal. Similar to the axis of *Embrithosaurus*, the body of the pleurocentrum narrows anteroposteriorly ventrally. Positioned anteroventrally on either side of the midline, the anterior rim of the pleurocentrum has anteroventrally facing, oval, faceted surfaces (Fig. 5.22B). A deep transverse groove extends on the ventral surface between the anterior and posterior rims. On the anterior rim of the lateral pleurocentrum, the diapophysial process for articulation with the head of the ribs, is short and laterally directed, as in *Embrithosaurus*.

Dorsal to the diapophysis, is the anterodorsally directed process of the prezygapophyses with its articular facet damaged. The postzygapophyses are very short and extend horizontally only a short distance from the posteromedial corner of the prezygapophyses.

The neural canal is covered posteriorly by an unidentified small, thin, broken bone fragment, along with a fragment of a small osteoderm. Anteriorly, the canal is filled with matrix but appears to be dosoventrally flat.

Posterior cervical vertebrae (3rd to 5th vertebrae) (Fig. 5.22) (labelled as "2", "3", and "4" on the fossils respectively)

Apart from the 3rd vertebra being smaller, the 3rd, 4th and 5th vertebrae share a number of characteristics. Compared to the dorsal vertebrae, the posterior cervical vertebrae are mediolaterally very narrow, as a result of very short and small pre- and postzygopophyses and differences in the parapophysis and the diapophysis.

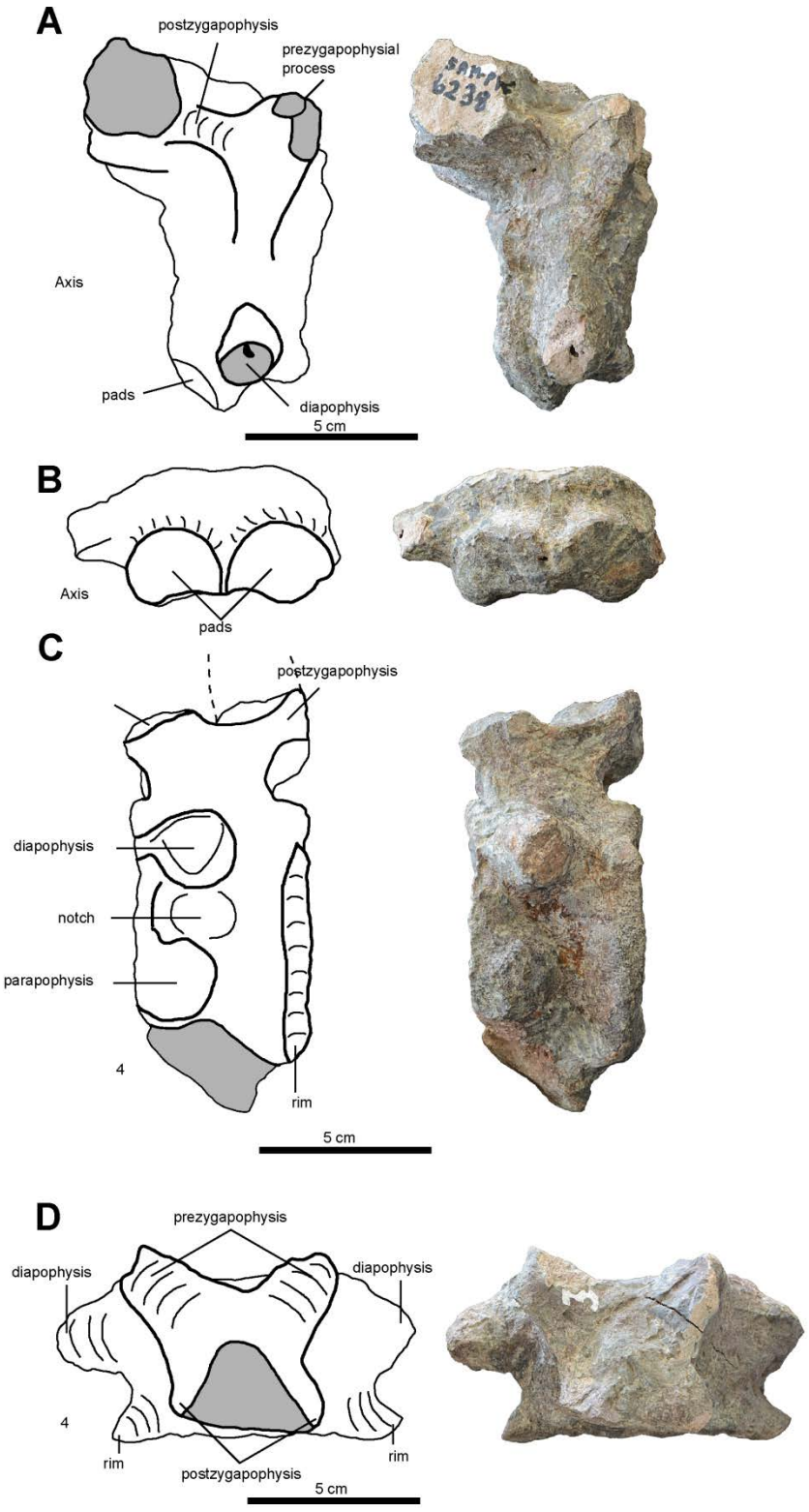


Figure 5.22: Photographs and interpretive drawings of the vertebrae of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), axis in right lateral view, (B), axis in ventral view, (C), 4th vertebra in left lateral view, (D), 4th vertebra in dorsal view. Dorsal to the top of the page in (A) and (C), anterior to the top of the page in (B) and (D).

Laterally, on the anterior rim of the centrum of the fourth vertebrae, two distinct processes carry the articular facets for the heads of the ribs: very low down, the parapophysial facet for articulation with the ventral part of the head is knob-like, rectangular with relatively sharp edges, slightly vertically elongated, and situated on a process that extends up to 14 mm laterally, forming part of the anterior border of the centrum.

Higher up on the lateral rim, the diapophysial facet, which articulates with the dorsal part of the head of the rib, is also rectangular with sharp edges, and positioned 7mm more posteriorly than the parapophysis**,** and on a process that extends laterally and slightly posteriorly, 20 mm. As in *Embrithosaurus*, these two process are linked by the anterior rim of the centrum which is thickened into a ridge, with a deep notch behind the ridge. A vertical groove separates the diapophysial and parapophysial processes from the posterior rim of the centrum, which is thickened and laterally flared posteriorly.

Similar to *Embrithosaurus* the anteroventral border of the fifth centrum, shows a wide, flattened area, which tapers posteriorly to form a longitudinal midline ridge.

The fourth and fifth centra are amphicoelous, with the anterior and posterior sides equally concave, and the posteroventral surface of each centrum is slightly swollen and convex, producing a rounded posterior lip-like protrusion. The fourth vertebra is possibly notochordal as the central hole of the centrum is very deep, yet still filled with matrix. The neural canal is large and ovoid in cross section and slightly dorsoventrally flattened.

The processes bearing the prezygapophyses are very slender, and short on the fourth and fifth vertebrae. They have mediolaterally narrow and anterposteriorly elongated dorsally facing articular facets. The postzygapophyses are well developed on only the fifth vertebra and extend posterolateraly from the posterolateral base of the neural spine.

Only the 5th vertebra preserves a partial anteroventral portion of the neural spine and is triangular in cross section (in contrast, the fifth neural spine of *Embrithosaurus* is diamond-shaped), anteriorly pointing, with a sharp to rounded anterior edge. The height of the neural spine cannot be determined. It is not possible to confirm the slant of the neural spines of the posterior cervical vertebrae, which are forward leaning in *Embrithosaurus.*

Dorsal vertebrae (6th to 16th vertebrae) (Figs. 5.23, 5.24, 5.25)

The anterior dorsal vertebrae (6th to 10th vertebrae) are poorly preserved and weathered, and the posterior dorsal vertebrae (11th to 16th vertebrae) are much better preserved.

All the dorsal vertebrae are very similar, varying only in the size and proportions of certain features along the vertebral column. The large centra of the dorsal vertebrae are similar in size to the centrum of the last posterior cervical vertebra (the 5th vertebra). Mediolaterally the dorsal vertebrae are much wider than the cervicals as a result of the expanded laterally projecting transverse processes (see below).

The centra of the dorsal vertebrae are amphicoelous, with deeply concave anterior articular facets. It is interesting to note that the posteroventrally extended overhanging lip-like projections on the posterior surfaces are much more robust than they are in the cervical vertebrae. On average, the centra are slightly anteroposteriorly flattened, and therefore slightly mediolaterally wider than anteroposteriorly long. They are not as flat as the cervicals.

The dorsal centra of SAM-PK-6238 share many features with those of the holotype of *Embrithosaurus*. Centra of the dorsal vertebrae are more mediolaterally constricted than in the cervicals, the vertical grooves on the lateral sides are very deep, and the anterior and posterior rims of each centrum flare laterally to become thin and elongated. Approximately half way up each centrum, the centrum is medially pinched, creating a midline, bar-like, cylindrical

swelling as the ventral-most portion of each centra. Ventrally, the anterior and posterior rims of the posterior dorsal centra curve towards each other. On all dorsal vertebrae, the ventral surface of the centrum lacks the distinct longitudinal midline ridge of the posterior cervicals.

It is important to note that in agreement with the situation in the holotype of *Embrithosaurus*, from the 6th vertebra backwards, the separate and distinct parapophysial and diapophysial articulations fuse into a single vertical flange, creating a transverse process with a single lateral facet.

On the damaged 6th vertebra of SAM-PK-6238, the transverse process shows the same features as those of the 6th to 9th vertebrae of the holotype of *Embrithosaurus*: the process produces a lateral facing facet comprising a tall, thin, flat, laterally facing, dorsal portion; and a wide, round, bowl-shaped, shallow, posterolateral facing ventral portion (Fig. 5.23). On the lateral side of the vertebrae, the ventral facet is very low and almost indistinguishable from the side of the body of the centrum, and reaches ventrally far down to almost reach the ventral surface of the centrum and the dorsal part of the transverse process does not extend laterally very far. The 7th and 8th vertebrae consist of little more than weathered centra and yield almost no morphological information.

The 9th to 16th vertebrae are similar in overall morphology (Figs. 5.24, 5.25). The lateral facet of the transverse process has changed to comprise only one tall, thin, laterally facing facet with a ventral portion that is thick and rounded, with a slightly concave, faceted surface facing posterolaterally. More dorsally, the lateral facet is very thin and narrow, before extending and thickening posteriorly, to create a concave posterolateral facet. In all these vertebrae, the transverse process is large, the ventral portion projects laterally 30-45 mm out of the side of the body of the centrum and the dorsal portion about twice as far, extending up to 60-75 mm laterally. The lateral edge of the transverse process is oblique in anterior or posterior view.

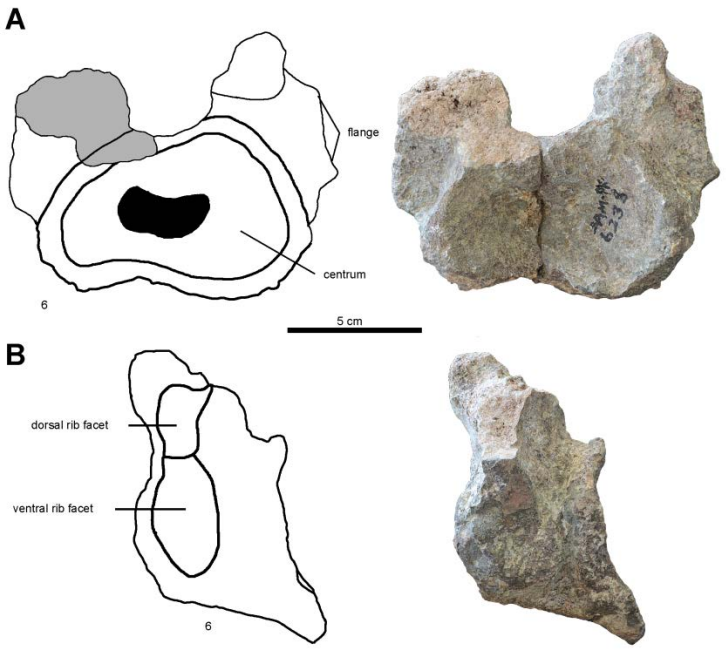


Figure 5.23: Photographs and interpretive drawings of the 6th vertebra of SAM-PK-6238 (*Nochelesaurus alexanderi*), (A), in anterior view, and (B), in left lateral view. Dorsal to the top of the page.

The ventral edge of the transverse process is positioned between 40-60 mm above the ventral edge of the centrum and shifts slightly higher up on more posterior vertebrae. Dorsally, the transverse process is swollen and thickened mediolaterally, and has a thinner, curved, plate-like anterior extension to the prezygapophysis. The transverse process is vertically oriented, with the dorsal portion more posterodorsally oriented, as seen in the holotype of *Embrithosaurus*.

The prezygapophyses are preserved only from the 10th to 16th vertebrae and are all similar, very flat, dorsally and slightly anteriorly facing, and at the end of short processes that extends anterodorsally from the swollen dorsal part of the transverse flange. As with the vertebrae of the holotype of *Embrithosaurus*, the prezygapophysial processes gradually increase in robustness posteriorly and also in mediolateral width.

As seen in *Embrithosaurus*, the postzygapophysial processes of *Nochelsaurus* are much larger and significantly increase in size and length posteriorly. They extend

posterolaterally from the lateral base of the neural spine, and the distal ends curve anteriorly. On the more anterior vertebrae they are mediolaterally much narrower than the transverse processes, but posteriorly they reach the width of the transverse processes.

The neural spines of the anterior dorsal vertebrae are dorsoventrally shorter (+-40 mm high) than those of the taller posterior dorsal vertebrae (+-70 mm high), similar to the condition found in *Embrithosaurus*. Neural spines of all the dorsal vertebrae are four-sided, diamond shaped in cross section, with sharp anterior, posterior, and lateral edges. On the anterior dorsal vertebrae (11th to 13th vertebrae, Figs. 5.24, 5.25), the anterior edges are rounded, the spines are mediolaterally wider (60-65 mm) than long (40-55 mm), and the dorsal surface of each spine is concave with a deep, midline longitudinal groove (also present in te 9th to 13th vertebrae of *Embrithosaurus* and the 5th to 9th vertebrae of *Bradysaurus baini*). The posterior dorsal vertebrae (14th to 16th vertebrae) have very sharp anterior edges, are anteroposteriorly longer (55–60 mm) than mediolaterally wide (40–45 mm), and their dorsal surfaces are convex and ruguse. The dorsal surface has small pits and larger hollows and sometimes a central, large hollow, but no anteroposterior midline grooves (also present in the 14th to 19th vertebrae of *Embrithosaurus* and the 10th to 18th vertebrae of *Bradysaurus baini*). All the dorsal vertebrae spines are vertical to slightly forward leaning.

The neural canal is very large (Fig. 5.25). Above the neural canal, the posterior side of the vertebrae have the thick horizontal bar of the hyposphene, which articulates with the facet of the hypantrum on the anterior side of posterior vertebra. The hypantrum of the anterior surface is much less robust than the posterior hyposphene. Above the hyposphene and hypantrum are two depressions, separated by a vertical midline ridge.

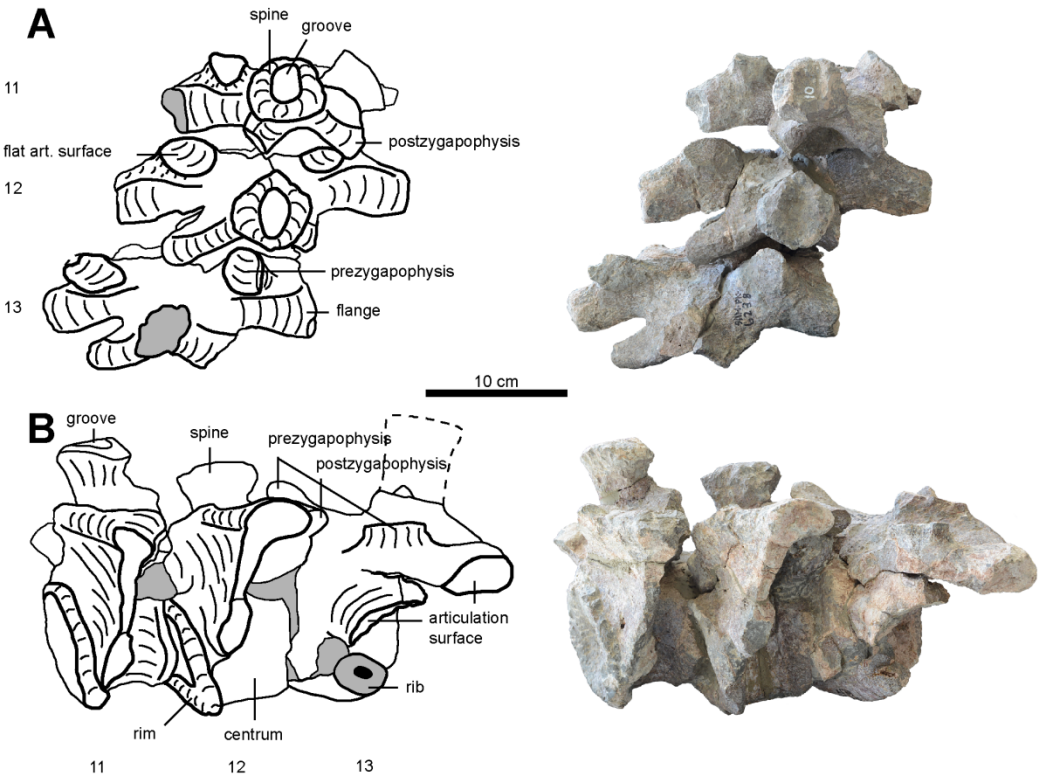


Figure 5.24: Photographs and interpretive drawings of the 11th-13th vertebrae of the SAM-PK-6238 (*Nochelesaurus alexnderi*), (A), in dorsal view, and (B), in left lateral view. Anterior to the top of the page in (A), dorsal to the top of the page in (B).

Poor historic preparation precludes the confirmation of notochordal centra in any of the dorsal vertebrae of SAM-PK-6238, but have been reported for a juvenile specimen of *Deltavjatia* (Tsuji 2010, 2013).

Ribs

All of the preserved presacral vertebrae of SAM-PK-6238 (axis to 16th vertebrae), have facets for rib articulation. SAM-PK-6238 preserves several dozen disarticulated and isolated partial rib fragments, including several well preserved rib heads, all single-headed (holocephalous).

The fused diapophysis and parapophysis on the 6th to 16th vertebrae, create a single, long, lateral facet and indicate that the rib articulations were single headed (holocephalus). Most of the rib fragments are thick (35 mm wide) with long shafts (410 - 560 mm), gently curved, with large, dorsoventrally elongated

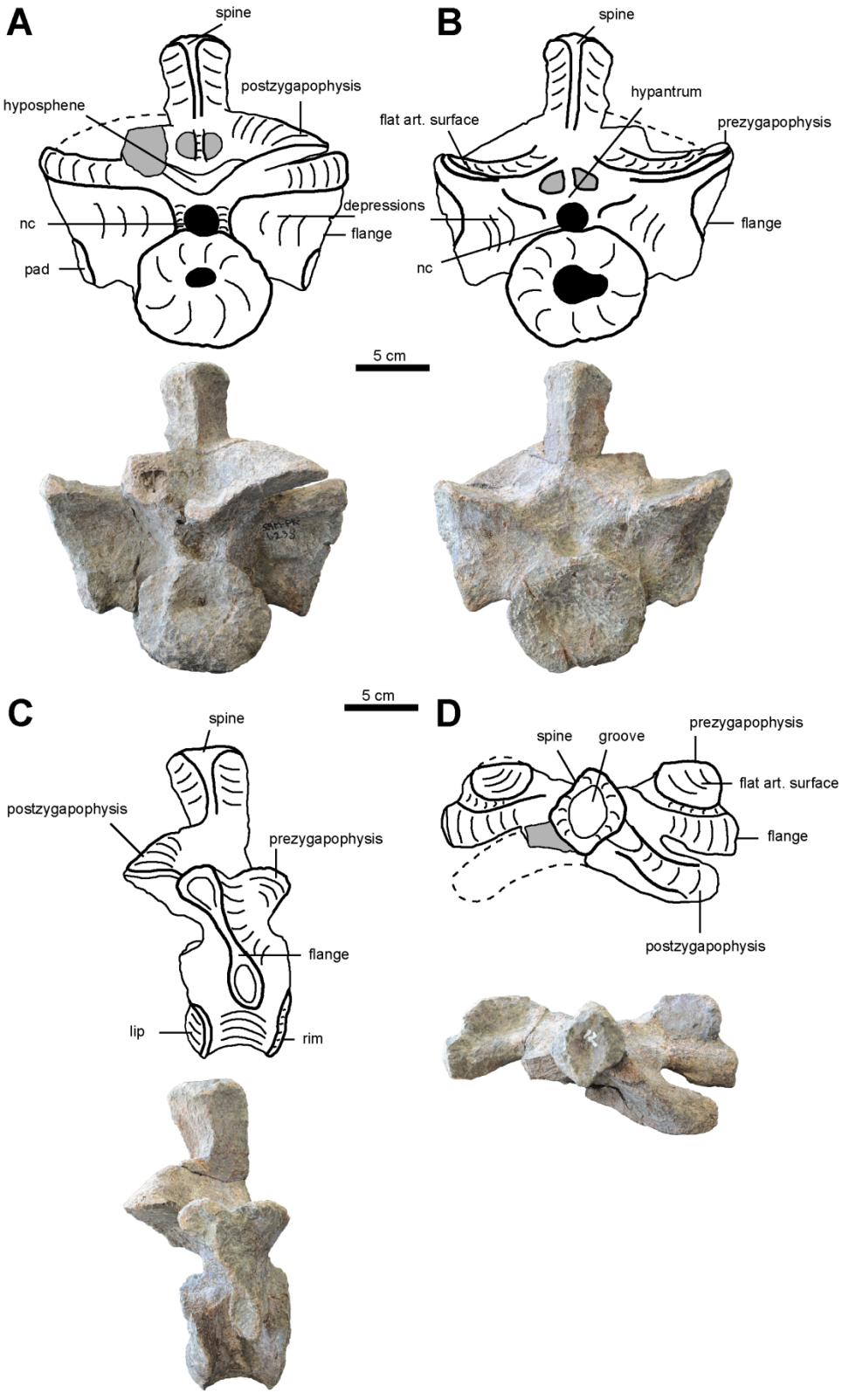


Figure 5.25: Photographs and interpretive drawings of the 13th vertebra of the SAM-PK-6238 (*Nochelesaurus alexnderi*), (A), in anterior view, (B), in posterior view, (C), in right lateral view and (D), in dorsal view. Dorsal to the top of the page in (A), (B) and (C). Anterior to the top of the page in (D).

heads, with elongated figure-of-eight articular facets for articulation with the long facet of the fused diapophysis and parapophysis of the dorsal vertebrae. These must have articulated with the posterior dorsal vertebrae, covering the largest, heaviest part of the rump of the animal. These large partial ribs have a distinct horizontally flat and thin, flange of bone on the anterior side, extending distally 80 mm, between 20 mm to 100 mm from the proximal rib head. Proximally, the long shaft of these ribs are convex anteriorly and concave posteriorly. All the long rib fragments taper distally and are oval in cross section.

5.4.5 Osteoderms (Fig. 5.26)

The holotype of *Nochelesaurus* preserves a plate of bone comprising at least seven large osteoderms (45-55 mm wide). They are rounded, to straight edged, five sided (roughly pentagonal).

The scutes are high (30-40 mm), robust and strongly convex. Unlike the flat, thin, low, disc-like periphery (5-7 mm high) of *Embrithosaurus*, the periphery of each boss of *Nochelesaurus* is high and thick (15-20mm) accounting for half the height of each osteoderm. In addition, each scute has a very distinct, clearly delimited, central boss, which is noticeably wide (25-40 mm) and high (15-20 mm above the perhiphery) accounting for the other half the height of the osteoderm. In *Embrithosaurus*, the central bosses are not as wide as in *Nochelesaurus*. In *Nochelesaurus*, some central bosses are roughly round (almost perfectly round on boss no 4 and 7, Fig. 5.26) whilst others are irregularly shaped, comprising tab-like, rugosities (boss no 1, 2, 5 and 6 Fig. 5.26). There are small, circular pits on the central bosses.

Lateral to each central boss, the peripheries of each osteoderm have less ornamentation than the central bosses and are therefore smoother, apart from a few small circular pits, and lack the regular radial ridges present in *Embrithosaurus*.

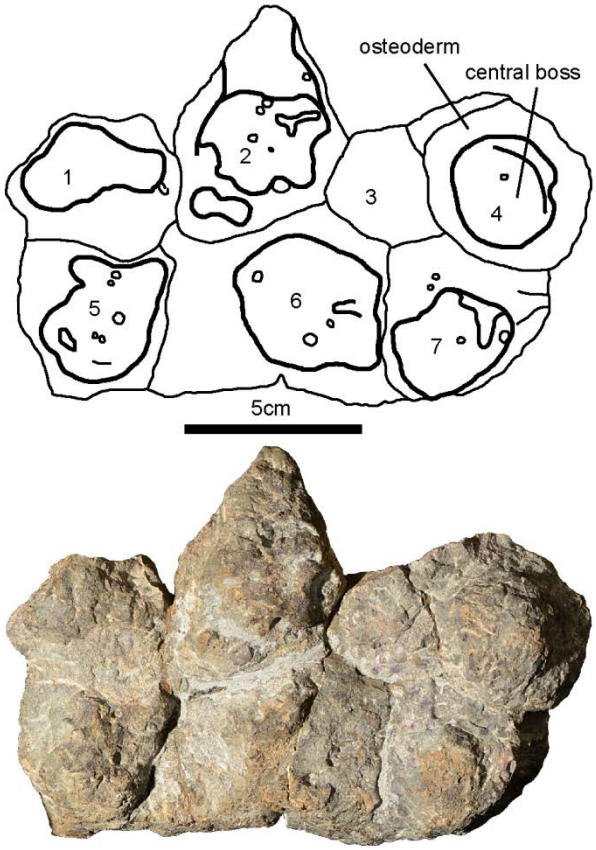


Figure 5.26: Photograph and interpretive drawing of the osteoderms of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239), in dorsal view.

6. CHAPTER SIX: POSTCRANIAL DESCRIPTION OF *BRADYSAURUS BAINI*

6.1 Introduction

British anatomist and palaeontologist H.G. Seeley visited South Africa in 1889 and collected two relatively complete pareiasaur specimens. These he described in detail (Seeley 1892). He assigned the more fragmentary specimen (NHMUK R1970) to *Pareiasaurus bombidens* (Owen 1876) and erected a new species, *Pareiasaurus baini*, for the very complete specimen (NHMUK R1971), represented by an almost complete skull and postcranium. This very complete, well prepared and historically important specimen is currently (2019) articulated and mounted on permanent display at the Natural History Museum in London.

Later, Watson (1914b) made NHMUK R1971 the holotype of *Bradysaurus baini,* in his classification system, as he recognised the earlier named *Pareiasaurus* to comprise specimens with an extensive covering of body osteoderms, a feature lacking in the scantly covered NHMUK R1971.

Bradysaurus baini was retained by Haughton and Boonstra (1929a) who provided a very brief cranial diagnosis, Boonstra (1934a) greatly expanded the diagnoses of the species, based solely on crania. The postcranium of *Bradysaurus baini* was described in the series of pareiasaurian papers published by Haughton and Boonstra over 1929-1934 (i.e. manus, Boonstra 1929a; pes, Boonstra 1929b; hind limbs, Haughton & Boonstra 1930b; fore limbs, Boonstra 1932b; dermal armour, Boonstra 1934b; and vertebrae and ribs, Boonstra 1934c).

Lee (1994, 1997a) recognised three cranial autapomorphies for *Bradysaurus baini* and noted postcranial differences between the taxon and the other middle Permian South African pareiasaurs. The postcrania of this species has not been described in detail since Boonstra's piecemeal descriptions in the 1930s (Boonstra 1934a, b, c).

As the complete postcranial description of *Bradysaurus baini* (Seeley 1892) is 127 years old, this chapter aims to re-describe in detail the postcranial elements of *Bradysaurus baini*. As in the previous postcranial descriptive chapters of this project, particular emphasis is placed on describing distinguishing features compared to the anatomically similar co-occurring South African pareiasaurs and to postcranial anatomical features which influence phylogenetic characters and states.

6.2 Material

6.2.1 Holotype

Refer to Chapter Two, Material and methods

6.2.2 Referred material

Refer to Appendix A for a list of referred specimens of *Bradysaurus baini*.

6.2.3 Comparative material

Refer to Chapter Two, Material and methods.

6.2.4 Literature consulted

Refer to Chapter Two, Material and methods.

6.2.5 Preservation and preparation

Refer to Chapter Two, Material and methods.

6.2.6 Holotype horizon and locality

Refer to Chapter Two, Material and methods.

6.3 Systematic Palaeontology

REPTILIA Laurenti, 1768

PARAREPTILIA Olsen, 1947

PAREIASAURIA Seeley, 1888

PAREIASAURIDAE Cope, 1896

BRADYSAURUS Watson, 1914

Bradysaurus baini Seeley, 1892

6.4 Postcranial description

This description is based primarily on the holotype of *Bradysaurus baini* NHMUK-R1971 and important referred specimens NHMUK R1970, and SAM-PK-5002. A few specific instances of other specimens are also used, and are referred to in the text.

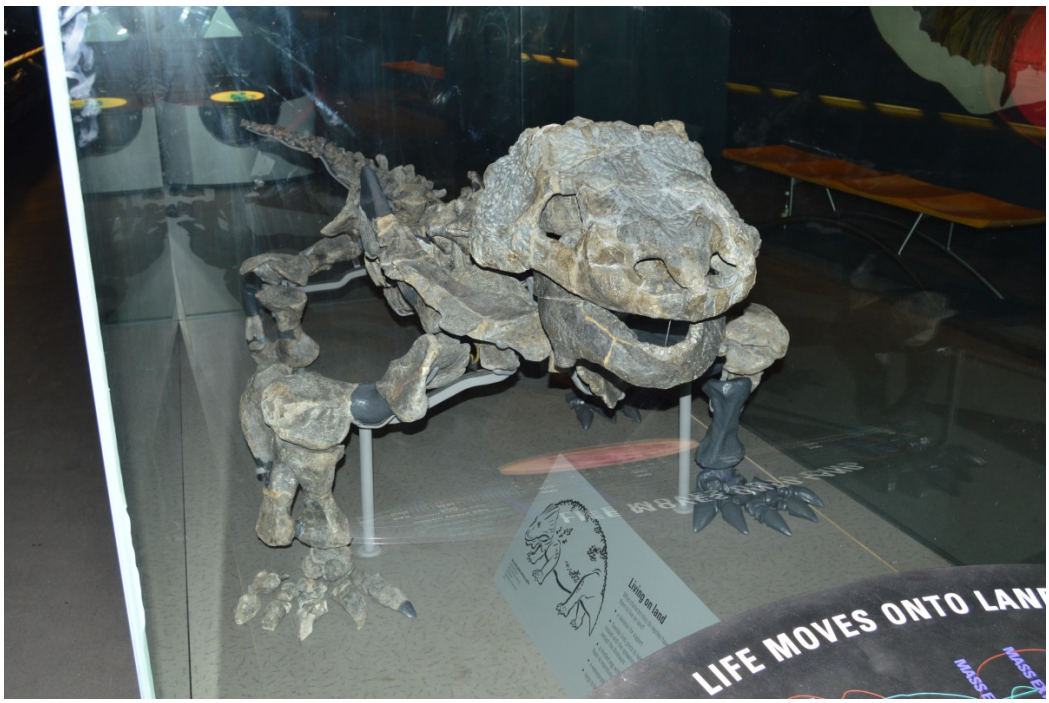


Figure 6.1: Photograph of the mounted holotype of *Bradysaurus baini* (NHMUK R1971), affectional nicknamed "Fred" by museum staff, on display in the "From the beginning" permanent exhibit, Natural History Museum, London.

6.4.1 Shoulder girdle

The shoulder girdle of *Bradysaurus baini*, as in all pareiasaurs, consists of paired scapulocoracoids, clavicles and cleithra, and the single interclavicle.

The holotype of *Bradysaurus baini* preserves a complete left scapulocoracoid (Fig. 6.2), apart from a small missing piece at the posteroventral corner of the posterior coracoid, with complete left cleithrum. The right scapulocoracoid is not as well preserved as most of the coracoid plate is damaged and the distal scapula blade is missing. Most of the interclavicle and of both clavicles are preserved.

Scapulocoracoid (Fig. 6.2)

As in all well preserved specimens of middle Permian pareiasaurs from South Africa, ventral to the glenoid fossa the lateral surface of the corocoid plate undulates with three wavy bulging areas and four corresponding low depressed regions between these raised bulges. The swollen process of the medial side of the scapula blade, located immediately above the articulation of the clavicle, is low and wide in the holotype and in specimen SAM-PK-5002 (the blade is 60 mm mediolaterally wide, but the medial bulge is less than 10 mm high in the holotype). This medial swelling is typical of all large co-occurring pareiasaurian taxa.

The anteroposterior width of the base of the scapula blade of the holotype, just above the dorsal edge of the acromion process is 110 mm. It is important to note the short, wide scapula blade. Distally, the scapula blade is widely flared (anteroposteriorly 200 mm) which is almost twice the basal anteroposterior width, and the preaxial and postaxial margins are strongly curved, especially the preaxial margin (Turner *et al*. 2015 character 88). Sub-adult specimen SAM-PK-5002 flares slightly less, from 85 mm at the base to 190 mm distally. The total lengths of the scapula blades of the holotype of *Bradysaurus baini,* including the acromion process is only 440 mm, significantly shorter than the 490 mm measured for *Nochelesaurus* (SAM-PK-6238). The glenoid fossa is of a typical

morphology for this group: anteroposteriorly elongated (180 mm left, 200 mm right), oriented about 25^0 obliquely anterodorsally above the horizontal ventral border of the coracoid plate. The scapula blade length is a little over two times the anteroposterior diameter of the glenoid fossa (Turner *et al*. 2015 character 87).

In comparison with other middle Permian pareiasaurs from South Africa, *Bradysaurus baini* has a short, wide scapula blade, with extreme distal flaring, similar to *Embrithosaurus*, but quite different from the longer, anteroposteriorly narrower and only very slight distal flaring of *Nochelesaurus*. Distally, as in *Embrithosaurus* and *Nochelesaurus*, both the lateral and medial surface of the scapula blades are highly rugose and covered with vertical striations and ridges.

The acromion process, situated above the supraglenoid buttress is the largest in this this group: long (145 mm) and high (45 mm) making a rectangular flange. The short dorsal margin is notched, and the short ventral margin more straight at a right angle to the scapula blade. The flat plate-like acromion is gently convex laterally and concave medially as in *Nochelesaurus* (Turner *et al*. 2015 character 89).

The inner (medial) surfaces of both scapulocoracoids show the prominent dorsoventral groove of the subscapular fossa, which is long (80 mm), wide (20 mm) and deep (20 mm), and is the largest of the middle Permian South African pareiasaurs (see Table 4.1). Indeed, the sub-adult *Bradysaurus baini* specimen SAM-PK-5002 has the largest subscapular fossa observed during the completion of this project (100 mm long, 45 mm wide, 40 mm deep). The subscapular fossa is positioned 55-60 mm behind the anterior border of the scapula (see Table 4.1), slightly further posteriorly than *Embrithosaurus* and *Nochelesaurus*.

The large coracoid foramen is positioned in the ventral corner of the long, vertical subscapular fossa of the medial surface of both scapulacorocoids.

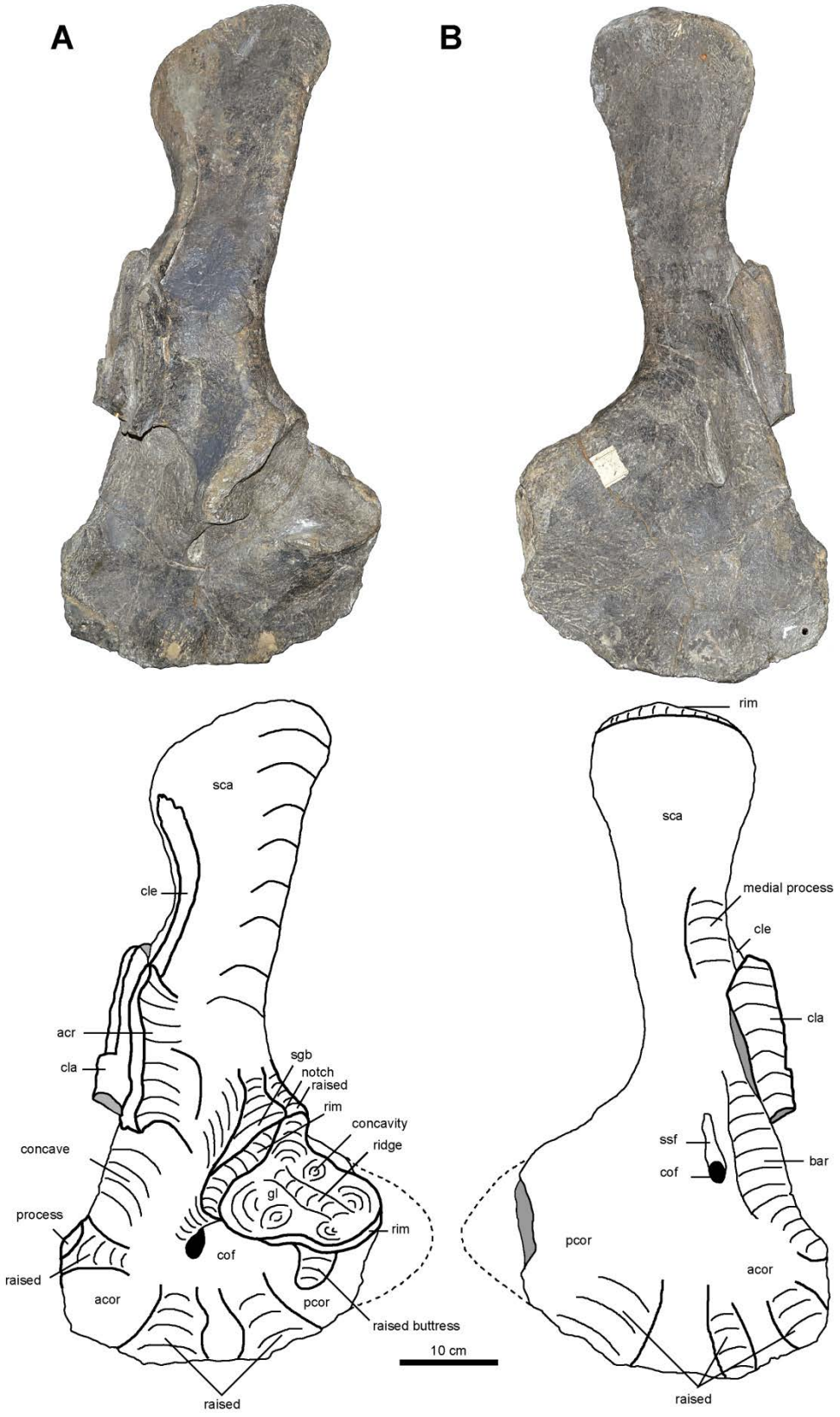


Figure 6.2: Photographs and interpretive drawings of the left scapulocoracoid of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), in lateral view, and (B), in medial view. Dorsal to the top of the page.

As in *Nochelesaurus* and *Embrithosaurus* the foramen passes through the coracoid plate almost vertically, and very slightly laterally, to emerge on the lateral surface of the anterior coracoid 40-50 mm below the anteroventral corner of the glenoid fossa. The foramen here is dorsoventrally oval (33 mm high, 16 mm wide).

The thickened anterodorsal supraglenoid buttress of the glenoid fossa is massive and has sharp ventral edges. There is a distinct groove (20 mm anterodorsally, 30 mm dorsoventrally) on the rim of the fossa, just posterior to the supraglenoid buttress, similar to the groove in the holotypes of *Nochelesaurus* and *Embrithosaurus* (CGP CBT 112). The supraglenoid buttress creates a large anterior facet in the glenoid fossa, and faces posteroventrolaterally. The posterior facet of the glenoid fossa is horizontally flat, with a posterior portion facing dorsolaterally and an anterior portion facing more dorsally. As in *Nochelesaurus* and *Embrithosaurus*, the posterior facet of *Bradysaurus baini* is supported by a particularly robust and thick shelf-like buttress (only slightly smaller than the supraglenoid buttress) with a swelling ventrally under the rim, on the lateral surface.

Between the anterior and posterior facets, the glenoid has a low (< 10 mm high), oblique, raised ridge (30 mm wide, 60 mm long) which is also present in *Nochelesaurus* and *Embrithosaurus* (CGP CBT 112). This oblique ridge covers the centre of the glenoid anterodorsally and has shallow concavities above and below it. The lower depression is quite deep.

Assuming a vertical posterior border of the scapula blade, the angle to the dorsal border of the posterior corocaoid is 125^0, which is very similar to the angles measured for *Nochelesaurus* and *Embrithosaurus* (Turner *et al*. 2015 character 90).

The narrow ventral edge of the anterior and posterior corocoid (the plate) is irregular and uneven with numerous small bumps, notches and indentations. On the anterior coracoid rim, anteroventral to the glenoid, the rim is swollen and

thickened to nearly twice the average mediolateral thickness of the coracoid plate, producing a knob-like process, covering 50 mm dorsoventrally and 30 mm anteroposeriorly of the lateral surface. This region is not well preserved on the holotypes of *Embrithosaurus* or *Nochelesaurus*, but referred *Embrithosaurus* specimen CGP CBT 112 has a similar swollen process, so it is most likely common to the group of pareiasaurs. On the anterior rim, between the knob-like process and the acromion process, the coracoid is very concave laterally.

Cleithrum (Fig. 6.2)

The cleithrum is very well preserved and complete on the anterolateral margin of left scapula blade of NHMUK R1971. It is 220 mm long and thin and curved anteriorly, as is the anterior margin of the scapula blade. Dorsally, the cleithrum thins mediolaterally to fuse with the scapula blade. The ventral base rests on the dorsal surface of the notched acromion process and articulates with the lateral edge of the clavicle (Turner *et al*. 2015 character 91).

Interclavicle (Fig. 6.3)

The interclavicle is broken along the midline and preserved in two large portions: the right clavicular arm is articulated with the right scapula and the left arm attached to a separate block containing the left clavicle. Only a small dorsal portion of the median stem of the interclavicle is preserved.

The transverse bar of the interclavicle is typical for large pareiasaurs, robust and the anterior surface is deeply grooved (as in *Embrithosaurus* and *Nochelesaurus*) for occlusion with a sharp, triangular wedge-shaped posterior process of the clavicles. Laterally, the lateral extensions of the interclavicle are 220 mm long and taper anteroposteriorly and dorsoventrally to end in a “cup-shaped” tip (as in *Embrithosaurus* and *Nochelesaurus)*.



Figure 6.3: Photograph of the partial left clavicle and interclavicle of the holotype of *Bradysaurus baini* (NHMUK R1971), in anterior view. Dorsal to the top of the page.

Clavicles (Figs. 6.2, 6.3)

Most of the left clavicle is well preserved and articulated to the left lateral extension arm of the interclavicle (Fig. 6.3). Separately, the distal end of the left clavicle is attached to the left scapula (Fig. 6.2). The right clavicle is articulated with the right lateral extension of the interclavicle on the right scapula. The clavicles are gently curved and anteroposteriorly flattened.

Anteriorly, the flat surface is convex at the dorsal and ventral edges and the lateral portion has a shallow groove. Medially the bone is triangular in cross section due to a wedge-shaped posterior process, for articulation with the anterior groove of the interclavicle.

The clavicle has a short an wide posteroventrally extended process (10-15 mm high and 110 mm mediolaterally wide) which is very similar in size and dimensions to the same feature seen on *Nochelesaurus* (SAM-PK-6238: 90 mm wide, 10 mm high) and the holotype of *Embrithosaurus* (SAM-PK-8034: 80 mm wide, 20 mm high), but it is slightly wider than in both those taxa and extends less than *Embrithosaurus*. Interestingly and perhaps diagnostically, both *Bradysaurus baini* (NHMUK R1971, SAM-PK-5002) and *Nochelesaurus* (SAM-PK-6239, SAM-PK-6238) lack the distinct notch just medial to this posteroventral process of *Embrithosaurus* (SAM-PK-8034).

Distally, the posterodorsal border of the clavicle is swollen and thickened into an almost cylindrical shape, also seen in *Nochelesaurus*, with a hollow depression anterior to it. As in *Nochelesaurus*, the distal lateral tip the clavicle is triangular in cross section.

6.4.2 Forelimbs

Humerus (Fig. 6.4)

The left humerus of the holotype of *Bradysaurus baini* consists of only the very wide distal half and the proximal half has been completely fabricated. The right humerus, which forms the basis of this description, is very complete apart from a postaxial piece of the entepicondyle and most of the short shaft of the humerus. Seeley (1892: 360) noted that the shaft of the right humerus was broken during preparation and that he could not be certain as to the original alignment of the two ends of the humerus to each other. Seeley attached the distal and proximal ends to each other in virtually the same plane, with torsion of only 10-20^0 between the two ends. Therefore, the holotype of *Bradysaurus baini* does not reveal the torsion in the humerus of the species (Turner *et al.* 2015 character 92). The mounted *Bradysaurus baini* specimen at the Iziko South African Museum (SAM-PK-5624) shows humeral torsion of 70-80^0 in both humeri and SAM-PK-3718 shows 70^0 torsion in its partial right humerus.

Of the local middle Permian pareiasaurs, *Bradysaurus* has the widest distal humerus (290 mm holotype left humerus) measured anteroposteriorly across the ectepicondyle and entepicondyle, which is wider than the range of *Nochelesaurus* (235-260 mm) and much wider than the holotype of *Embrithosaurus* (230 mm).

The humeral ectepicondyle is very large, swollen and robust and is dorsoventrally more than twice as thick as the more gracile entepicondyle (Turner *et al.* 2015 character 99).

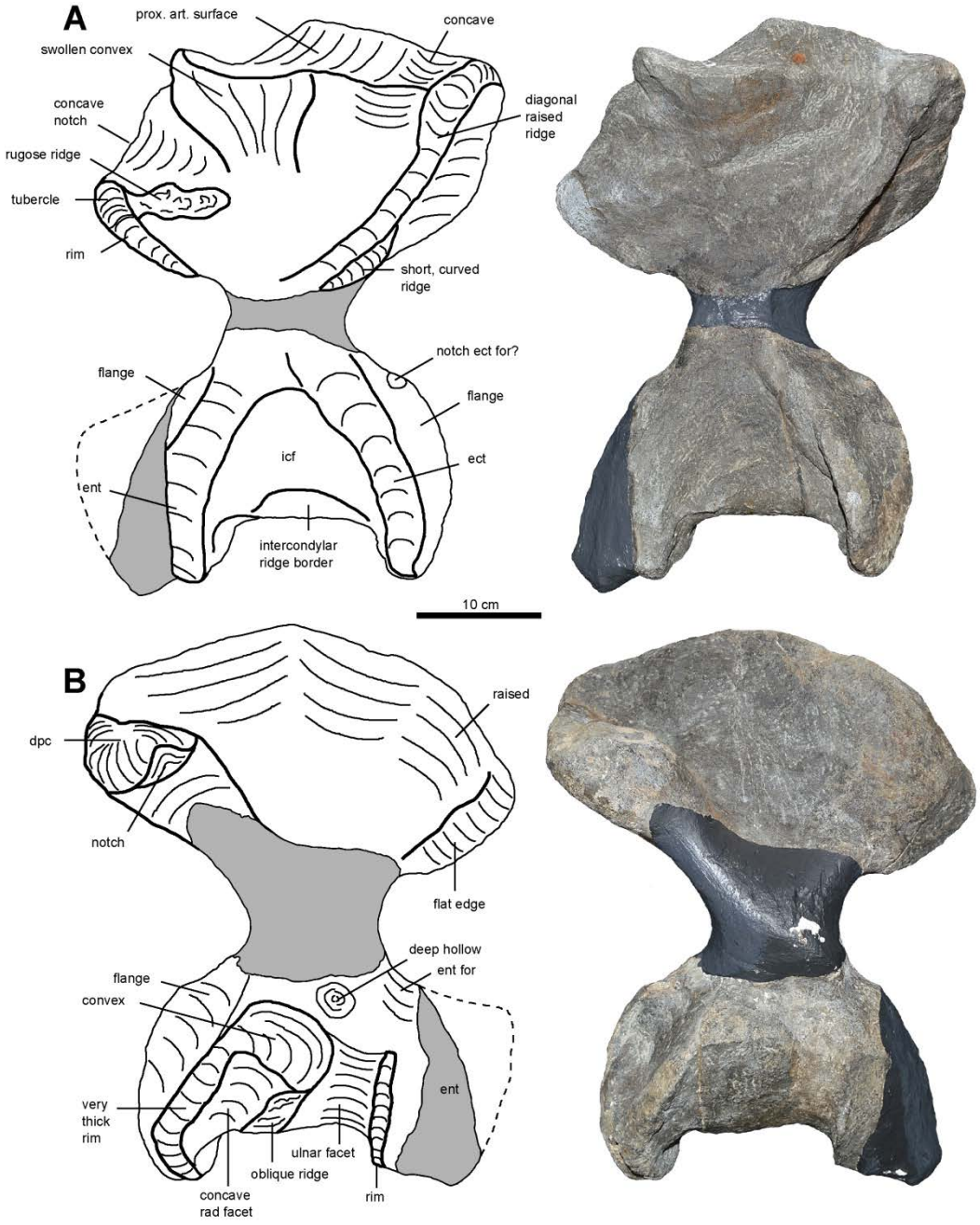


Figure 6.4: Photographs and interpretive drawings of the right humerus of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), in dorsal view, and (B), in ventral view. Medial to the top of the page.

A thin, expanded, wide flange is on the preaxial border of both large ectepicondyles (Turner *et al.* 2015 character 93). Identification of the small ectepicondylar foramen (present in all pareiasaurs according to Lee 1997b: 237) is uncertain on both sides, but a notch on the right humerus indicates its likely position (Turner *et al.* 2015 character 94).

The postaxial border of the smaller entepicondyle is reconstructed on the right humerus and damaged on the left. An entepicondylar flange is not preserved on either humerus (Turner *et al.* 2015 character 95). Only a small proximal section of the slit-like entepicondylar foramen of the right humerus is preserved, where the morphology is consistent with co-occurring middle Permian pareiasaurian taxa (Turner *et al.* 2015 characters 96 and 97).

Anteroposteriorly, the width of the proximal right humerus is very wide at 305 mm, similar in width to *Nochelesaurus* (SAM-PK-6238: 275 mm right humerus, 284 mm left humerus), and much wider than the holotype of *Embrithosaurus* (250 mm).

The ectepicondyles of the holotype of *Bradysaurus baini* project distally much further beyond the radial and ulnar articulation surfaces (44 mm left humerus, 49 mm right humerus) than does the holotype of *Embrithosaurus* (25 mm) or in specimens of *Nochelesaurus* (Holotype: left humerus, 35 mm; SAM-PK-6238: right humerus, 35 mm, left humerus, 40 mm) (Turner *et al.* 2015 character 98).

The triangular intercondylar fossa (olecranon fossa) is wide and forms a deep depression on the dorsal surface of the humerus of *Bradysaurus baini* (50 mm deep on the right, 40 mm deep on the left), in the same range as *Nochelesaurus* (Turner *et al.* 2015 character 103) but much deeper than *Embrithosaurus* (SAM-PK-8034: 20 mm). As with *Nochelesaurus*, this deep fossa suggests a prominent, large olecranon process of the ulna (see Ulna). The intercondylar fossa is much wider than the width of the proximal ulna (olecranon process) (Turner *et al.*2015 character 104).

The preaxial and postaxial margins of the intercondylar fossa are straight to gently outwardly convex, apart from the preaxial margin on the right humerus, which is very distinct and sharp edged as a result of distortion. As in all large middle Permian South African taxa, the dorsal distal margin of the fossa is formed by a gently concavely curved, wide and low, transverse ridge (intercondylar ridge border) which does not extend onto the distal side of the

humerus. This ridge separates the intercondylar fossa from the radial facet and the ulnar facet of the humerus (Turner *et al.* 2015 character 102).

The distal radial facet/condyle of the right humerus is dorsoventrally crushed so as to be flat and concave, creating an unnaturally sharp , very thick, preaxial border (Fig. 6.4). On the better preserved distal left humerus, the radial facet is typical for this middle Permian pareiasaurian group: large, round and bulbous (strongly convex), with a shallow concave portion distally. Proximal to the radial facet is a small hollow depression (present on all these large pareiasaurs.

The oblique ridge that separates the radial facet from the adjacent trochlear (ulnar) groove on the ventral surface of the humerus is poorly developed, low and indistinct. The postaxial (posterior) margin of the trochlear groove is formed by a distinct, raised, sharp-tipped pointed rim (Turner *et al.* 2015 character 101)**.**

The transverse and curved intercondylar ridge at the distal-dorsal edge of the humerus prevents the radial facet and the trochlear groove of the ventral side of the humerus from encroaching round onto the dorsal surface (Turner *et al.* 2015 character 100).

On the deeply concave ventral surface of the proximal humerus, the postaxial delto-pectoral crest is massive and robust, similar in size and shape to that of the referred *Nochelesaurus* specimen SAM-PK-6238 (90 mm wide) and also much wider than the narrow crest of the holotype of *Embrithosaurus* (70 mm). The ventral surface of the delto-pectoral crest is irregular, roughly convex and presents a “heart shaped” surface as does *Nochelesaurus*. Also aligned with *Nochelesaurus*, the ventral surface lacks the long, central, ventral groove of *Embrithosaurus*.

The prominent oblique, triangular ridge that dominates the dorsal surface of the proximal blade is prevalent. The short, curved, crescent-shaped, insertion point for muscle attachment, seen in *Nochelesaurus* (absent in *Embrithosaurus*) is

present on the humeral shaft, distal to the thick triangular ridge. The anterior long, thin ridge seen in *Nochelesaurus* and *Embrithosaurus* is present here.

The s-shaped proximal articulation surface of the head of the humerus is deep and has raised edges. As seen in all large *Tapinocephalus* Assemblage Zone pareiasaurs, the postaxial edge of the proximal blade comprises a thickened rim, and has a tubercle on the proximal-postaxial corner, where a rough, irregular, rugose, oblique ridge extends below a prominent notch, to reach the central region of the dorsal face of the blade.

Radius (Fig. 6.5)

NHMUK R1971 preserves the complete right radius in excellent condition. The morphology of the right radius is very typical of the large middle Permian South African pareiasaurs: short and stout, significantly shorter than the much longer ulna, with a roughly rectangular shaft. The proximal and distal ends are mediolaterally expanded with the proximal expansion slightly wider (125 mm) than the distal expansion (113 mm), as is the case with *Embrithosaurus*. The planes of the proximal and distal expansions are 45^0 to each other as is typical of the other middle Permian pareiasaurs.

In general morphology, the radius of *Bradysaurus baini* is similar to that of *Embrithosaurus*, and differs somewhat from *Nochelesaurus*. Like *Embrithosaurus,* the proximal expansion of the radius is slightly wider than the distal expansion, whereas the situation is reversed in *Nochelesaurus,* but these size differences are small and may not be important or diagnostic. In *Nochelesaurus*, the distal half of the radius is ventrolaterally expanded, a condition not present in the more symmetrical *Embrithosaurus* and *Bradysaurus* distal radii.

Similar to co-occurring pareiasaurian taxa, assuming an upright shaft orientation, the distal articulation surface is not on a horizontal plane and instead creates an oblique angle about 35^0 from the horizontal plane (which is 20^0 in *Nochelesaurus*

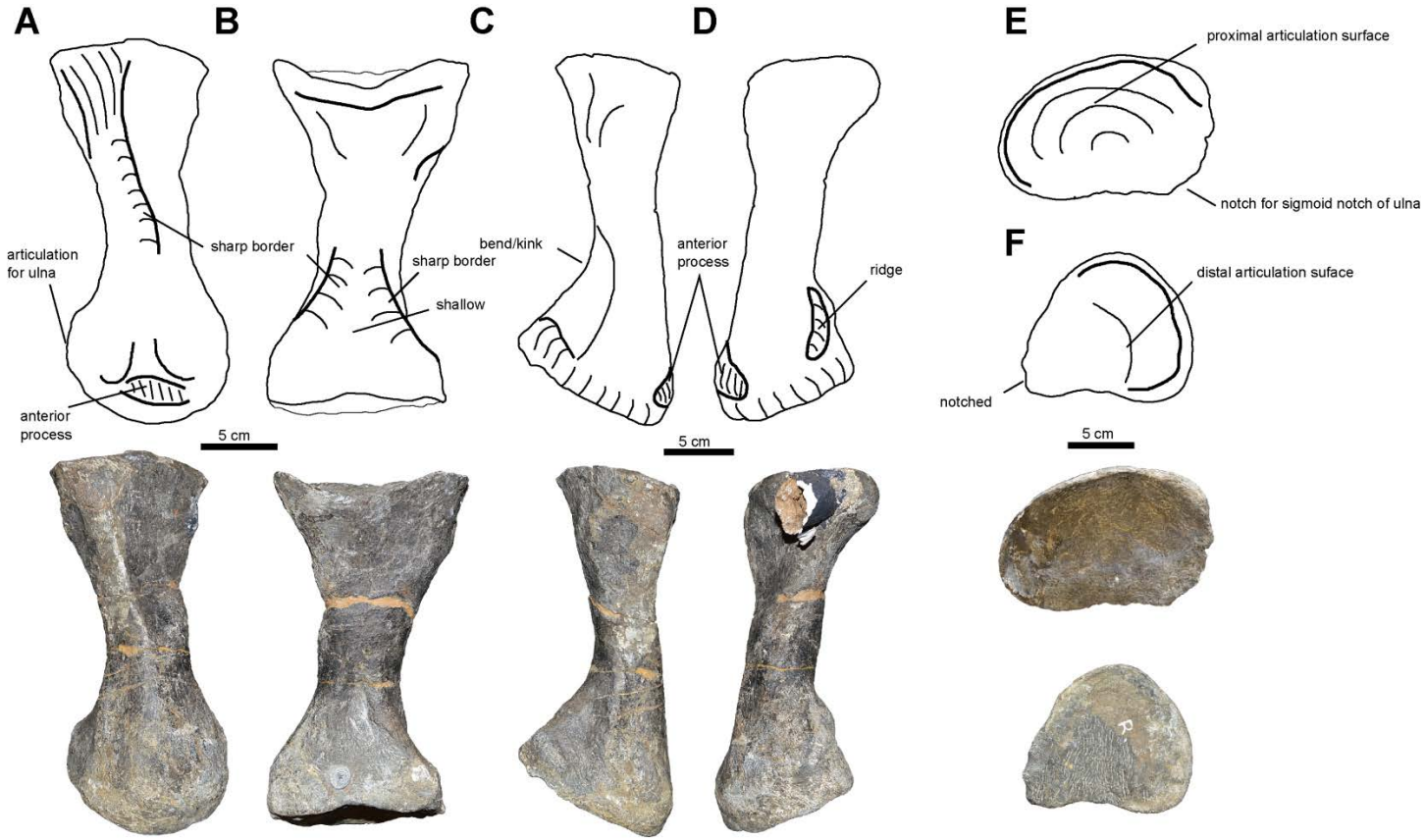


Figure 6.5: Photographs and interpretive drawings of the right radius of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), in anterior view, (B), in posterior view, (C), in lateral view, (D), in medial view, (E), in dorsal view, (F), in ventral view. Dorsal to the top of the page in (A), (B), (C) and (D). Anterior to the top of the page in (E) and (F).

and *Embrithosaurus*), exaggerated in *Bradysaurus baini* through compression and distortion of the specimen as there is a distinct bend or kink on the posterior side (Fig. 6.5C). Both the proximal (ovoid) and distal (triangular) articulation surfaces are deeply concave and equally deep.

The posterior side of the radius is deeply concave between the sharp, vertical lateral and medial borders, as commonly seen in these pareiasaurs. The distinct vertical ridge of the medial side of the distal shaft, seen in *Nochelesaurus*, is also present in *Bradysaurus baini,* and lacking in *Embrithosaurus.* The anterior process of the radius, is not large as in *Nochelesaurus*, and is similar in size to the smaller, lower, less distinct and bulbous condition seen in *Embrithosaurus*.

Ulna (Figs. 6.6, 6.7, 6.8)

The right ulna of the holotype is complete and well preserved. On the left ulna, a large section of the distal shaft has been reconstructed and a large section of the proximal articular surface and medial sigmoidal process and the sigmoidal notch, has been sheared off. There are deep, dorsoventrally long, erosional cavities on the lateral and medial surfaces of the proximal left ulna. The right ulna is mediolaterally compressed and as a result is about 20 mm narrower than the left.

As seen in referred *Nochelesaurus* specimen SAM-PK-6238, the ulna of *Bradysaurus baini* is dorsoventrally long (370 mm) and is significantly longer than the short ulna of *Embrithosaurus* (295mm). As in all large middle Permian South African pareiasaurs, the proximal postaxial side of the ulna forms a straight, thickened, very rugose “bar”. Similar to *Nochelesaurus*, the bar consists of two distinct regions separated by a bend on the postaxial side: the distal portion of the bar is long, almost cylindrical and mediolaterally narrow; the proximal portion is mediolaterally thicker, postaxially flatter, with square-edged sides, and mediolaterally widens significantly. The length of the proximal portion of this bar measures 90 mm dorsoventrally obliquely, similar to *Nochelesaurus* specimens (90 mm) and quite different from the holotype of *Embrithosaurus* (30 mm). The

proximal articulation surface of the ulna is longer in the holotypes of *Bradysaurus baini* (130 mm) and *Nochelesaurus* (130 mm) than in the holotype of *Embrithosaurus* (90 mm).

A large, deep sigmoidal (radial) notch is present and bordered dorsally by the lateral and medial and sigmoidal processes. As in *Nochelesaurus* and *Embrithosaurus*, the medial process extends further anteriorly from the sigmoidal notch (50 mm) than the lateral process (25 mm). The medial process is triangular with a rounded tip, and the short lateral process is also rounded. The process on medial rim of the proximal articular surface, at the postaxial base of the medial sigmoidal process, is small, low and rounded (as in in *Nochelesaurus*) and not as distinct as in *Embrithosaurus*.

The proximal articular surface is divided by a swollen ridge (20 mm wide), although more vertically oriented and not obliquely as in *Nochelesaurus*, whereas the ridge is absent in *Embrithosaurus*. The surface faces primarily anteriorly (Turner *et al.* 2015 character 105).

Olecranon processes are present on both ulnae of the holotype, but are morphologically very different. On the right ulna, the olecranon process is very large (Fig. 6.7A) (45 mm in dorsoventral height, extending anteriorly 30 mm beyond the proximal articular surface) (Turner *et al.* 2015 character 106) and abruptly ends the proximal articular surface, where a distinct “lip-like” overhanging ledge prevents the hooked articular surface from passing over onto the proximal surface. This large olecranon process, of the right ulna, above the well-defined proximal articular surface, is in general agreement with Seeley (1892) who mentioned a slightly higher figure of “2.5 inches” (62 mm).

Interestingly, the olecranon process on the left ulna is significantly smaller (Fig. 6.7C) extending only 15 mm dorsoventrally above the articular surface, one third as much as the right ulna, indicating a significant lack of bilateral symmetry.

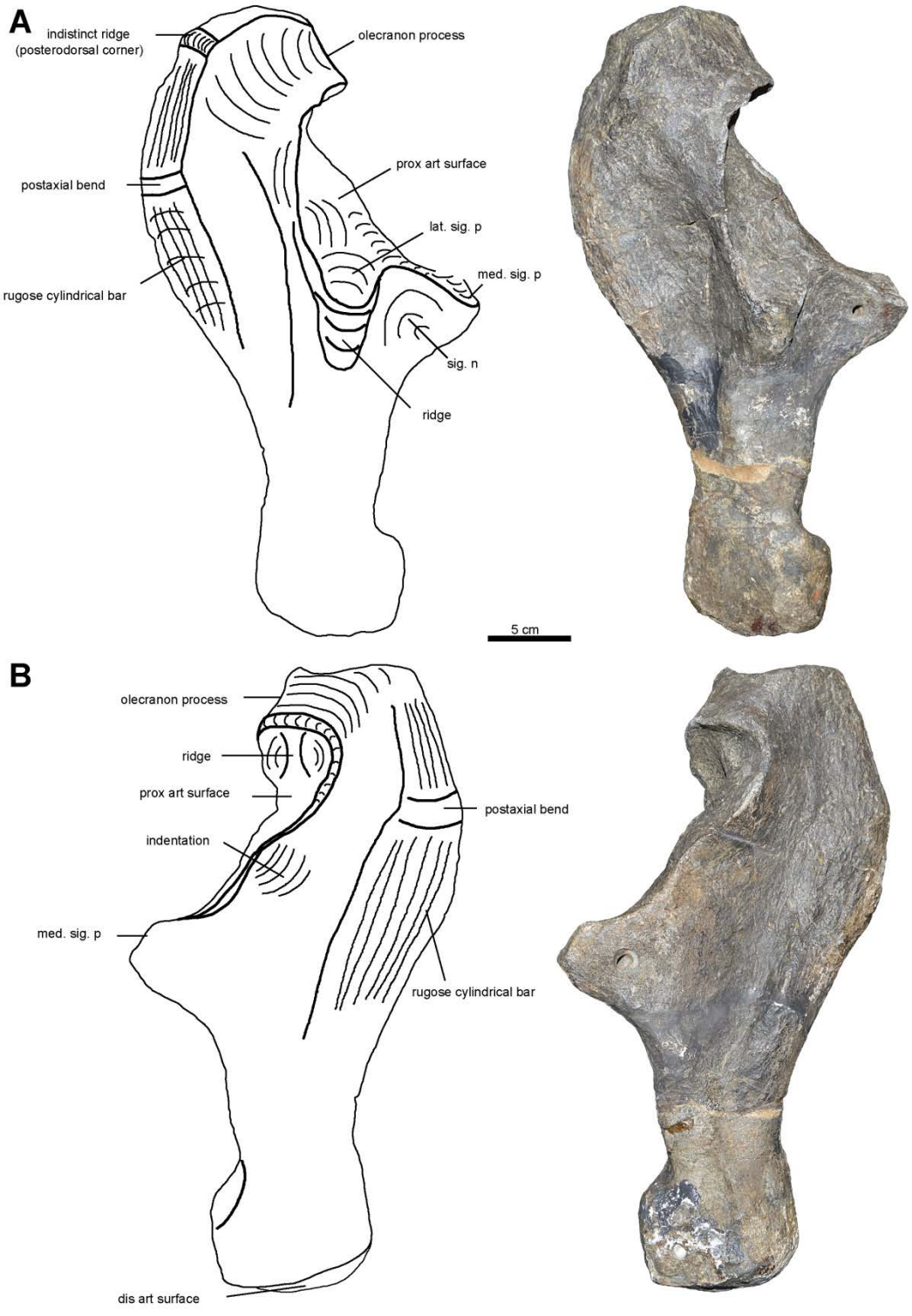


Figure 6.6: Photographs and interpretive drawings of the right ulna of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), in lateral view, and (B), in medial view. Proximal to the top of the page.

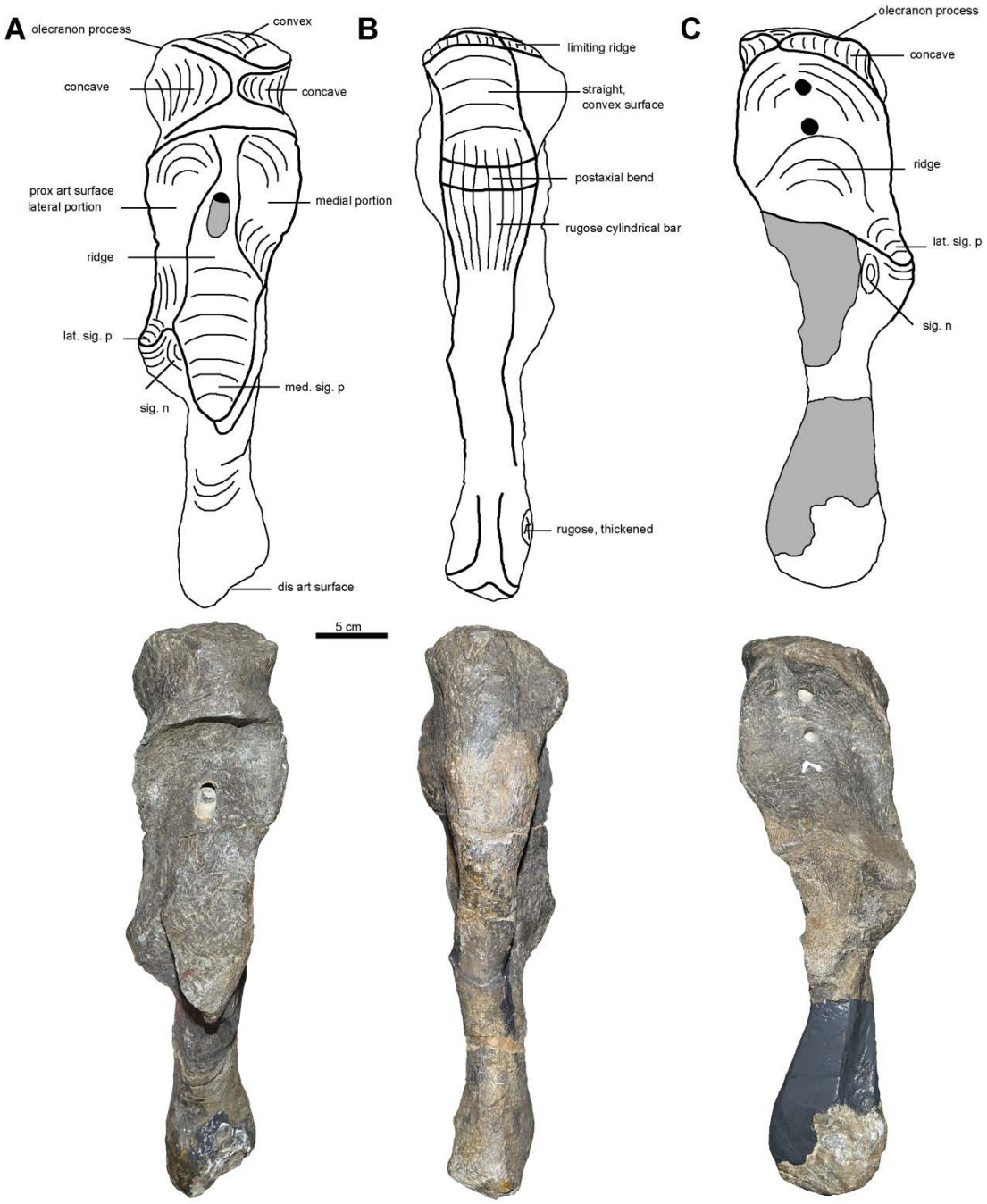


Figure 6.7: Photographs and interpretive drawings of the ulnae of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), right ulna in anterior view, (B), right ulna in posterior view, and (C), left ulna in anterior view. Proximal to the top of the page.

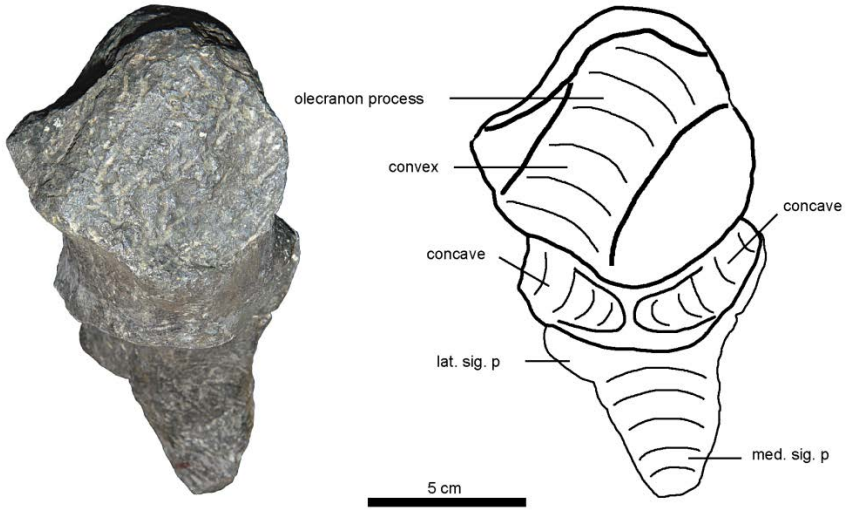


Figure 6.8: Photograph and interpretive drawing of the right ulna of the holotype of *Bradysaurus baini* (NHMUK R1971), in proximal view. Posterior to the top of the page.

In *Bradysaurus baini*, the olecranon processes are formed anterodorsally by two overhanging ledges, which are concavely curved projections of the lateral and medial surfaces of the ulna, that meet each other anteriorly. Dorsally the olecranon process is convex. In referred *Nochelesaurus* specimen SAM-PK-6238, anterodorsally only the lateral side of the olecranon process curves medially, and constricts the ulna, but does not meet the lateral side and the olecranon process is very low (20 mm).

A transverse limiting ridge (Fig. 6.6A)(as in the holotype of *Nochelesaurus*, but not in the holotype of *Embrithosaurus*) is present at the posterodorsal corner of the ulna of *Bradysaurus*, and separates the proximal olecranon process from the postaxial bar (Turner *et al.* 2015 character 105).

Manus

Since the manus and carpus of the holotypes of *Embrithosaurus* and *Nochelesaurus* are not preserved, the description here of the manus and carpus of *Bradysaurus baini* does not include comparative species morphology and is brief.

Most of the right carpus and manus is preserved and was arranged by Seeley (1892) into five digits. The principal carpus is a large rounded element, dorsally convex for reception with the concave articular surface of the distal radius (Seeley 1892, Boonstra 1929a). As noted by Seeley (1892) two small carpals are attached. As arranged by Seeley (1892) there are 5 rows (digits) of one metacarpal and three phalanges each, including a large terminal claw phalange per row. One digit appears to have four phalanges (Seeley 1892, Boonstra 1929a). Boonstra (1929a) records Seeley's (1892) phalangeal formula as 3, 4, 4, 3, 3 for this specimen.

6.4.3 Hindlimbs

Femur (Fig. 6.9)

The right femur of NHMUK R1971 is complete, and severely dorsoventrally crushed to measure only 55 mm in dorsoventral thickness at the narrowest point of the shaft, compared to the undistorted left femur which measures 85 mm dorsoventrally at the narrowest point of the shaft. The left femur comprises only the shaft and the medial condyle, as the head and large lateral condyle are reconstructed.

The right femur of the holotype of *Bradysaurus baini* is of typical length for middle Permian South African pareiasaurs (415 mm long) and the anteroposterior width of the proximal head (200 mm) is the same as that of the holotype of *Nochelesaurus*, and slightly narrower than that of *Embrithosaurus* (210 mm). The narrowest point of the shaft is anteroposteriorly the widest (135 mm) compared to the other middle Permian South African pareiasaurs: 120 mm for *Nochelesaurus* and 110 mm in *Embrithosaurus*. The expanded distal condyles are also anteroposteriorly the widest (190 mm) compared to the other middle Permian South African pareiasaurs: 170 mm *Embrithosaurus*, 155 mm *Nochelesaurus*. The torsion of the planes between the proximal and distal articulations is only 10^0 on the crushed right femur (probably due to the

dorsoventral crushing effect), whereas the less distorted left femur shows the more typical condition (30^0) of torsion, present in the other middle Permian South African pareiasaurs.

The proximal articulation surface of the head of the femur is dorsoventrally narrow, due to crushing. The posterodorsal notch, just proximal to the major trochanter is shallow (also present in *Embrithosaurus* and *Nochelesaurus*). Preaxially, the proximal articulation surface is gently convex and curves slightly distally before terminating at a 90^0 sharp bend (Turner *et al.* 2015 character 120). The formoral head creates an angle of about 40^0 from the plane of the femoral shaft (Fig. 6.9), identical to the situation in *Embrithosaurus* and *Nochelesaurus*.

The major (external) trochanter of *Bradysaurus baini* is small as it protrudes posteriorly only a short distance, 10 mm (NHMUK R1971, SAM-PK-5002) beyond the postaxial edge of the femur (Turner *et al.* 2015 character 122). Dorsoventrally it is quite swollen to approximately the same amount as in the holotypes of *Embrithosaurus* and *Nochelesaurus* (35 mm each). Sub-adult specimen SAM-PK-5002 is slight thinner at 30 mm (Turner *et al.* 2015 character 121). The tubercle present on the posterodorsal corner of the femur of *Nochelesaurus*, immediately dorsal to the major trochanter, is not present in *Bradysaurus baini* or *Embrithosaurus*, but this difference is insignificant.

The postaxial flange is very typical of middle Permian South African pareiasaurs as it extends distally from the major trochanter over the entire length of the shaft of the femur to the lateral condyle (220 mm) (Turner *et al.* 2015 character 123**)**.

As in all of these similar South African pareiasaurs, both femora of NHMUK R1971 show the femur to be consistently wide over the entire length of the shaft (Turner *et al.* 2015 character 124) to slightly outwardly bulging, as the postaxial edge of the postaxial flange is straight to slightly convex (bulging) in

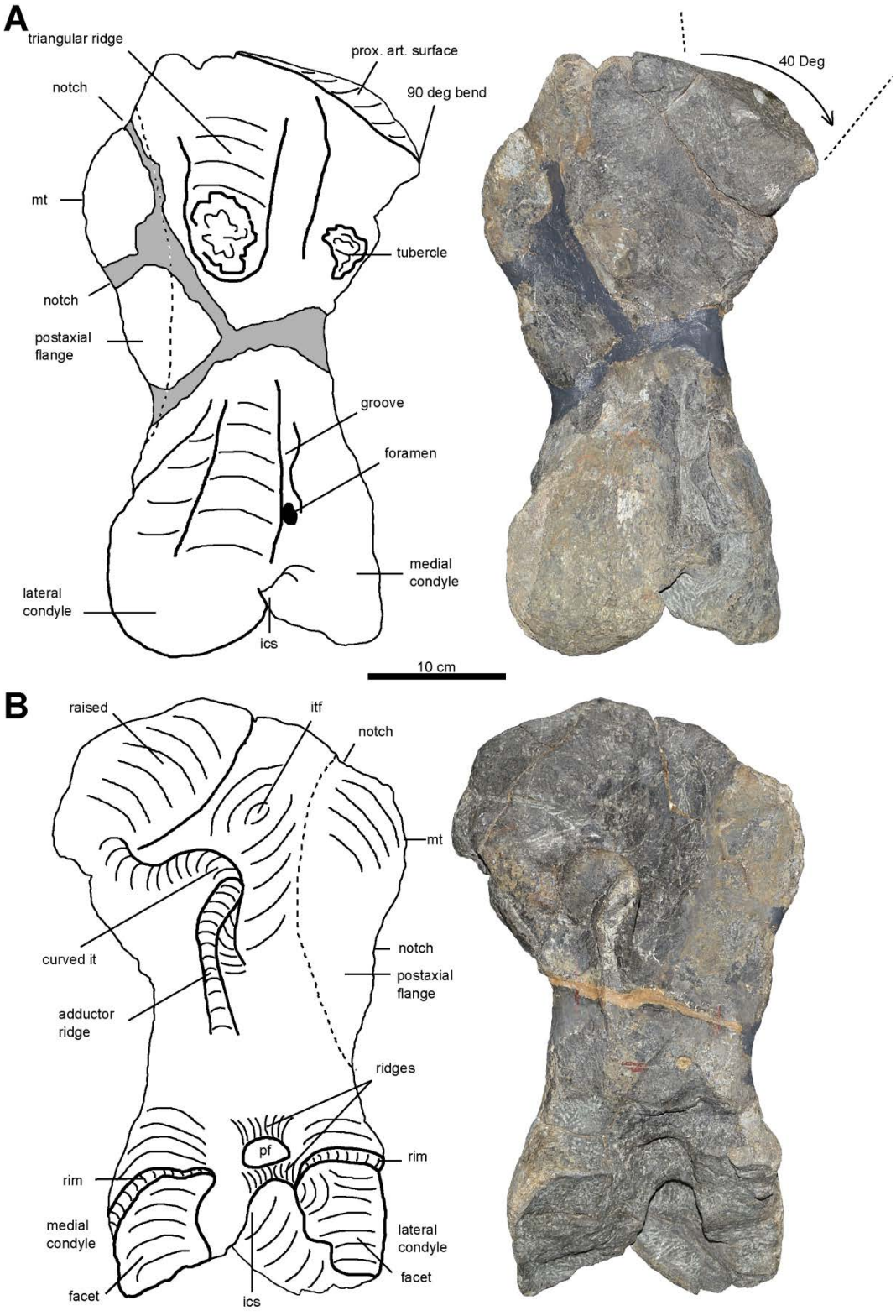


Figure 6.9: Photographs and interpretive drawings of the right femur of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), in dorsal view, and (B), in ventral view. Proximal to the top of the page.

dorsal or ventral view. The dorsoventral thickness of the flange increases distally, as in all middle Permian South African pareiasaurs.

A triangular ridge for muscular attachment dominates the dorsal surface of the proximal portion of both femora, low on the crushed right femur, it is massive, raised, round and rugose on the better preserved left femur. As in *Embrithosaurus* and *Nochelesaurus*, a small, low, tubercle is present anterior to this ridge, on the preaxial border (Fig. 6.9A).

It is important to note the morphology of the highly diagnostic internal (minor) trochanter. Broken off on the left femur, the right femur shows the minor trochanter forming a massive, curved, "flattened coin" shaped process, protruding ventrally from the proximal portion of the straight adductor ridge. Proximally it is strongly curved to be concave anteriorly and convex posteriorly (Turner *et al.* 2015 character 125). A more gently curved but protruding internal trochanter is present in *Embrithosaurus*, whilst *Nochelesaurus* exhibits a very different straight and low internal trochanter. In *Bradysaurus*, the internal trochanter extends posteroventrallly very far (40 mm in NHMUK R1971, 30 mm in SAM-PK-5002) beyond the shaft of the femur, compared to *Embrithosaurus* (30 mm) and *Nochelesaurus* (10 mm). In *Bradysaurus baini* (NHMUK R1971, SAM-PK-5002) and *Embrithosaurus* (SAM-PK-8034) the proximal edge of the internal trochanter emerges ventrally abruptly perpendicularly (90^0) out of the femur (and obliquely in specimens of *Nochelesaurus*).

The dorsal surface of the distal right femur is damaged but the left side shows the typical shallow groove containing the large nutritive foramen. The size, shape and orientation of the medial and lateral condyles and articular facets are typical for this group of middle Permian pareiasaurs. Similarly, the intercondylar sulcus is deep ventrally and the popliteal fossa on the ventral surface is large and wide. The large lateral condyle extends distally only 20-30 mm beyond the edge of the medial condyle in the holotype, but much further in SAM-PK-5002 (50 mm left, 40 mm right) and 30-40 mm in the holotype of *Embrithosaurus*). In the holotype

of *Nochelesaurus* it extends the furthest, 70 mm, beyond the edge of the medial condyle.

Tibia (Fig. 6.10)

The right tibia of the holotype of *Bradysaurus baini* is complete, but anteroposteriorly crushed. Most of the proximal half of the left tibia is reconstructed in plaster, apart from a small posterolateral piece. The morphology of the tibia is typical for this group of middle Permian pareiasaurs, with expanded proximal and distal ends and a constricted shaft and with the proximal expansion mediolaterally much wider than the distal expansion. The proximal and distal planes of the tibia are not greatly angled to each other (only about 20^0 on the complete right tibia).

Posteriorly, the proximal depression is shallow and the distal one deeper (possible due to crushing) and the diagonal ridge that extends between these depressions is well developed. As in all middle Permian South African pareiasaurs the proximal lateral border of the proximal depression houses a rough, rugose, irregular, wide tubercle and rough, highly rugose proximal and distal articulation surfaces are present, implying a thick cartilaginous covering.

Anteriorly, the cnemial crest is well developed and there is a short lateral twist or overhang over the deep, vertical, lateral excavation (Turner *et al.* 2015 character 126).

The proximal articulation surface of the right tibia is damaged and missing a small piece anterolaterally. This surface shows extreme dorsoventral height of the oblique ridge (40 mm), being about twice the height of the same feature (20 mm) in the holotypes of *Embrithosaurus* and *Nochelesaurus*, which fits in the intercondylar sulcus groove of the femur. Unfortunately, the extreme dorsoventral height of this ridge on the right tibia cannot be confirmed on the left tibia, which is reconstructed proximally. Ultimately this does not matter as all other specimens of *Bradysaurus baini* do not have such a high ridge.

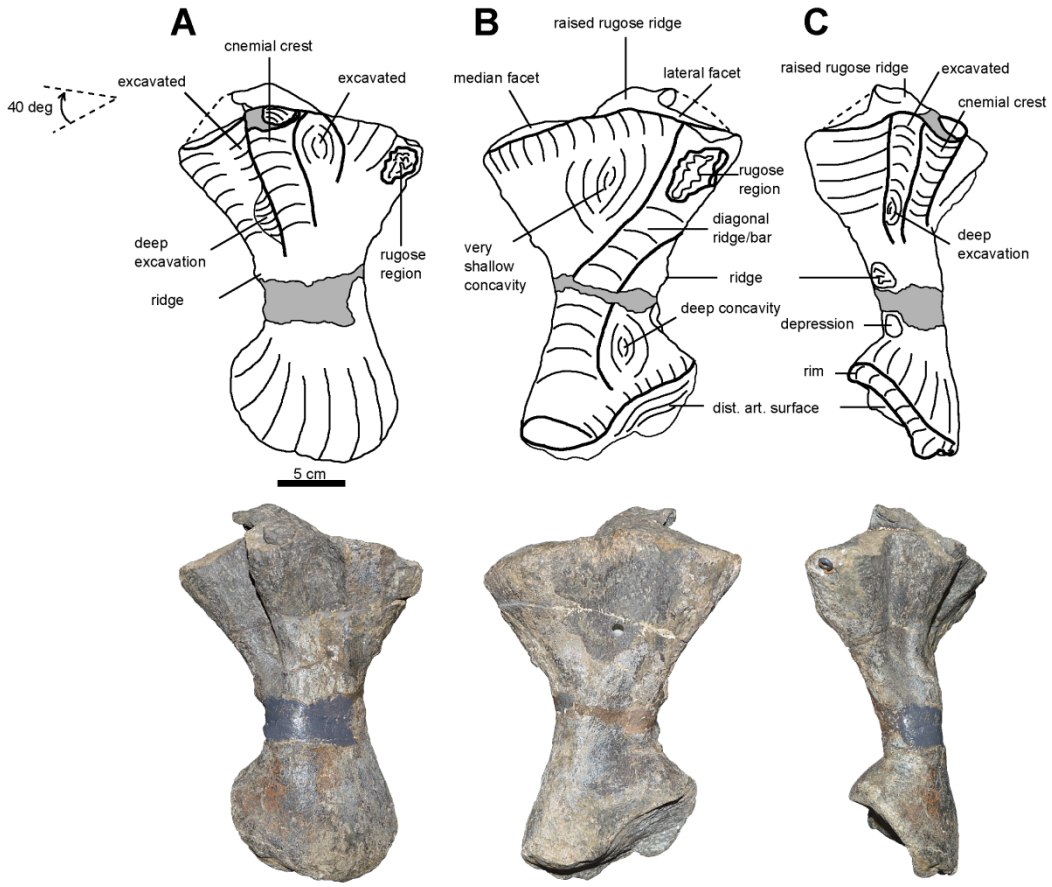


Figure 6.10: Photographs and interpretive drawings of the right tibia of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), in anterior view, (B), in posterior view, and (C), in lateral view. Proximal to the top of the page.

The large medial facet is slightly convex and faces dorsally. As in all taxa in this group, the smaller lateral facet is bent to face dorsolaterally. The angle of the planes between the medial and lateral facets is small (40^0), similar to *Nochelesaurus* specimens, and different from the larger (60^0) angle in the holotype of *Embrithosaurus*. Proximally the tibia of *Bradysaurus baini* is mediolaterally wide (180 mm).

The distal articulation surface is typical for large middle Permian South African pareiasaurs: the large lateral facet is shallowly concave, and the smaller medial facet comprises a convex, raised portion posteriorly and a very shallow, depressed, concave portion anteriorly. A shallow notch is present on the posterior margin of the distal articulation surface, between the lateral and medial facets. The distal articulation surface of the right tibia is not horizontally

oriented, but instead creates an oblique angle about 45^0 from the horizontal plane.

Possibly diagnostic, the right tibia of *Bradysaurus baini* shares with *Nochelesaurus* a mediolaterally wide distal tibia, caused by a distal ventromedial expansion and the distal ventrolateral side being upturned. On the lateral edge of the shaft of the tibia is an elongated rugose ridge, just dorsal to a vertical depression, both of which are also present in *Nochelesaurus*, whilst *Embrithosaurus* shows the same depression and lacks the rugose ridge.

Fibula

The left fibula of the holotype of *Bradysaurus baini* consists of only the distal half, and the right fibula is also incomplete, preserving the distal half and a partial shaft. The shaft is typically narrow. Distally, the fibula of *Bradysaurus baini* is very similar to the fibulae of the holotypes of *Embrithosaurus* and referred *Nochelesaurus* specimen SAM-PK-6238. It is widely expanded with a straight lateral side and a severely flared/concave medial side. Distally, a rugose region or tubercle is present on the medial side of the fibula, as seen in *Nochelesaurus* and *Embrithosaurus*.

The distal articular surface forms an elongated diamond-shape in cross section, and is damaged and distorted posteriorly. The planes of the distal and proximal expansions are each offset by 45^0 from a horizontal plane.

Tarsus (Fig. 6.11)

The holotype of *Bradysaurus baini* preserves both left and right astragalocalcania. Broom (1903) described a (now lost) large tarsal element in the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034) as very similar to the astragalocalcania of the holotype of *Bradysaurus baini*. In NHMUK R1971, both astragalocalcania are 5 sided and roughly rectangular. The posterior surface is flattened, slightly concave and rectangular, and the margins form a raised rim around the bone. The centre of the ventral surface shows a long, groove (65 mm

long, about 10 mm deep) which is open at the dorsal/proximal margin (here 15 mm wide) and extends towards the centre of the bone where it widens to 30 mm. The groove terminates at the posterior opening of a large foramen.

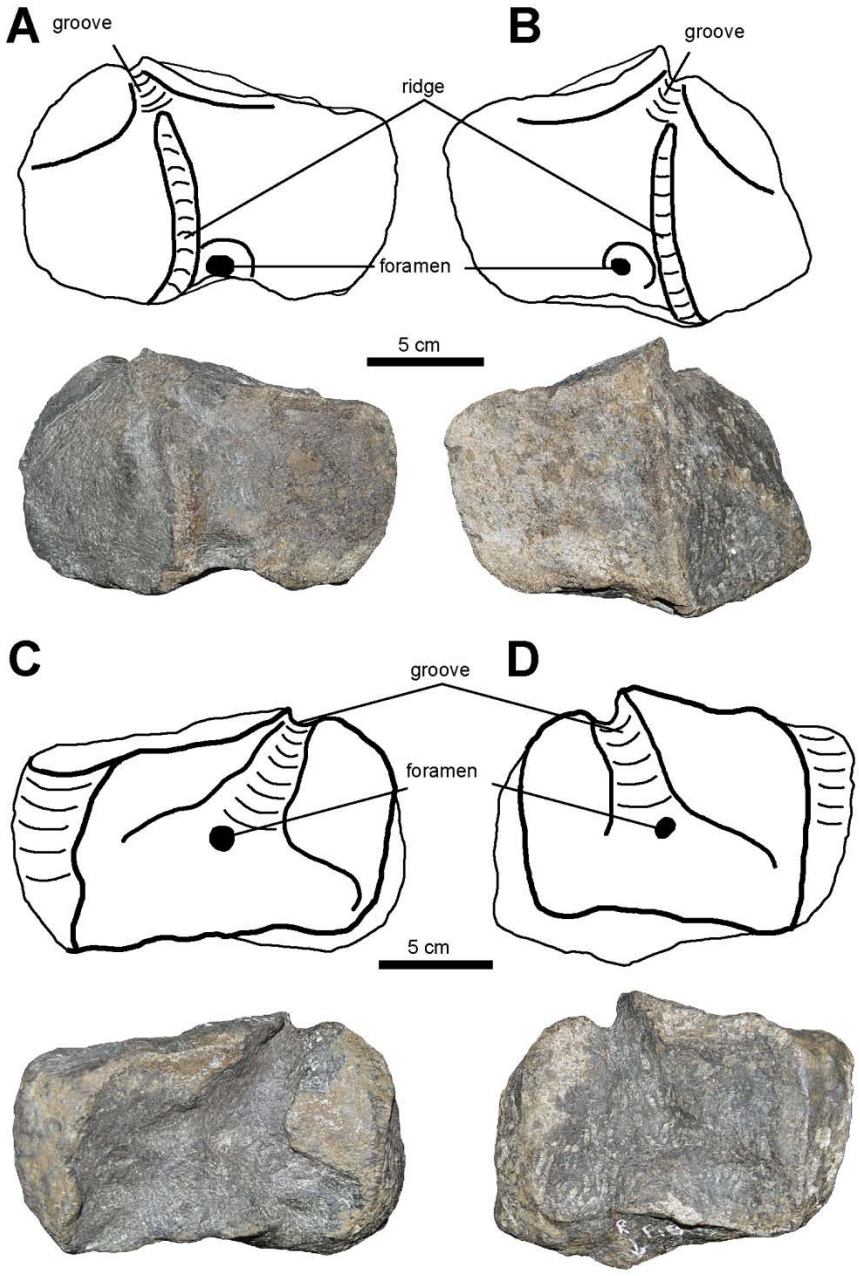


Figure 6.11: Photographs and interpretive drawings of both (left and right) astragalocalcania of the holotype of *Bradysaurus baini* (NHMUK R1971), (A) and (B) in dorsal views, (C) and (D), in ventral views. Posterior to the top of the page.

The anterior articulation surface comprises a roughly equally sized, concave and a convex portion, separated by a slightly curved, 20-25 mm high, oblique, vertical, swelling. Both left and right elements show a large foramen (5 mm wide) on the anterior side, near the centre, within the convex articulation, just below the dorsal/proximal margin.

Pes

Since most of the pedes of the holotypes of *Embrithosaurus* and *Nochelesaurus* are not preserved, the pes of *Bradysaurus baini* cannot be critically compared and is not described here. Specimen NHMUK R1971 preserves the right pes, arranged by Seeley (1892) for which he assigned five digits, with short, broad flattened metatarsals, with three phalanges, including the terminal claws.

6.4.4 Pelvic Girdle

The pelvis of the holotype of *Bradysaurus baini* is virtually complete, well preserved and well prepared, with only a few small isolated regions crushed, distorted or filled with plaster. The pelvis is noticeably low and wide in comparison with the narrow and high pelvis of *Embrithosaurus*. As with *Embrithosaurus*, the sutures between the ilium, ischium and pubis are strongly fused and not discernible.

Ilium (Figs. 6.12, 6.13, 6.14)

Anterodorsally, the iliac blade is long (290-310 mm) compared to that of *Embrithosaurus* (260 mm) because of the slightly longer anterior process (130 mm) compared to that of *Embrithosaurus* (90 mm) (Turner *et al.* 2015 character 110). The posterior process is slightly shorter (at 50 mm) than the length of *Embrithosaurus* (60 mm) (Turner *et al.* 2015 character 112).

The anterior and dorsal margins of the anterior processes are very wide (25 mm mediolateraly wide) compared to the narrower 15-20 mm width in *Embrithosaurus*) and are flat, sharp edged, with slightly raised rims.

Unlike *Embrithosaurus schwarzi*, the iliac blades of the holotype of *Bradysaurus baini* are complex. The posterior half of the iliac blade is vertically oriented and is flat and thin, but the dorsal margin of the posterior process curves medially inwards a short distance (25 mm) towards the midline, giving the posterior blade a convex shape posterodorsally (Figs. 6.13A, 6.14B, left blade, NHMUK R1971, SAM-PK-5002). The anterior half of the iliac blade is not oriented vertically as the anterior process everts or bends upwards (facing the blades upwards) forming an angle of 55-60^0 outwards from a parasagittal vertical plane (Fig. 6.12A: NHMUK R1971, SAM-PK-5002) (Turner *et al.* 2015 character 111).

Posteriorly, the vertical and straight iliac blades are oriented parallel to each other and to the parasagittal plane (Fig. 6.13A: NHMUK R1971, SAM-PK-5002). In the holotype, the left blade is aligned with the parasagittal plane; the right blade is directed slightly laterally outwards, by 10^0 off a parasagittal plane, anteriorly diverging (Fig. 6.13A). Anteriorly, the blades are not parallel to each other and to the parasagittal plane, but are sharply concavely curved laterally outwards and the anterior ends of the anterior process are oriented roughly 45^0 off the parasagittal plane, diverging anteriorly, with the anterior tip of the anterior process extending up to 80 mm laterally from the sagittal plane in NHMUK R1971, SAM-PK-5002 (Fig. 6.13A) (Turner *et al.* 2015 character 111).

The neck of the ilium of *Bradysaurus baini* is directed horizontally (anterodorsally), only about 30^0 above the horizontal plane (Fig. 6.14A) compared to that of *Embrithosaurus*, which has a more vertical shaft orientation, about 60^0 anterodorsal from the horizontal. (The orientation of the shaft described here assumes that the dorsal edge of the anterior process of the sacral blade is oriented slightly below a horizontal plane, such that the orientation of the sacral vertebrae is horizontal and slightly ventral, as they would have been in life position (Turner *et al.* 2015 character 113).

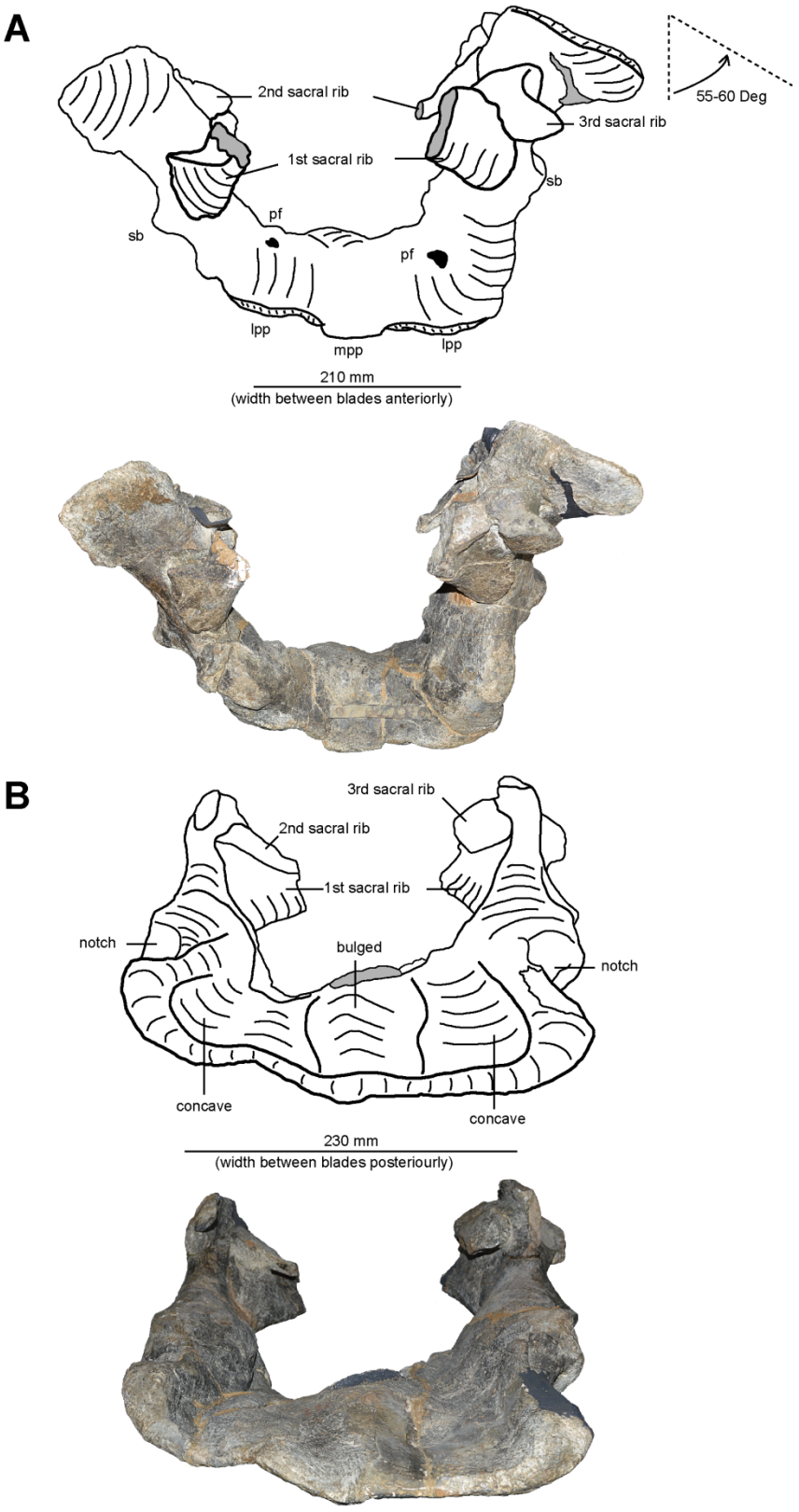


Figure 6.12: Photographs and interpretive drawings of the pelvis of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), in anterior view, and (B), in posterior view. Dorsal to the top of the page.

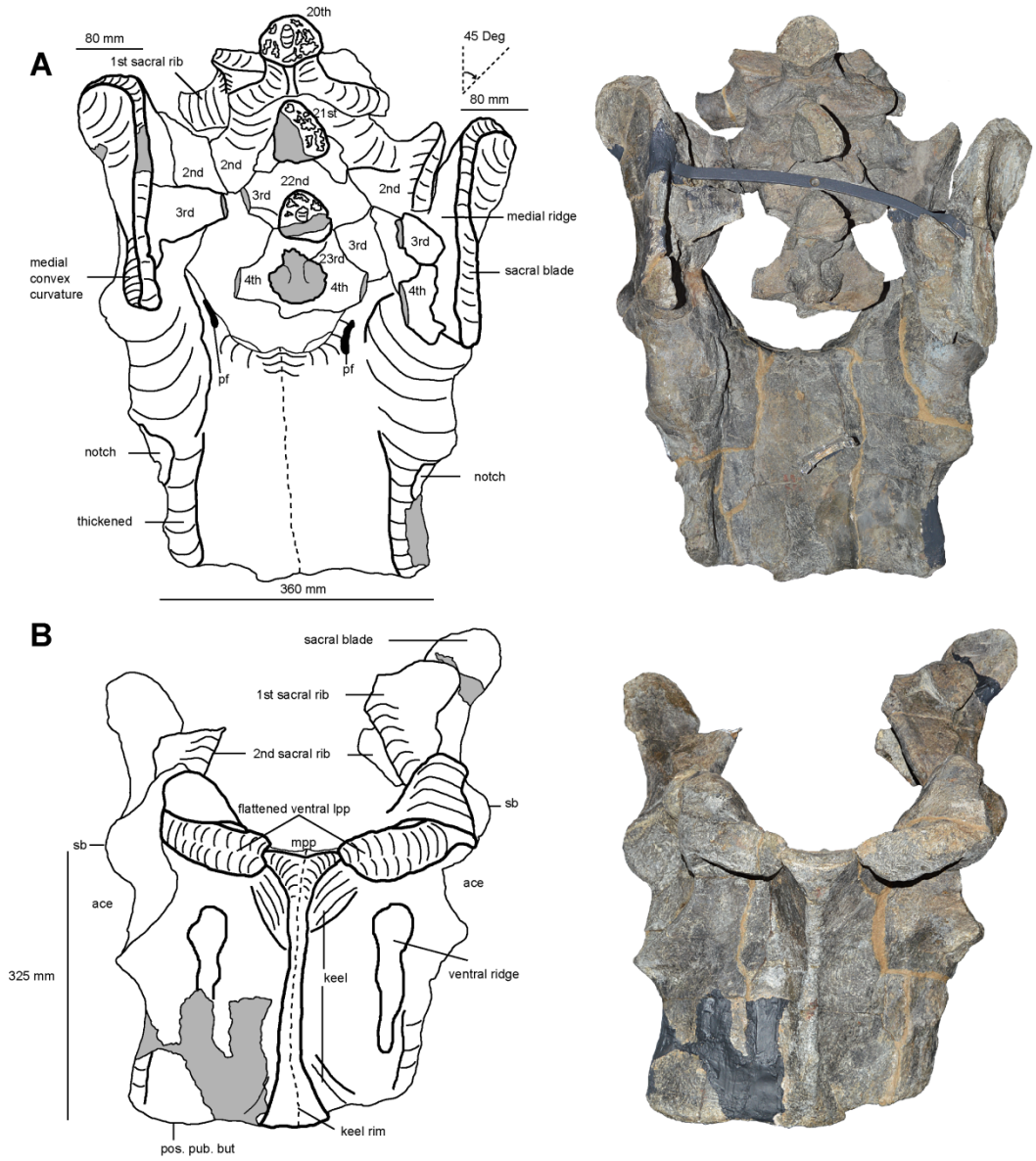


Figure 6.13: Photographs and interpretive drawings of the pelvis of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), in dorsal view, and (B), in ventral view. Anterior to the top of the page.

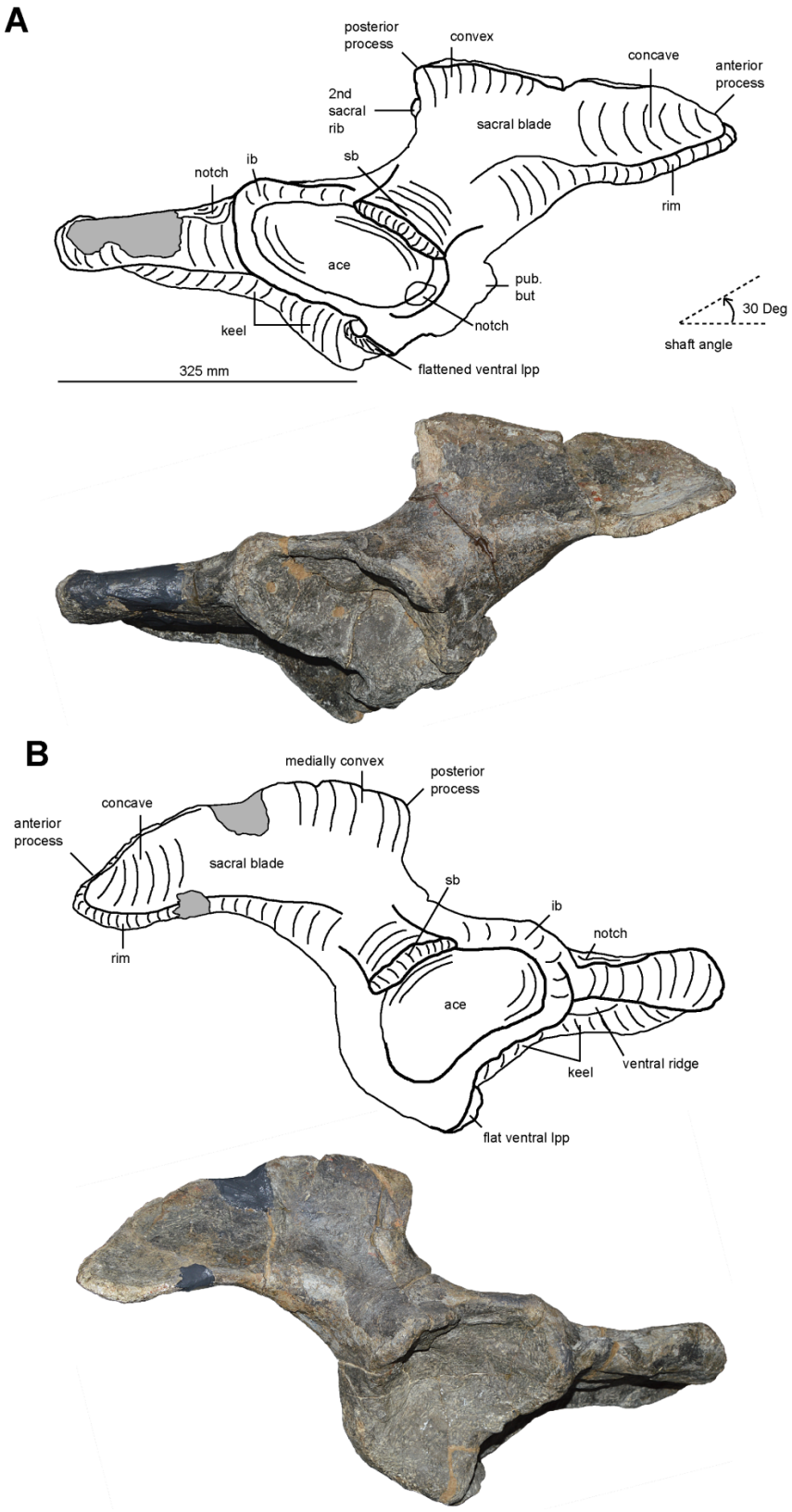


Figure 6.14: Photographs and interpretive drawings of the pelvis of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), in right lateral view, and (B), in left lateral view. Dorsal to the top of the page.

The medial process of the iliac blade which articulates with the first sacral rib is horizontally to anterodorsally oriented and is prominent, protruding 40 mm medially from both iliac blades, a similar morphology to that seen in *Embrithosaurus*.

The acetabulum is large and noticeably oval (anteroposteriorly elongated, dorsoventrally flattened), longer than the rounder acetabulum of *Embrithosaurus,* partially exaggerated by dorsoventral crushing (Fig. 6.14). Three thickened regions are prominent: as in *Embrithosaurus* the dorsal supra-acetabular buttress under the shaft of the ilium is the largest and protrudes laterally 35 mm, forming an almost perfect semi-circular overhanging dorsal "lip" to the acetabulum (Turner *et al.* 2015 character 114). The ischial buttress on the posteroventral corner of the acetabular rim, supports the posterior puboischiatic plate. The pubic buttress is the least robust of the three, as in *Embrithosaurus*, and is low and flattened. The shallow and indistinct notch on the anterior acetabular rim just above the dorsal edge of the pubic buttress, which is present in the holotype of *Embrithosaurus,* is also present in *Bradysaurus baini* (Turner *et al.* 2015 character 115).

Pubis (Figs. 6.12, 6.13, 6.14)

The puboischiatic plate of the pelvis of *Bradysaurus baini* is very different from that of *Embrithosaurus*. It is wide, measuring 360 mm between the lateral edges of the lateral pubic processes anteriorly, and the same width posteriorly, between the posterolateral edges of the posterior pubic buttress (Fig. 6.13A). The puboischiatic plate of *Embrithosaurus* is much narrower, measuring 305 mm wide anteriorly and 290 mm wide posteriorly (Figs. 4.18, 4.19). In *Bradysaurus baini*, dorsally between the iliac blades the plate is wide, measuring 210 mm anteriorly and 230 mm posteriorly (Fig. 6.12). In contrast the much narrower pelvis of *Embrithosaurus* measures about half of the width of *Bradysaurus baini* between the iliac blades, 95 mm anteriorly and 130 mm posteriorly (Fig. 4.18A, B).

The puboischiatic plate of *Bradysaurus baini* is anteroposteriorly extremely long, measuring 325 mm (Fig. 6.13B) in the holotype, compared to the much shorter 220 mm in the holotype of *Embrithosaurus* (Fig. 4.19B) (Turner *et al.* 2015 character 118).

The puboischiatic plate of *Bradysaurus* is horizontally flat, and dorsally slightly raised or bulged (convex) along the midline (more so over the anterior half). Posteriorly there are wide and shallow longitudinally elongated depressions either side of the bulged midline (Fig. 6.13). In *Embrithosaurus*, the dorsal surface of the anterior plate between the blades is not flat and bulged at the midline, but strongly and deeply concave, lacking shallow dorsal depressions posteriorly.

The ventral surface of the puboischiatic plate of *Bradysaurus* is flat and forms a broad plate. It has a midline, ventrally directed v-shaped "keel", which is mediolaterally narrow, measuring anteriorly 60-70 mm across (Fig. 6.13B). In *Bradysaurus* there is a low longitudinal ventral ridge on either side of the keel (Fig. 6.13B). In contrast, *Embrithosaurus*, lacks longitudinal ventral ridges either side of the keel and the the ventral surface of the puboischiatic plate is not flat, as it forms steep sides of a more sharply angled, wider keel, measuring at least 100 mm in *Embrithosaurus* (Fig. 4.19B). In both *Bradysaurus* and *Embrithosaurus*, the ventral keel narrows in the middle (Figs. 6.13, 4.19).

Surprisingly, the maximum dorsoventral thickness (80 mm) of the narrow pelvic symphysis or keel of NHMUK R1971, is almost as thick as that of the holotype of *Embrithosaurus* (90 mm). Sub-adult *Bradysaurus baini* SAM-PK-5002, measures 70 mm (Turner *et al.* 2015 character 119). As in *Embrithosaurus*, the keel of *Bradysaurus* is not level: the anterior half slopes anteroventrally downwards at about 25-30^0 below the horizontal plane, and the posterior half is horizontally oriented and level (Fig. 6.14).

Anteriorly, the dorsal surface of the plate curves sharply downwards, forming an 80 mm high vertical wall that supports each lateral pubic process (Fig. 6.12A) (Turner *et al.* 2015 character 116).

The anterior margin of the pubis of NHMUK R1971 has a wide median pubic process (75 mm wide). However there are differences compared to the median pubic process of *Embrithosaurus*. In *Bradysaurus*, it is rectangular to square with perpendicular sides, and extends only 10 mm ventrally below the lateral pubic processes (Turner *et al.* 2015 character 117). In *Embrithosaurus*, it forms a curved "tongue" and extends anteroventrally much further (50 mm). Lateral to the median process, *Bradysaurus baini* has mediolaterally wide lateral pubic processes (140 mm wide) which are horizontally flattened over most of their ventral surface and only curve upwards at the lateral extremes. In the holotype of *Embrithosaurus*, the lateral process are slightly shorter mediolaterally (120 mm) and curve or direct upwards over their entire length.

Ischium (Figs. 6.12, 6.13, 6.14)

The ischium forms the posterior portion of the puboischiatic plate, which has been fully described (see pubis) and part of the acetabulum (see ilium). The posterior rim of the ischium is very thin in *Embrithosaurus* (less than 10 mm thick). In *Bradysaurus baini* it is slightly thicker, 15 mm, and is much thicker and higher at the lateral sides of the posterior pubic buttress, which form longitudinally thickened bars or cylinders (Figs. 6.12, 6.13, 6.14) measuring 30 mm wide, 40 mm high.

6.4.5 Vertebral column and ribs

The holotype of *Bradysaurus baini* preserves an almost complete vertebral column, but the historic preparation was rough and superficial compared to the good preparation of the long bone elements. The anterior cervicals (atlas and axis) are isolated. A large articulated block contains the 3rd to 12th vertebrae, i.e. the posterior cervicals (3rd, 4th and 5th vertebrae) and most of the dorsal

vertebrae (6th to 12th vertebrae). The rest of the dorsal vertebrae (13th to 18th vertebrae, and a partial 19th vertebra) are contained in a separate block (Turner *et al.* 2015 character 80). As a result of the articulated blocks, only the dorsal, lateral and ventral surfaces of most vertebrae are accessable, and most of the anterior and posterior sides are not. The sacral vertebrae (20th to 23rd vertebrae) are in a separate block. The 24th to 27thcaudal vertebrae are articulated, the 28th to 37th are articulated, and lastly the 38th to 50th are articulated.

Ribs

Most of the ribs of the holotype of *Bradysaurus baini* are not preserved, apart from several almost complete dorsal ribs articulated to the block of the 13 th-19th dorsal vertebrae. There are four sacral ribs attached to the 20th to 23rd vertebrae.

There are no cervical ribs preserved. Five long ribs are attached to the left lateral side of the 8th, 9th and 10th dorsal vertebrae. These ribs are almost complete, 600 mm long. On the right side, ventrally, are the proximal-most 120 mm of five long ribs. The left side rib heads are single headed and have articular surfaces 90-100 mm dorsoventrally long, and are s-shaped, and double lobed. The single lateral facet of the fused diapophysis and parapophysis of the posterior dorsal vertebrae, create a long single, lateral facet and indicate that the rib articulations were single headed (holocephalus).

Sacral ribs (20th-23rd vertebrae) (Fig. 6.13)

As in *Embrithosaurus*, the medial portions of the sacral ribs are attached to the vertebrae and the lateral portions to the inside of the iliac blades. The first sacral rib (attached to the 20th vertebra) is anterodorsally oriented and robust, especially on the left where medially it is anteroposteriorly 60 mm long, dorsoventrally 50 mm high, and much more robust than the last ribs of the last prescaral vertebra (on the 19th vertebra).

The second sacral rib (on the 21st vertebra) is the most robust on the sacrum and overall forms a high, anterodorsally oriented wall (+-30 mm anteroposteriorly).

The medial portions are attached to the sacral vertebra (Fig. 6.13) where it is dorsoventrally high (110 mm) and it is also anteroposteriorly long (50 mm). Laterally, the second sacral rib enlarges anterodorsally and terminates with a deep, concave, lateral facet for articulation with the convex bulge of the medial iliac blade, best seen on the right (Fig. 6.13A). The medial sides of both iliac blades preserve large, lateral sacral ribs, covering a large portion of the anteroventral medial surface of each iliac blade (Fig. 6.13B)(as in *Embrithosaurus*)

The third and fourth sacral ribs are similar to each other. They are much smaller than the first two sacral ribs (medially: 30 mm anterodorsal length, 25 mm dorsoventrally high) and are oriented almost horizontally, and so appear dorsoventrally flattened, thin, plate or "sheet like" (Turner *et al.* 2015 character 108). On the medial illiac blades, portions of these lateral ribs are preserved as widened sheets (3rd sacral rib on the left, 3rd and 4th on the right) (Fig. 6.13A)

Anterior cervical vertebrae (Atlas: 1, Axis: 2)

Atlas (1st vertebra) (Fig. 6.15)

The atlas and axis are preserved separately and have been very crudely prepared. The paired left and right neural arches of the atlas (atlantal arches), reported in *Embrithosaurus* by Boonstra (1934c) are not preserved.

A large, long and curved, left atlantal intercentrum is articulated with the occipital condyle of the skull. It covers the posteroventral and posterolateral left side of the occipital condyle and is not preserved on the right. It forms a concavely curved, posterodorsal surface for reception with the convex bulge of the anterior surface of the atlas (Turner *et al.* 2015 character 79).

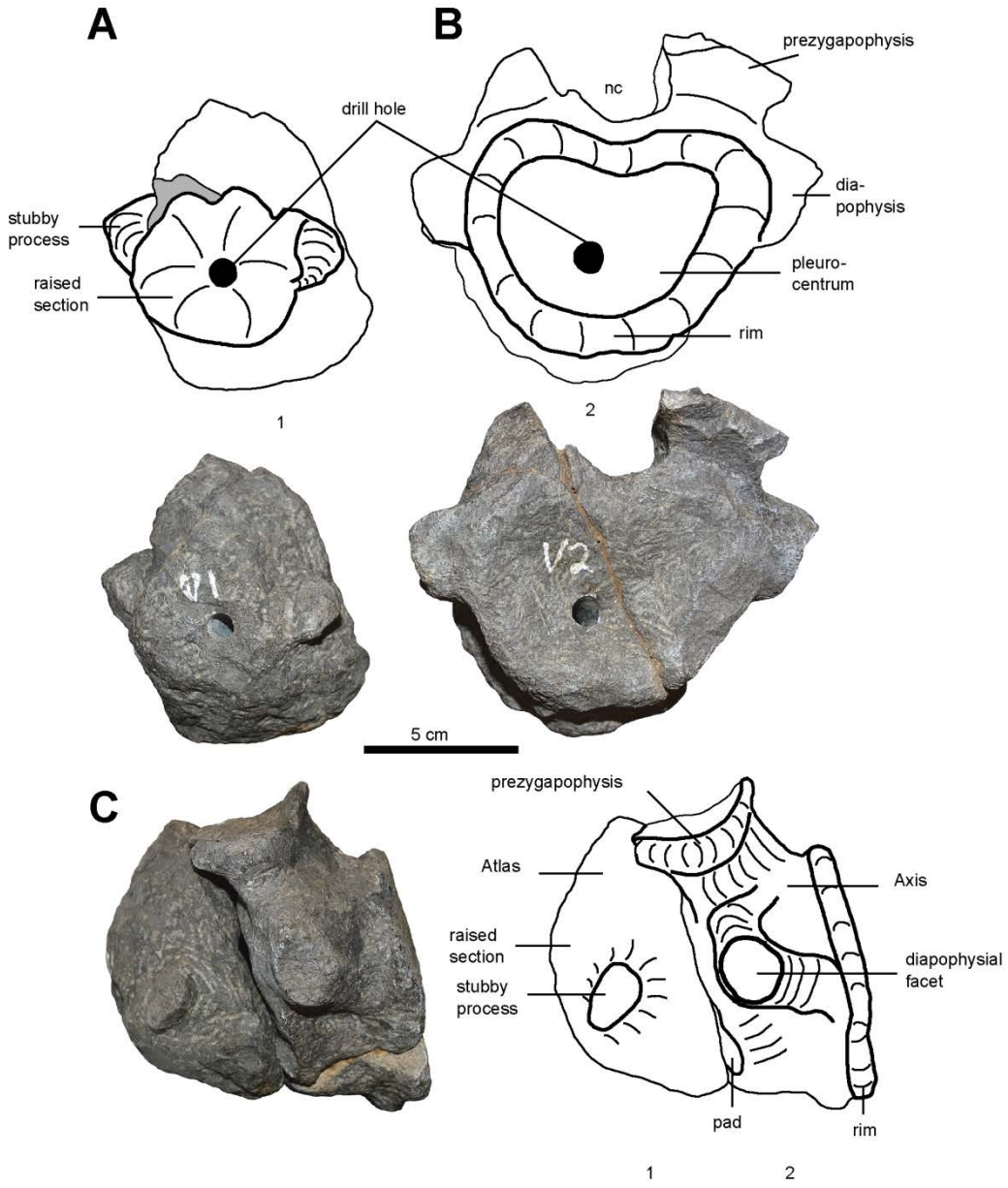


Figure 6.15: Photographs and interpretive drawings of the vertebrae of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), atlas in anterior view, (B), axis in anterior view, and (C), atlas and axis in left lateral view. Dorsal to the top of the page.

As in *Embrithosaurus*, the anterior side of the pleurocentrum of the atlas is easily identifiable as a dominant dome, strongly convex, with a raised central section for articulation with the concavity on the posterior side of the occipital condyle of the skull. The posterior side of the atlas is deeply concave.

On the lateral surface of the atlas, is a small, stubby, ovoid process, oriented anteroventrally, also seen in *Embrthosaurus* (although as a more vertical, thin,

facet). The process is much larger on the right side. Posterior to the process is deep, thin, vertical groove as in *Embrithosaurus*.

The posterior border of the atlas is sharply rimed, apart from the posteroventral edge which is ventrally flattened.

The dorsal surface of the atlas is poorly prepared and appears as a convex bulge, a dorsal extension of the central, anterior bulging of the centrum of the atlas, but this is probably uncleared matrix. As in *Embrithosaurus* this region is deeply concave and accommodates the open neural canal.

Axis (2nd vertebra) (Fig. 6.15)

The paired neural arch of the axis is not preserved and the neural canal is cleanly prepared and open. The pleurocentrum is concave anteriorly and posteriorly. Laterally the laterally facing diapophysial process, for articulation with the head of the ribs, is short and stubby, vertical to slightly anterodorsally oriented and placed on the anterior rim of the lateral pleurocentrum, presenting a flat and slightly concave, tear-drop shaped, diapophysial facet, similar to *Embrithosaurus*.

The axial pleurocentrum is anteroposteriorly flattened and ventrally tapering. Laterally, below the diapophysis is a depressed hollow. The posterior border of the axis is much thicker and more robust than the anterior rim.

The prezygapophysis is not well preserved but on the better preserved right side, anterodorsal to the diapophysial process, is a short upwardly directed process for articulation with the atlantal neural arches (which are not preserved). No postzygapophyses are preserved.

Posterior cervical vertebrae (3rd, 4th and 5th vertebrae)

The posterior cervical vertebrae (3rd, 4th and 5th vertebrae) are articulated in a long block containing the 3rd to 12th vertebrae. The 3rd vertebra is much smaller than the 4th and 5th vertebra, which are larger and similarly sized. The pre- and postzygopophyses are shorter and smaller than those of the dorsal vertebrae.

As in *Embrithosaurus* and *Nochelesaurus*, the anterior rim of each centrum carries the lower positioned parapophysial process and facet. The facet is roughly square to round on a short and blunt process and is most prominent on the 4th vertebra. On the 5th vertebra, the parapophysial process and facet is vertically elongated, low and partially fused to the higher diapophysial process and facet. Interestingly, this fusion is only seen from the 6th vertebra backwards in specimens of *Embrithosaurus* and *Nochelesaurus*.

Higher up on the lateral sides of these vertebrae, is the diapophysial process and its lateral facet. The diapophysial process is anteroposteriorly thin, vertically elongated, curves dorsally and extends backwards. The facet is round and small, only 10 mm in diameter on the 3rd vertebrae. On the 4th and 5th vertebrae the facet is vertically elongated. The size of the diapophysial process and facet on the 5th vertebrae is much larger than that of the 3rd and 4th vertebrae, and is more similar in size to the anterior dorsal vertebrae (6th to 9th vertebrae).

The diapophysial process on the 5th vertebra forms a wall-like, mediolaterally wide transverse flange. It extends laterally much further than in the preceding two vertebrae and is partially fused to the lower, irregular parapophysial process and facet. In *Embrithosaurus*, and *Nochelesaurus*, from the 6th vertebrae backwards, the separate and distinct parapophysial and diapophysial articulations fuse into a single vertical flange, creating a transverse process with a single lateral facet. In *Bradysaurus baini*, this seems to occur one vertebra earlier, i.e. on the 5th vertebra, compared to the 6 th vertebra of *Embrithosaurus*, and *Nochelesaurus.*

The anteroventral border of each centrum of the 3rd, 4th and 5th vertebrae, has a small ventral process, which tapers posteriorly and forms a longitudinal midline ridge. Each centrum projects anteroventrally, creating an anterior lip-like protrusion.

The prezygapophysial processes on the 3rd vertebra are broken off, but were clearly quite small and slender. On the 4th and 5th vertebrae they increase in size

where they are short, mediolaterally narrow, as in *Embrithosaurus*, with small articular facets compared to that of the dorsal vertebrae. The posterolaterally directed postzygapophyses of the posterior cervicals are also relatively narrow and short and gradually increase in overall size and robustness posteriorly from the 3rd to the 5th vertebrae.

The neural spines of the 3rd and 4th vertebrae are missing, but from the complete 5th neural spine, they leant forwards, similar to the situation in *Embrithosaurus*. The holotype of *Embrithosaurus* preserves a complete 5th neural spine, which is diamond-shaped in cross section, anteroposteriorly flattened and mediolaterally wide, matching the morphology of *Bradysaurus baini*. The dorsal surface of the 5th neural spine of *Bradysaurus baini* is deeply concave and bowl shaped, with a distinct and deep longitudinal grove that creates anterior and posterior notches in the dorsal margin of the neural spine. A similar groove is also present in *Embrithosaurus*.

Dorsal vertebrae (6th to 12th and 13th to 19th)

The dorsal vertebrae include the 6th to 19th vertebrae and are preserved in two large blocks, an anterior block containing the 3rd to 12th dorsal vertebrae and a posterior block containing the 13th to 19th dorsal vertebrae.

As is the case in *Embrithosaurus*, the dorsal vertebral column can be considered as two regions in which the vertebrae are similarly sized and proportioned: anterior dorsal vertebrae extend from the 6th to 9th vertebrae, and the posterior dorsal vertebrae extend from the 10th to 19th vertebrae.

Anterior dorsal vertebrae (6th - 9th vertebrae)

All of the anterior dorsals (6th to 9th vertebrae) are similar in morphology and increase in size posteriorly. Most notably, the postzygapophyses increase remarkably in size and mediolateral extent, and the single, laterally projecting, wall-like, transverse process, that first appears on the 5th vertebra, continues to increase in mediolateral extent and anteroposterior thickness posteriorly.

As in *Embrithosaurus* and *Nochelesaurus*, the transverse process has a obliquely slanted, dorsoventrally long facet, comprised mostly of a tall, thin ventrolateral facing dorsal portion, and a much smaller, bowl-shaped posterolateral facing ventral portion. The ventral facet is very low on the lateral side of the centrum, hardly protruding out of the lateral side of the centrum, and as a result is almost indistinguishable from the side of the body of the centrum.

The neural spines of 6th to 9th vertebrae are upright and the dorsal surfaces of the spines are mediolaterally narrower than the dorsal surfaces of the spine of the 5th vertebra. The neural spines of the three anterior dorsal vertebrae are dorsoventrally short (reaching +-40 mm above the postzygapophyses) compared to the taller posterior dorsal vertebrae (+-60 mm), similar to the condition found in *Embrithosaurus* and *Nochelesaurus*. All neural spines are four-sided and are diamond shaped in cross section. The dorsal surfaces of the neural spines of the 5th to 9th dorsal vertebrae are exposed and are concave with a longitudinal groove that notches the anterior and posterior rims.

Intercentra are preserved on the ventral surfaces between the 8th to 19th dorsal vertebrae. Superficially they look like osteoderms as they are ovoid, thin and disc-like and convex with rugose surfaces.

Posterior dorsal vertebrae (10th - 19th vertebrae)

The 10th, 11th and partial 12th vertebrae are preserved in the anterior block containing the 3rd to 12th vertebrae. The 13th to 19th vertebrae are all tightly occluded articulated and preserved in the second block.

The first two posterior dorsal vertebrae (10th and 11th vertebrae) are similar in morphology and differ from the 12th to 19th vertebrae. They have a very obliquely slanted lateral facet of the transverse flange, dorsoventrally extensive and thin, made of separated (long, thin) dorsal and (small, rounded) ventral facets on the 10th vertebra.

On the 11th and 12th vertebrae, the lower facet partially merged with the longer, vertical, dorsal facet and the ventral facet migrates dorsally up the side of the lateral body of the centrum, such that the dorsoventral height of the lateral surface of the transverse flange, begins to decrease, as in *Embrithosaurus.*

The 13th to 19th vertebrae are homogeneous. The centra are massive and deeply excavated laterally with thick anterior and posterior rims. Ventrally, the centra have a midline longitudinal ridge and the neural spines are upright.

The transverse processes of the 13th to 19th vertebrae decrease posteriorly in dorsovental height and the lateral facet of these transverse process comprises two almost equally sized lobes, dorsally and ventrally. The dorsal portion of the transverse flange extends further laterally than the ventral portion. But, moving posteriorly, the ventral portion reaches further laterally out of the side of the body of the centrum on each successive posterior vertebrae, such that the lateral facet therefore becomes more vertically oriented on each successive posterior vertebrae. The transverse flange also continues to shift higher up on the side of the centrum, in each successive vertebrae moving posteriorly.

The dorsal surfaces of the vertebral spines of the 10th to 18th vertebrae are obscured by osteoderms and the dorsal spines are as mediolaterally wide as they are anteroposteriorly long. The dorsal surfaces of these neural spines are convex and ruguse with small pits and sometimes a larger, central, shallow hollowed, rounded pit and apparently no longitudinal midline groove.

Several small disc-like osteoderms, with rugose surfaces, lie adjacent to these neural spines (see Osteoderms). There are no lumbar vertebrae (i.e. vertebra without rib facets (Turner *et al.* 2015 character 81).

Sacral vertebrae (20th-23rd vertebrae) (Fig. 6.13A)

There are four sacral vertebrae (20th – 23rd vertebrae) (Turner *et al.* 2015 character 82) preserved on a large block.

On the 20th and 21st vertebrae, the neural spines are the most massive on this individual (70 mm wide, 65 mm longitudinally) and the slightly convex dorsal surface of these neural spines is covered with rugose ornamentation. The ornamentation comprises several hundred irregular raised, <1 mm wide, ridges, generally placed in a zigzag or random pattern. There are also irregular, mottled (not circular) tiny pits. A longitudinal, very shallow, midline, groove (10 mm wide, 25 mm long) is present which does not notch or reach the anterior or posterior border of the dorsal spine. The neural spines decrease in size from the 22nd vertebrae backwards.

The centra of the four sacral vertebrae are the largest and are fused as evidenced by the fact that the ventral surface shows the rims of adjacent vertebrae fused together and no matrix is preserved between these rims.

The prezygapophyses of the first sacral vertebra (20th vertebra) are very large. It is important to note that dorsally, behind the prezygapophyses, the 20th vertebra has a wide, flattened, depressed region, bordered laterally by a sharp, raised longitudinal ridge (Fig. 6.13). This wide area supports the expanded first sacral rib. These features are also present in on the first sacral vertebrae(20th) of the holotype of *Embrithosaurus*.

The centra of the 20th and 21st vertebrae are the most robust of this individual, decreasing significantly posteriorly on the 22nd and 23rd vertebrae. Large, ventrally convex, wide, flat, intercentra are preserved posteroventral to the fused rims of the 20th and 21st dorsal vertebrae.

Caudal vertebrae (24th to 49th vertebrae) (Fig. 6.16)

The caudal vertebrae are preserved in three blocks: the 24 th to 27 th, the 28 th to 37 th, and the 38 th to 49 th vertebrae. Beyond the 49 th vertebra, there were several more vertebrae (Seeley 1892), which are no longer preserved, meaning there were more than the currently preserved 26 caudal vertebrae in *Bradysaurus baini*.

As in all pareiasaurs the caudal vertebrae gradually decrease in size moving posteriorly and are the smallest vertebrae. The size of the centra and neural spines decrease remarkably posteriorly. Of the first four caudals (24th to 27th vertebrae) only the 27th vertebra preserves a complete neural spine (Fig. 6.16A) which is dorsoventrally high (65 mm), triangular with a sharp anterior midline point, and a flatter, rounded posterior midline side. The dorsal surface of the neural spine is convex, lightly rugose with small pits. More posteriorly, the small, neural spines are anteroposteriorly longer than mediolaterally wide and present diamond-shaped dorsal surfaces.

On the first few caudals, the postzygapophysis are remarkably small, consisting of short (10 mm), stub-like processes, with concave pads for articulation with the prezygopophysis of the next vertebrae. The prezygapophyses are also small, but twice as long as the very tiny postzygapotheses. The transverse flange is large on the 24th and 25th vertebrae (dorsoventrally expanded, loped shape with a ventral and dorsal portion) and decrease posteriorly. From the 26th vertebra backwards, the transverse flanges become cylindrical and there are no lateral articulation surfaces as the transverse flanges end in a rounded stub.

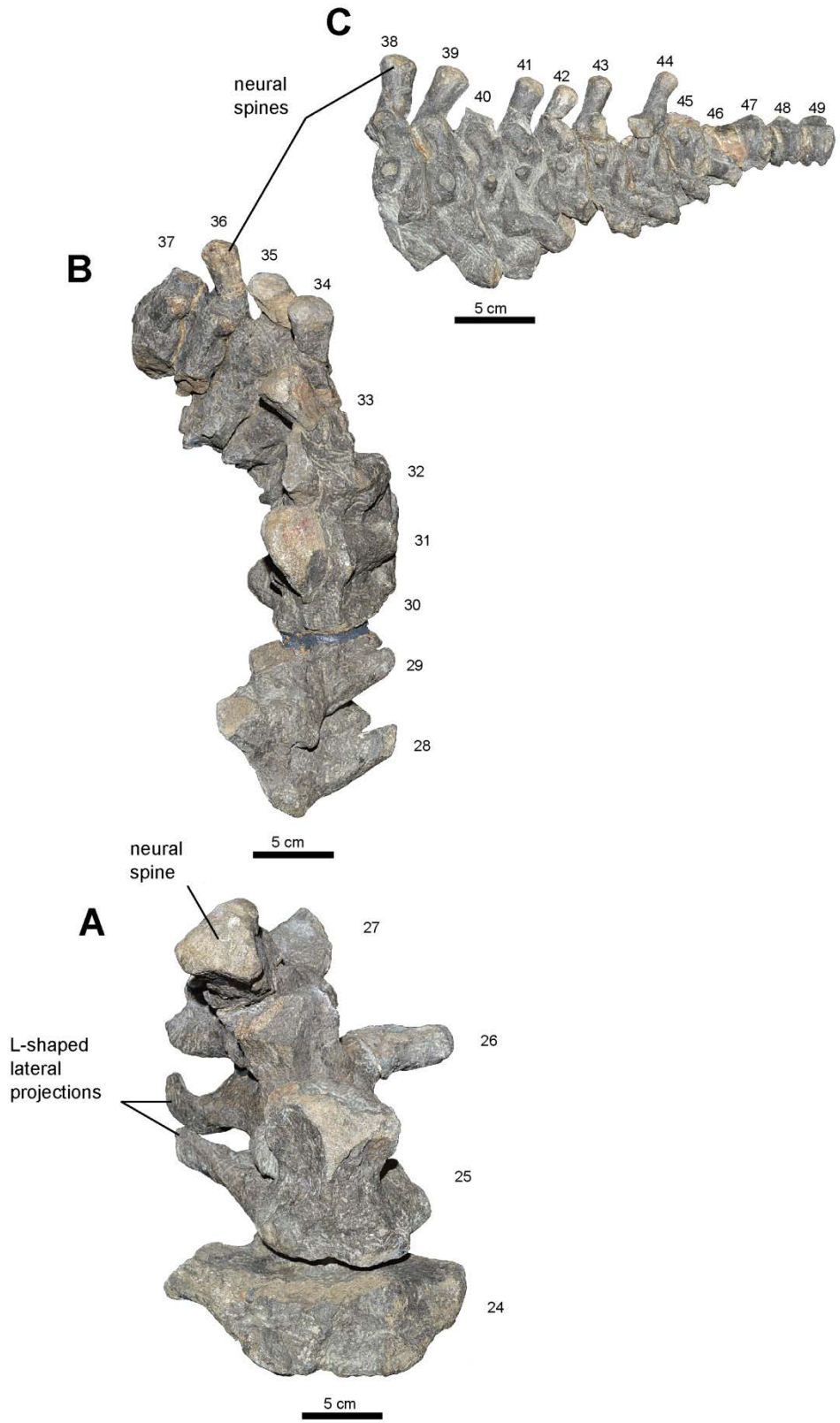


Figure 6.16: Photographs of the caudal vertebrae of the holotype of *Bradysaurus baini* (NHMUK R1971), (A), anterior caudals 24-27 in dorsal view, (B), caudals 28-37 in dorsal view, and (C), posterior caudals 38-49 in left lateral view. Posterior to the top of the page in (A) and (B). Dorsal to the top in (C).

The ventral surfaces of the 26th and 27th vertebrae have no intercentra or chevrons. Flattened V-shapd chevrons are present on the ventral surfaces of the 30th to 34th vertebrae, and the 38th to 45th vertebrae, decreasing in size posteriorly. On the 30th vertebrae the chevrons are large, 70 mm in dorsoventral height and 65 mm in mediolateral width at their articulation to the underside of each vertebrae. The chevrons decrease in size posteriorly, the last one on the underside of the 45th vertebra, measuring 25 mm high and 20 mm wide. On the underside of the vertebrae, on the posterior rim of each centra, are two flattened, slightly concave depressions, one either side of the midline and facing posteroventrally for articulation with the chevrons. These depressions are present on the 38th to 49th vertebrae.

6.4.6 Osteoderms

Osteoderms are preserved associated with the dorsal side of the 5th to 19th vertebrae. Seeley (1892) notes that a few osteoderms were found just behind the neck of the specimen, during excavations but were not retained. Juvenile *Bradysaurus baini* specimen CGP/1/2269 and the large specimen CGP/1/2268 from the Council for Geosciences, Pretoria, both preserve the entire neck shield arrangement of osteoderms.

The holotype preserves three osteoderm morphotypes positioned above the vertebrae. These are anterior dorsal osteoderms, the posterior dorsal osteoderms and small stud-like osteoderms.

Anterior dorsal osteoderms (6th -9th vertebrae) (Fig. 6.17A)

The 6th to 8th vertebrae have osteoderms preserved on the dorsal surface of the midline neural spines. Additionally there are two irregular rows of large osteoderms on the dorsal surface of the postzygopophysis, indicating an arrangement of five rows of scutes (Fig. 6.17A). Boonstra (1934b) in describing the armour of *Embrithosaurus,* noted a central row of the largest scutes, directly above the spinous neural processes, and two lateral rows of slightly smaller

osteoderms, also resulting in five rows, extending probably along the whole length of the back. The five longitudinal rows of osteoderms of *Bradysaurus* and *Embrithosaurus* (and presumably *Nochelesaurus*) contrast strongly with the much more extensive coverage of the more derived South African pareiasaurs, such as *Pareiasaurus serridens*.

In NHMUK R1971, the anterior dorsal scutes on the 3rd to 8th in the neck shield region, are not well prepared and their dorsal surfaces are partially obscured by a thin layer of matrix. At least seven osteoderms are present in the neck region (Fig. 6.17A). These are large osteoderms (roughly 55 mm medioalterally wide, 45 mm anteroposteriorly long), with a strong convex curvature dorsally. They are round to roughly 5 sided pentagons and low (18-20 mm dorsoventally). Although the dorsal surface of the osteoderms are evenly and smoothly convex, they each show a very slightly thickened centre, or a very slightly raised central region, creating a large, indistinct or incipient central boss, 25-30 mm wide, covering most of the osteoderm. There is light ornamentation consisting of very fine (1 mm wide) , very short (2-4 mm long), straight to slightly curved , radial ridges, with shallow, very thin depressions or troughs in between, occurring both on the incipient central boss and on the periphery, mostly on the periphery. There are also just a few, very small, very shallow, circular pits on a minority of these scutes. Sub-adult *Bradysaurus baini* specimen SAM-PK-5002 preserves four large anterior dorsal osteoderms, consistent with all these features.

The 11th vertebra of the holotype has two smaller osteoderms (roughly 30 mm wide) on the postzygopophysis, with the same ornamentation style and features (Fig. 6.17A).

Posterior dorsal osteoderms (10th -19th vertebrae) (Fig. 6.16B)

The osteoderms on the 13th to 19th vertebrae are smaller (25-30 mm wide) than the anterior dorsal osteoderms and are flat, low, thin and disc like. These osteoderms are not well prepared and are covered in a thin layer of matrix on

the holotype. They are convex and lack a central boss. Most of these scutes have a

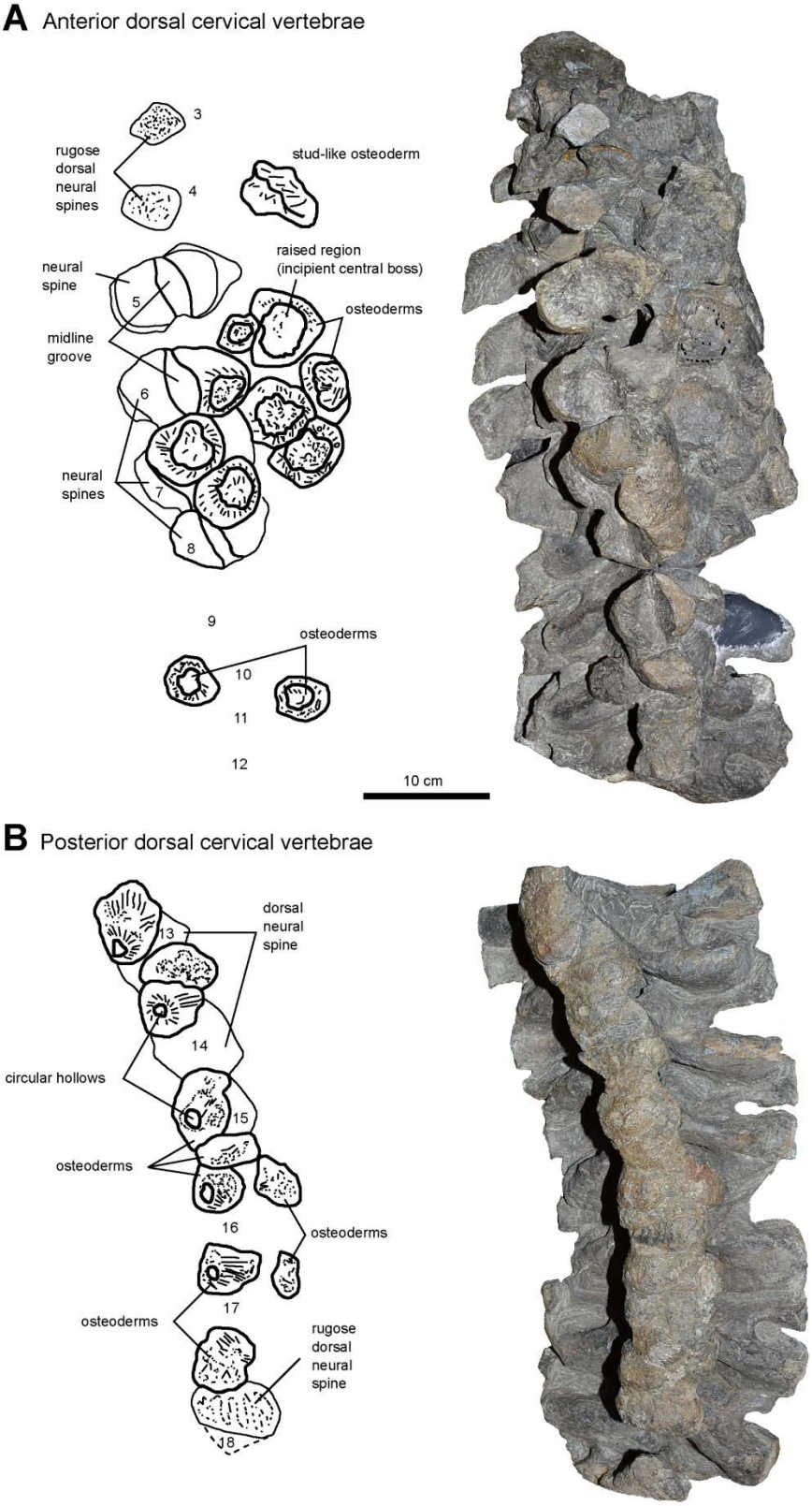


Figure 6.17: Photographs and interpretive drawings of the osteoderms of the holotype of *Bradysaurus baini* (NHMUK R1971), (A) osteoderms preserved on the 3rd to 12th dorsal vertebrae in dorsal view, and (B), osteoderms preserved on the 13th to 19th dorsal vertebrae in dorsal view. Anterior to the top of the page.

small, well defined, shallow, central circular hollow, (6-8 mm wide). The same very light ornamentation style as seen on the anterior dorsal osteoderms are present: very fine (1 mm wide) , very short (2-4 mm long), straight to slightly curved, radial ridges, with shallow, very thin depressions or troughs in between. There are very small, very shallow, circular pits on a minority of these scutes.

These scutes are arranged predominantly directly on top of the midline neural spines of the vertebrae on the holotype. A minority of the scutes lie between the spines (such as between the 15th and 16th spines, Fig. 6.17B) with scutes that are smaller than the diameter of the dorsal neural spines. At least five scutes are positioned lateral to the neural spines over the 13th to 19th vertebral sequence.

The exposed dorsal surface of the 18th neural spine is ornamented, rugose, gently convex (as seen in *Embrithosaurus*) and lacks a midline groove. This ornamentation is very similar to the ornamentation of the osteoderms in this region.

7. CHAPTER SEVEN: DISCUSSION OF ANATOMICAL DIFFERENCES BETWEEN MIDDLE PERMIAN PAREIASAUR SPECIES

7.1 Introduction

This chapter provides a detailed comparative discussion of the middle Permian pareiasaur species from South Africa, organised into two main sections: 1) anatomical discussion (cranial first, followed by postcranial), and 2) taxonomic discussion. This leads to the conclusion that consistent and valid morphological differences exist between *Bradysaurus baini*, *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi* and that these characters can be reliably used to differentiate between the three species.

7.2 Cranial anatomical discussion

7.2.1 Tooth cusp numbers

The holotype of *Embrithosaurus schwarzi* (SAM-PK-8034) was first described by Broom (1903), a paper in which he mistakenly assigned it to *Pareiasaurus serridens*. Van den Brandt (2016) and Van den Brandt *et al.* (2019) produced the first detailed cranial description and updated diagnosis for this taxon, in which he discussed likely reasons for the incorrect referral to *Pareiasaurus serridens* by Broom (1903) as a combination of distortion and poor preparation, creating the misleading appearance of ventral marginal cheek bosses and a very smooth skull with low and indistinct cranial bosses, features of *Pareiasaurus serridens* (Lee 1994, 1997a). At the time, specimen SAM-PK-8034 was the first pareiasaur from the *Tapinocephalus* AZ bearing more than usual number of seven marginal cusps on the teeth (with nine cusps present). This is more similar to *Pareiasaurus serridens* which has 9-11 cusps (Lee 1994, 1997a) which probably influenced Broom's incorrect referral.

Van den Brandt (2016) and Van den Brandt *et al.* (2019) discussed the number of cusps on the dentition of *Tapinocephalus* AZ pareiasaurs, and, as per most

previous authors (e.g. Haughton and Boonstra 1929a, Boonstra 1934a, and Kuhn 1969) accepted only specimens with nine cusps on wider teeth and more regularly spaced or evenly distributed marginal cusps, in *Embrithosaurus.* Considering only skulls, Van den Brandt (2016) and Van den Brandt *et.al.* (2019) rejected the range of seven to nine cusps per tooth that was accepted by Broom (1903) and Lee (1994, 1997a) to define *Embrithosaurus*. Lee (1994, 1997a, pers. comm) assigned a range of seven to nine cusps to *Embrithosaurus* to accommodate two specimens in *Embrithosaurus* which both have only seven cusps on the upper jaw teeth*:* NHMUK R7782 and CGP CBT 112. Lee contended that the seven cusped CGP CBT 112 be referred to *Embrithosaurus* based on the presence of three pelvic autapomorphies. Based on the cranium only, Van den Brandt (2016) and Van den Brandt *et.al.* (2019) did not assign a positive identification to this specimen. Having subsequently studied the postcrania of *Tapinocephalus* AZ pareiasaurs, I now agree with Lee (1994, 1997a) in assigning CGP CBT 112 to *Embrithosaurus.*

Lee (1994, 1997a) also tentatively assigned the historic, seven cusped specimen NHMUK R7782 to *Embrithosaurus* through a process of elimination. Van den Brandt (2016, *et.al.* 2019) did not assign an identification to this specimen as it exhibits a combination of features of both *Bradysaurus* and *Embrithosaurus*, but I now agree with Lee and tentatively assign this specimen to *Embrithosaurus* (see Appendix A). Consequently the cranial diagnosis for *Embrithosaurus* has been updated to accommodate a range of dental marginal cusps and is now seven (elongated) or nine (wider) cusped teeth. It is important to note that the direct study of 240 pareiasaurs for this project, has increased the range of the numbers of dental marginal cusps in all valid species (see below) and dental variability now seems common among the middle Permian South African pareiasaurs.

7.2.2 Derived dentition recognised in middle Permian pareiasaurs

It has long been known (Haughton and Boonstra 1929a, Boonstra 1934) that the basal pareiasaurs possess different shaped teeth to the more derived forms, but

these differences have not been discussed in detail. In comparison with derived pareiasaurs, the tooth crowns of basal species are “leaf-shaped” and the more derived forms are “fan-shaped”, two discrete morphologies which are explained in Table 7.1.

Basal pareiasaurs: “leaf”-shaped tooth morphology	**Derived pareiasaurs: “fan”-shaped tooth morphology**
Teeth relatively more dorsoventrally elongated so appearing longer	Teeth dorsoventrally elongated, but relatively less, and so appearing shorter
Teeth relatively less anteroposteriorly (mesial-distally) expanded so appearing narrower	Teeth relatively more anteroposteriorly (mesial-distally) expanded so appearing wider or broader
Relatively few cusps per tooth	Relatively more cusps per tooth
Cusps irregularly arranged (gaps between cusps inconsistent, variable in size: small to wide)**.**	Cusps arranged regularly around the crown with consistent sized gaps or spaces between cusps
Larger spaces or gaps between the cusps	Smaller spaces or gaps between cusps
Symmetrical or non-symmetrical mesial and distal cusp arrangements	Symmetrical mesial and distally cusp arrangements
Longer individual marginal cusps that project far out of the crown	Shorter or lower individual marginal cusps that do not project far out of the crown

Table 7.1: Comparison of tooth morphology of leaf-shaped (basal pareiasaurs) and fan-shaped (derived pareiasaurs), compiled from personal observations and Haughton and Boonstra (1929a), Boonstra (1934a), Lee (1994, 1997a, Lee *et al.* 1997), and Tsuji (2013).

In all basal South African pareiasaurs, the marginal cusps on the lower jaw teeth are not regularly distributed around the crown, as the spaces between the cusps vary. More derived pareiasaurs, such as *Pareiasuchus nasicornis* (Lee *et al.* 1997), *Deltavjatia* (Tsuji 2013) and *Scutosaurus* (Lee 1994) show more regularly spaced cusps with consistent, even spaces between each cusp and this is an important phylogenetic character (Turner *et al.* 2015, phylogenetic character 66).

The teeth of all basal South African pareiasaurs have crowns that are leaf-shaped. For a long time it has been known that specimens of *Embrithosaurus* present a more derived tooth morphology because of the larger number of cusps (Broom 1935, Lee 1994, 1997a). This project has identified several specimens of

both *Nochelesaurus alexanderi* and *Bradysaurus baini* that have more than seven cusps on the maxillary and mandibular teeth (see Appendix E, Tables 1 and 2), meaning that *Embrithosaurus* can no longer be distinguished as the sole middle Permian pareiasaur with teeth having more than seven cusps. The presence of a greater number of cusps is phylogenetically important (Lee 1994, 1997a, Turner *et al.* 2015, phylogenetic characters 69 and 70) as cusp numbers increase in the more derived taxa. However, despite the higher number of cusps now recognised in all middle Permian South African pareiasaurs, only *Embrithosaurus* has wider upper and lower jaw teeth (a few specimens of *Bradysaurus baini* have wider lower jaw teeth).

The apparently unique *Nochelesaurus* condition reported by Van den Brandt (2016), of a very low cusp at the base of the anterior (mesial) margin of all lower jaw teeth and certain upper jaw teeth, which creates a non-symmetrical cusp arrangement, is no longer unique to *Nochelesaurus*. This study has recognised a specimen of *Bradysaurus baini* (NHMUK R49426) with a similar very low basal cusp on only the posterior (distal) margin. This means that both *Nochelesaurus* and *Bradysaurus* can display non-symmetrical cusp arrangements on their mandibular teeth. *Embrithosaurus* alone presents a symmetrical cusp arrangement on all its teeth.

Another important finding first reported by Van den Brandt (2016) for *Nochelesaurus* is the medially positioned cusps on lower jaw teeth and the incipient horizontal cingulum ridge. This study has now identified medially positioned cusps on lower jaw teeth in specimens of both *Bradysaurus baini* and *Nochelesaurus* (see Appendix E, Table 2). This project further recognised the presence of an incipient lingual cingulum on lower jaw teeth of *Nochelesaurus* in the holotype and referred specimen SAM-PK-6238. This has not yet been found in any other middle Permian South African pareiasaur. The presence of lingual cingulum ridges on pareiasaurian teeth have been considered a derived character (Turner *et al.* 2015, phylogenetic character 72 and 73) up till now.

Another important finding first reported by Van den Brandt (2016) for *Nochelesaurus* is the presence of one to three vertical ridges on the lingual surface of the mandibular teeth. This study has now found similar features on specimens of *Bradysaurus baini* as well (see Appendix E, Table 2). The presence of lingual vertical ridges on mandibular pareiasaurian teeth have been considered a derived character (Turner *et al.* 2015, phylogenetic character 71).

7.2.3 Tooth orientation and jaw morphology

Boonstra (1934a) was the first to describe two very different and contrasting pareiasaurian jaw morphologies concerning the shape of the maxilla and the orientation of the upper jaw teeth. Boonstra (1934a) noted that a maxilla which is only slightly curved ventrally holds vertical teeth, whereas one that is strongly inwardly curved ventrally holds inwardly directed teeth.

Most pareiasaurs have a maxilla that is only slightly curved ventrally and the upper jaw teeth point straight down. Lee (1994, 1997a) included three taxa that show exceptions to the typical condition. He noted that *Scutosaurus* has vertical and slightly outwardly pointing upper jaw teeth as an autapomorphy for that taxon. Lee (1994, 1997a) considered the inwards pointing (medially inflicted) upper jaw teeth of *Pareiasuchus nasicornis* and *Bradysaurus baini* as an autapomorphic condition in these two taxa and created a phylogenetic character (number 27) for the condition (Lee 1997b). Jalil and Janvier (2005) reported anteroventrally oriented upper jaw teeth in *Arganaceras* which is more exaggerated than the slightly forward pointing teeth upper jaw teeth of *Scutosaurus*. Turner *et al*. (2015) published a list of autapomorphies per species wherein they removed the inwards pointing upper jaw teeth character of *Pareiasuchus nasicornis* and *Bradysaurus baini* as an autapomorphy (since the condition occurs in more than one taxon), and retained the inward condition for these two taxa as a state of character 67 in their phylogenetic analysis.

Van den Brandt (2016) maintained that the backward pointed upper jaw teeth in specimens of *Bradysaurus baini* was a taphonomic effect and the result of dorsoventral crushing, exaggerating the naturally slightly inward orientation. However, my direct study of several *Scutosaurus* specimens confirmed that the taxon consistently displays slightly outwardly oriented upper jaw teeth, despite the often severely distorted and crushed skulls, suggesting that even severe cranial distortions do not significantly affect the orientation of the upper jaw teeth. This implies that the inward pointing upper jaw teeth of specimens of *Bradysaurus baini* is probably a real feature of the taxon and not the result of cranial distortions. Moreover the inwards pointing upper jaw teeth of *Bradysaurus baini* specimens is always accompanied by a curved ventral maxilla, with a wide horizontally oriented ventral portion just above the tooth row, which accommodate the long, curved roots of backwards pointing teeth. In ventral view, the inwardly curved maxilla and horizontal upper jaw teeth obscure the anterior and lateral portions of the palate of *Bradysaurus baini*, whereas in *Embrithosaurus* and *Nochelesaurus* this obstruction is not present and there is only a slightly curved ventral maxilla with teeth that point downwards.

Interestingly, personal observation has shown that the orientation of the upper jaw teeth is not consistent along the tooth row. The posterior maxillary teeth are often horizontally flattened and medially inwardly pointing in many specimens of all species of middle Permian South African pareiasaurs. Accordingly the orientation of the upper jaw teeth should be defined by only the premaxillary and anterior maxillary teeth.

The holotypes of *Nochelesaurus alexanderi*, *Bradysaurus baini* and *Embrithosaurus schwarzi* have lower jaws that are significantly smaller than the upper jaw. When the jaws are closed, the lower jaw teeth pass well inside of the upper jaw teeth, by several centimetres, and they do not contact each other. No tooth wear can be seen on the cusps or crowns of any of the teeth of these holotypes or on in any pareiasaur skull studied for this project. Indeed no tooth

wear patterns have been described for any pareiasaur in the literature. The considerable distance between upper and lower jaw teeth and the resulting lack of tooth wear lead Haughton and Boonstra (1930a:264) to propose that pareiasaurian teeth do not occlude, do not directly cut nor grind vegetation, but merely serve as "rugosities to prevent the soft vegetation from slipping out after a mouthful has been taken".

Lee *et al.* (1997) in his description of *Pareiasuchus nasicornis* included a discussion of the functional morphology of the pareiasaurian dentition, jaw occlusion, the cheek flanges, and the angular boss on the lower jaw. He explains how the uninterrupted, even cutting edge of pareiasaurian dentition characteristic of herbivores, employs a cropping action which does not require contact between the upper and lower jaw teeth, and instead slide closely past one another in a scissor-like action. According to Lee, this explanation accounts for the reason why pareiasaurian teeth never show wear facets or other signs of tooth wear. Lee *et al.* (1997) discussed how the depressed jaw articulation of pareiasaurs (well below the tooth row) produces a posteriorly directed force during occlusion. This creates a shearing action to facilitate cropping of tough plant matter, limiting pareiasaurs to cropping bits of vegetation before swallowing in the absence of anteroposterior sliding (propalinal) movement at the jaw articulation. Using Lee's discussion, we can understand how the seemingly strange inwards pointing upper jaw teeth of *Bradysaurus baini* (and *Pareisuchus nasicornis*) would still be functional, supporting the contention that this strange morphology is real and is not due to distortion.

Niche partitioning (differing diets) may be responsible for generating the unique jaw and tooth morphology of *Bradysaurus baini* compared to *Embrithosaurus* and *Nochelesaurus,* helping to separate three species of similar size, enabling them to coexist without competing for 2-3 million years, while the rocks of the upper Abrahamskraal Formation were being deposited.

7.2.4 Cranial ornamentation

Pareiasaurian cranial ornamentation style (size and morphological shape of the bosses, ridges, grooves and pits) and sculpturing patterns (placement) varies significantly between different taxonomic groups and even individual taxa. Where specific distinguishing pareiasaurian ornamentation exists, they are justifiably used by most authors to identify different taxa. *Pareiasaurus serridens* is diagnosed as possessing a reticulated network of uniformly fine raised ridges and small pits, and lacking central bosses on each element (Lee (1994, 1997a). *Deltavjatia* has distinctive subcircular, "lozenge-shaped" bosses that produce a "pustule-like" pattern on the skull roof and flat areas with radiating depressed grooves (no raised ridges) emanating from central bosses (Tsuji 2013). Lee (1994, 1997a) distinguishes *Anthodon* as being covered by a network of shallow, smooth pits, widely spaced, and with no raised bosses or raised ridges.

According to Lee (1994, 1997a) all large middle Permian South African pareiasaurs have the same general cranial sculpturing style and pattern consisting of low, rounded bosses in the centre of each bone, with regular, wide, low, ridges radiating outwards. Lee (1994, 1997a) and Van den Brandt (2016) noted the more distinctive bosses on the posterior margins of the cheeks (quadratojugal and squamosal) present in *Nochelesaurus* as an important distinguishing feature amongst the co-occurring South African pareiasaurian taxa.

I disagree with Lee that all middle Permian South African pareiasaurs have the same general cranial ornamentation style of low, rounded bosses. *Bradysaurus baini* and *Embrithosaurus schwarzi* certainly have low, rounded, indistinct, smooth bosses, but the cranial sculpturing of most specimens of *Nochelesaurus* is more distinctive and is not only on the posterior cheek (see chapter 8: Taxonomic review and diagnoses). Here cranial bosses are higher, longer, more conical and more pointed, especially the bosses on the posterior edge of the quadratojugal, including the corner cheek boss (see below). Other examples

include the more distinct and larger central boss on the frontal, the more distinctive bosses on the lateral surface of the quadratojugal, the larger boss on the posterolateral edge of the squamosal, and the more distinct orbital marginal bosses of the prefrontal, postfrontal and postorbital. The lack of a distinct maxillary boss in *Nochelesaurus* is an exception to the general rule of more distinctive cranial ornamentation in this taxon.

As noted by Van den Brandt (2016) the distinct large, wide, midline boss at the nasal-frontal contact present on the holotype of *Nochelesaurus alexanderi*, has not been observed on any other basal South African pareiasaur specimen and this feature of the holotype is probably an anomaly or pathology of the individual specimen.

The morphology of the corner cheek boss on the quadratojugal of pareiasaurs has been identified by several authors as diagnostically important and even autapomorphic. In *Deltavjatia* this boss is autapomorphic in being long, flattened and rectangular in all adult specimens (Lee 1994, 1997, Tsuji 2010, 2013). *Provelosaurus americanus* is diagnosed by two prominent cylindrical bosses at the posteroventral corner of the quadratojugal (Cisneros *et al.* 2005). In *Elginia* (Newton 1893), *Arganaceras* (Jalil and Janvier 2005) and *Scutosaurus* (Lee 1994) the corner boss is very long, pointed and horn shaped, and in *Obirkovia* it is conical (Bulanov and Yashina 2005). The shape of the corner boss in *Nochelesaurus* can be used to differentiate it from *Bradysaurus baini* and *Embrithosaurus schwarzi* as it is larger, much longer than wide, and more prominent, and sometimes presents a long, thin neck, followed by a raised distal rim.

7.2.5 Presence, absence and shapes of cranial bones

The different appearance of the postfrontal in basal South African pareiasaurs when viewed dorsally (externally) compared to ventrally (internally) has caused much confusion and disagreement amongst previous authors. Watson (1914b)

used internal sutures only and illustrated a very small, mediolaterally elongated postfrontal in his cranial description of a referred specimen of *Embrithosaurus schwarzi* (NHMUK R7782).

Boonstra (1934a), based on both internal and external sutures, noted the postfrontal to be much larger than the size figured by Watson (1914b), and detailed the bone as longitudinally elongated in most if not all pareiasaurs. Conversely, Lee (1994, 1997a) declared that all pareiasaurs possess mediolaterally elongated postfrontals which as a result show a feeble contribution to the orbital margin and are relatively small cranial bones and designed a phylogenetic character around this point (Turner *et al*. 2015, character 34). Broom (1924) noted the postfrontal as relatively large and roughly square (as large as the prefrontal) in a juvenile specimen of a large pareiasaur, with easily identifiable sutures, speculating that this specimen is either a different species to Watson's (1914b) specimen (*Embrithosaurus schwarzi* NHMUK R7782) or that the large postfrontal bone may appear smaller when viewed internally, the method used by Watson (1914b). Broom's (1924) juvenile skull, now lost, seems to be a different species (probably a specimen of *Bradysaurus baini*) as it has a narrow postparietal and a large, roughly square postfrontal, features which agree with specimen CGP/1/2269, a juvenile *Bradysaurus baini*.

Van den Brandt (2016) and Van den Brandt *et al.* (2019) in his cranial description of the holotype of *Embrithosaurus*, explicitly noted and described the contrasting shape of the postfrontal viewed internally compared to externally, documenting the external shape as longitudinally elongated and large and the internal shape as mediolaterally elongated and small. Since the internal sutures are more secure than the external ones, Van den Brandt (2016) and Van den Brandt *et al.* (2019) concluded it best to define the postfrontal in *Embrithosaurus* as mediolaterally elongated.

Based on the holotypes and additional well preserved skulls with identifiable sutures, I propose that different pareiasaur species from the middle Permian of South Africa present two different postfrontal morphologies: 1) small: mediolaterally elongated in *Embrithosaurus schwarzi* and 2) large: square to slightly longitudinally elongated in *Nochelesaurus alexanderi* and *Bradysaurus baini*. It is important to note that these two morphologies do not influence phylogenetic character 34 (Turner *et al.* 2015) wherein the postfrontals of all pareiasaurs are scored as mediolaterally widened (about two times as wide as long, making no or only a feeble contribution to the orbital rim). This is because, despite the two different morphologies of the postfrontals of the middle Permian South African pareiasaurs, the bone always makes a feeble contribution to the orbital rim in all species, and therefore has been scored as such. These three taxa have all been phylogenetically scored as mediolaterally elongated in this project as in all pareiasaurs, as this phylogenetic character is used to group all pareiasaurs together in a clade.

Nochelesaurus, *Embrithosaurus* and *Bradysaurus* do not possess septomaxillae. A pareiasaurian septomaxilla has been described only once, in *Anthodon* (Boonstra 1934a) which Tsuji *et al.* (2013) suggests is a misinterpretation and propose a loss of the septomaxilla as characteristic for all pareiasaurs. This study concurs with Tsuji *et al.* (2013).

The supernumerary bone, which is present in several derived pareiasaurs, is not present in any of the basal South African pareiasaurid species. When present, this is a small triangular bone on the posterior margin of the skull roof, wedged between the postparietal and supratemporal. Lee (1994, 1997a) discussed the absence of the supernumerary element amongst all basal South African pareiasauria taxa. He noted its appearance only in the more derived pareiasaurian taxa, and proposed an ordered phylogenetic character (absent -> small -> large). Interestingly, the middle Permian South African pareiasaurs exhibit two distinct morphologies of the postparietal: 1) a narrow postparietal in

Bradysaurus and *Embrithosaurus*, and 2) a wide postparietal in *Nochelesaurus*. The most secure confirmation of a narrow postparietal in *Bradysaurus baini* is from the clearly identifiable sutures of specimen CGP/1/2269, a well preserved juvenile skull. Van den Brandt *et al.* (2019) described unambiguous external cranial sutures confirming a narrow and square postparietal on the holotype skull of *Embrithosaurus schwarzi*, disagreeing with Boonstra (1934a) that *Embrithosaurus* has a transversely wide postparietal. Van den Brandt *et al.* (2019) acknowledged that an unidentified internal suture suggests a wide postparietal in the holotype *Embrithosaurus.* The holotype of *Nochelesaurus* and referred *Nochelesaurus* specimen SAM-PK-6238 show obvious sutures confirming wide postparietals. Intriguingly, there is a specimen of *Bradysaurus baini* (SAM-PK-12216), with identifiable sutures, that has a narrow postparietal with small triangular supernumerary bones on either side. This is the only example of supernumerary bones present on a skull, out of more than 200 middle Permian South African pareiasaur specimens studied. Possibly, the presence or absence of the supernumerary bone in these basal pareiasaurs requires more work.

7.2.6 Lower jaw considerations

Is the morphology of the lower jaw and particularly the angular boss diagnostic? Haughton and Boonstra (1930a) produced a detailed study of the pareiasaurian mandible, noting the difficulty of using the morphology and features of the mandible for identification and concluding that specimens of the same genus have very dissimilar mandibles and conversely that very dissimilar skulls have similar mandibles. My research confirms the limited use of the morphology of the lower jaw in middle Permian pareiasaurian species for taxonomy as no reliable consistent pattern emerges. From the work of Tsuji (2010) it is evident that the size and shape of the pareiasaurian angular boss grows during ontogeny in *Deltavjatia* indicating that the size of the angular boss cannot be used for taxonomic purposes.

The morphology of the angular boss is highly variable in different middle Permian pareiasaurian species: from short to long, small to large and bulbous ("tennis-ball" shaped) to conical or horn shaped, to proximally swollen ("claw" shaped) to distally swollen (see Appendix E, Table 6). With so much variation and no consistent patterns, one must caution against using the morphology of the angular boss in species identification. However, the angular boss appears often to be, but is not always, largest in specimens of *Embrithosaurus* and *Nochelesaurus* and smaller in specimens of *Bradysaurus*, including very large skulls of *Bradysaurus*.

7.2.7 Morphology of the distal paroccipital process of the opisthotic

An important diagnostic character is the morphology of the distal end of the paroccipital process of the opisthotic. One of the three cranial autapomorphies of *Bradysaurus baini* put forward by Lee (1997a: 247) is that of a "greatly swollen" distal paroccipital process of the opisthotic. Van den Brandt (2016) and Van den Brandt *et al.* (2019) interpreted this brief description as comprising two features: 1) an anteroposteriorly expanded distal portion, and 2) an oblique, dorsomedially elongated, posteriorly projecting, knob-like process on the medial edge of the posterodorsal corner of the paroccipital process.

Van den Brandt (2016) and Van den Brandt *et al.* (2019) recorded the anteroposterior extent as the same in *Embrithosaurus* and *Nochelesaurus,* but to be much larger in *Bradysaurus baini*. He noted the dorsomedial posterior process as absent in *Nochelesaurus* and as present, but smaller in *Embrithosaurus* than in *Bradysaurus baini*. Personal study of over 200 pareiasaur specimens for this project, allows further clarification. The smaller posterior process of *Embrithosaurus* and the larger one of *Bradysaurus* are 1) dorsomedially elongated, and 2) positioned on the medial edge of the posterodorsal corner of the paroccipital process, well above the posteroventral edge of the paroccipital process. In *Nochelesaurus*, there is no distinct dorsomedially elongated posterior

process at the medial edge of the posterodorsal corner of the paroccipital process. However, sometimes the posteroventral edge of the distal paroccipital process is gently swollen to form a low, wide, dorsolaterally elongated posterior process. These features have been extensively used for species identifications in this project.

7.2.8 Sub adult holotypes and their implications: *Embrithosaurus schwarzi* and *Bradysaurus seeleyi*

The holotypes of *Bradysaurus baini* (NHMUK R1971) and *Nochelesaurus alexanderi* (SAM-PK-6239) are large, adult specimens. However, the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034) is slightly smaller and appears to be a sub-adult. The cranium is smaller and the basal skull length is shorter (315 mm) compared to the larger NHMUK R1971 (370 mm) and SAM-PK-6239 (363 mm) (see Table 7.2). The angular boss of the holotype of *Embrithosaurus* is relatively small considering the size of the skull and provides evidence that the skull belongs to an individual that is and not fully mature, since Tsuji (2010) showed that the size of the pareiasaurian angular boss grows disproportionally more with increasing size of individual skulls in ontogeny in *Deltavjatia*.

Similarly, most of the postcranial elements are slightly shorter and more gracile in *Embrithosaurus* than in the larger holotype specimens of *Bradysaurus baini* and *Nochelesaurus alexanderi* (e.g. the length of the femur, radius and tibia are all slightly shorter in the holotype of *Embrithosaurus*, see Tables 4.3, 4.5, and 4.6). Sub-adult or juvenile features that separate the holotype specimen of *Embrithosaurus schwarzi* from the larger holotypes of *Bradysaurus baini* and *Nochelesaurus* (and the large *Embrithosaurus* specimen CGP CBT 112) are: the lack of an olecranon process on the ulna, which severely shortens the length of the ulna; the absence of the prominent vertical scar for muscle attachment on the fibula; and the unfused nature of the last sacral vertebrae (22^{nd} to 23^{rd} vertebrae).The holotype of *Embrithosaurus* has a small but distinct maxillary boss which would most likely increase in size with ontogeny.

Specimen #	Midline	Left	Right	Size Range
CGP CBT 112	350	400	400	Adult
NHMUK R1971	370	405	434	Adult
SAM-PK-6239	363		403	Adult
SAM-PK-6238	370		420	Adult
SAM-PK-3718	345	400	392	Adult
SAM-PK-8944	370	400	400	Adult
SAM-PK-5624	360	385	385	Adult
SAM-PK-5002	360	345	380	Late Sub-adult
SAM-PK-8034	315	350	360	Sub-adult
NHMUK R49426	300	325	340	Sub-adult
SAM-PK-6240	310	335	340	Juvenile
SAM-PK-5012	290 est.	320 es	320	Juvenile
CGP/1/2269	260	290	290	Juvenile
SAM-PK-4350	250	265	265	Small Juvenile
SAM-PK-9095	240	280	280	Small Juvenile

Table 7.2: Skull length measurements of middle Permian pareiasaurs in millimetres. Midline: longitudinal length from the posterior edge of the dorsal premaxilla to the posterior edge of the midline occipital flange; Left: perpendicular length from the posterior edge of the dorsal premaxilla to the posterior edge of the left-most corner of the occipital flange; Right: perpendicular length from the posterior edge of the dorsal premaxilla to the posterior edge of the right-most corner of the occipital flange.

The holotype of *Bradysaurus seeleyi* (NHMUK R49426) is certainly a sub-adult specimen and is smaller than the sub-adult holotype of *Embrithosaurus schwarzi* in basal skull length (see Table 7.2). The postcrania are noticeably smaller and more gracile in NHMUK R49426 than the sub-adult holotype of *Embrithosaurus* and NHMUK R49426 has been identified as a sub-adult or juvenile *Bradysaurus baini* (see Chapter 8, Taxonomic review and diagnoses).

7.3 Postcranial anatomical discussion

As the postcranial morphology of *Embrithosaurus*, *Bradysaurus* and *Nochelesaurus* are very similar to each other, this postcranial discussion will concentrate on the differences. As is evident from the descriptive chapters, the

postcranial skeleton of *Nochelesaurus* is not as well-known as that of *Embrithosaurus* and *Bradysaurus,* as the holotype and referred specimens of *Nochelesaurus* used in the postcranial description do not preserve the pelvis.

7.3.1 Sacral vertebrae

Historically, there has been disagreement regarding the number and nature of pareiasaurian sacral vertebrae and ribs. Seeley (1892) noted four sacral vertebrae in *Pareiasaurus* (*Bradysaurus*) *baini* (identified as a sacro-lumbar, a true sacral, and two sacro-caudals), noting the first two ribs as massive and that all four vertebrae produce sacral ribs that all support (reach) the ilium. Broom (1903), in describing *Embrithosaurus schwarzi*, considered only the first two sacral vertebrae as definitely sacral, as he applied the strict definition and explicit criteria of considering only vertebrae as true sacrals when they have both: 1) fused, anchylosed or coalesced centra; and 2) sacral ribs that extend to articulate or fuse with the ilium. Broom (1903) noted that only two vertebrae satisfy these criteria. In the holotype of *Embrithosaurus schwarzi*, the centra of the first three sacral vertebrae (20th , 21st and 22nd) are clearly fused together as no matrix is present ventrally between the centra (Figs. 4.28, 4.30) and the centra of the 22nd to 23rd vertebrae are unfused and are separated by matrix infill ventrally (Fig. 4.30). Two large, conspicuous sacral ribs extend from the first two sacral vertebrae (20th and 21st) to articulate with the medial surface of the ilium, which Broom considered as true sacrals. The 22nd and 23rd vertebrae present much smaller sacral ribs, with only the medial portions preserved (Fig. 4.30) and with no lateral articulation with the ilium preserved.

Watson (1914b) considered *Embrithosaurus* and *Bradysaurus* as having four vertebrae in the sacrum. Boonstra (1934c) produced a comprehensive vertebral study and compared the vertebral columns of 46 South African pareiasaurian specimens. He drew many of his conclusions primarily from the complete vertebral column of a large *Tapinocephalus* AZ specimen excavated by himself (SAM-PK-9168) identified at the time as a specimen of *Bradysaurus seeleyi*. He

noted four sacrals as the typical large adult basal pareiasaurian condition. Boonstra (1934c:58) remarked that all four pareiasaurian sacrals are usually fused or coalesced in the majority of specimens, but not always so (as is the case in the sub-adult holotype of *Embrithosaurus*) and that the fourth sacral rib did not reach the ilium, but was probably attached ligamentously.

Lee (1997b) notes at least four sacral vertebrae in all pareiasaurs and exactly four in all basal South African taxa, except for *Nochelesaurus*, where the condition is unknown. Lee (1997b) also noted the first or anteriormost sacral rib as greatly distally expanded and the most robust, with all subsequent sacral ribs much more slender.

My research shows that there are four sacral vertebrae in *Embrithosaurus* and *Bradysaurus baini*, all four fused together in the large holotype of *Bradysaurus baini*, and the centra unfused between the last two sacral vertebrae of the holotype of *Embrithosaurus schwarzi,* as a result of incomplete growth in this sub-adult holotype specimen. The same probably applies to *Nochelesaurus*. I consider the sacrum to comprise four vertebrae (20th to 23rd vertebrae), as seen in all large *Tapinocephalus* AZ pareiasaur specimens, with the lateral articulation of the last two and smaller (22nd and 23rd vertebrae) sacral ribs often not preserved and probably ligamentous as proposed by Boonstra (1934c). Interestingly, in the holotype of *Embrithosaurus*, the first sacral rib (20th vertebra) is the largest and the second sacral rib (21st vertebra) is the second largest (SAM-PK-8034). In several specimens of *Bradysaurus baini*, the second sacral rib (21st vertebra) is the largest and the first sacral rib (20th vertebra) is smaller (e.g. NHMUK R1971 and NHMUK R49426).

7.3.2 Pelvic differences between *Bradysaurus* and *Embrithosaurus*

The holotypes of both *Embrithosaurus schwarzi* and *Bradysaurus baini* preserve nearly complete pelvic girdles, allowing for detailed comparison. Previous authors noted a number of differences. Watson (1914b) defined the genus

Bradysaurus and noted a few important postcranial features compared to that of the holotype of *Embrithosaurus*. Watson (1914b) contrasted the broad, low, flat pelvis and the large olecranon process of *Bradysaurus* with the narrow, rounded and high pelvis and the absence of an olecranon process in *Embrithosaurus*.
In fact, *Bradysaurus baini* is most securely distinguished from *Embrithosaurus* postcranially, by the shape and features of the pelvis.
Broom (1903) also noted the pelvis of *Embrithosaurus* (SAM-PK-8034) as quite different from the pelvis of *Bradysaurus baini* (NHMUK R1971) which was well illustrated and described by Seeley (1892). Broom (1903) noted the iliac crest of *Embrithosaurus* as anteriorly and outwardly (laterally) directed, the very strong (thick) pubic symphysis, and the prominent anterior midline expansion (median pubic process). All three of these features are present and valid. Haughton and Boonstra (1930b) provided a very detailed, systematic pelvic analysis for several species. For *Embrithosaurus* they noted the markedly thickened pelvic symphysis and the strong ventrally projecting carina (keel), even providing a figure to only illustrate the thickened keel (Text Fig.1:209). They systematically noted the pelvis as very high and narrow, with an upstanding (vertical) ilium, producing a sharp "v-shape" in anterior view. They also noted an anteriorly diverging iliac blade, producing a wide pelvis only anteriorly and dorsally. Also the anterior edge of the iliac blade as vertical, with no eversion (bending) and the practically flat lateral side of the blade. Haughton and Boonstra (1930b) note the symphyseal tongue of the anterior pubis as extending far forward. All these features are accurately and correctly described.
Lee (1997a) provided the most recent postcranial diagnoses for *Embrithosaurus schwarzi*, focusing on three pelvic features that he described as "unambigious autapomorphies" (Lee 1997a:251):

- A flat, non- everted anterior iliac blade. In dorsal view the anterior iliac blade has a ventral border which is not everted, such that this bone presents a thin edge when viewed dorsally. Lee notes that in all other pareiasaurs, the sacral

blade is slightly to greatly everted, presenting a wide lateral surface, when viewed dorsally.

- The iliac blades diverge anteriorly, making an angle of about 40^0 with the sagittal plane when viewed dorsally, and are not parallel. Lee notes that in all other pareiasaurs, the iliac blades are almost parallel.
- The pelvic symphysis is extremely thick, being almost half as deep as long, noting that in all other pareiasaurs the pelvic symphysis is much thinner.

Lee is correct in all these features of the pelvis of *Embrithosaurus*, and they have been fully described in the postcranial descriptive chapter (see chapter 4). Additional complimentary distinguishing pelvic features of *Embrithosaurus*, obtained through additional measurements and the use of more specimens, have now been described and added to the diagnosis: high, narrow v-shaped pelvis; pelvic shaft oriented anterodorsally 30^0 off the vertical plane; puboischiatic plate narrow, short and dorsally concave; thick and wide ventral keel with oblique lateral sides; median pubic process large, tongue shaped with rounded edges, extending far anteroventrally.

7.3.3 Olecranon process development the result of ontogeny

The morphology of the proximal ulna of *Embrithosaurus schwarzi* provides an interesting study. Broom (1903: 132) was the first to document the absence of an olecranon process in the holotype of *Embrithosaurus schwarzi* (see chapter 4). Clearly intrigued by this unique morphology, Broom (1903) explained how very different it is compared to the ulna of the holotype of *Bradysaurus baini*, where the ulna forms an overhanging, proximal lip or hook above the articular surface, creating a well-defined, enclosed socket, which clasps around the articular surface of the humerus. Broom offered no explanation for the absent olecranon of *Embrithosaurus*, noting only that the proximal ulna is otherwise well developed, and shows no sign of damage, fracture or a missing epiphysis.

Watson (1914b) considered the lack of an olecranon process in the holotype of *Embrithosaurus schwarzi* important enough to contribute towards the diagnostic features of the genus in his taxonomic classification.

Boonstra (1932c) analysed the ulna of a number of pareiasaur species and noted the absence of an olecranon process in the holotype of *Embrithosaurus*, explaining that "the articular surface passes gently over on to the proximal surface without being marked by a limiting ridge" (Boonstra 1932c:469), which is an accurate description. Boonstra (1932c) also noted the lack of an olecranon process in two other middle Permian pareaisaurs (*Bradysaurus vanderbyli:* SAM-PK-9169, SAM-PK-8941*,* and *Nochelesaurus alexanderi:* SAM-PK-8944) and a very weak or low olecranon process in *Dolichopareia angusta* (SAM-PK-6238). Boonstra (1932c) noted that all species that have an olecranon process have their proximal articulation surfaces terminated by a ridge anterodorsally, which forms the olecranon process, whereas in those without an olecranon process there is no anterodorsal limiting ridge, and the proximal articulation surface extends proximally. My study of these specimens shows that extreme variation exists in the morphology of the pareiasaurian proximal ulna between different specimens.

Lee (1997b:253) noted that he could not locate the ulnae of the holotype of *Embrithosaurus schwarzi* and stated that the lack of an olecranon process described and figured by Broom (1903) and Boonstra (1932c) was probably the result of incomplete preservation of the ulna. Lee went on to note that the complete ulnae of referred *Embrithosaurus* specimen CGP CBT 112 both show a prominent olecranon processes, which they do possess.

My research shows that the ulnae of the holotype *Embrithosaurus schwarzi* are complete with the right ulna very well preserved (see chapter 4). The somewhat eroded and weathered left ulna, matches the right ulna in terms of general shape and size, they are consistent with each other and show bilateral symmetry. There is no olecranon process on either ulna. As described by Broom

(1903) and Boonstra (1932c), the proximal articular surface passed over smoothly from anteriorly (preaxially) to proximally (dorsally) to posteriorly (postaxially). There is no anterodorsal limiting ridge or enclosed socked created anterodorsally by an olecranon process (which are present in both ulna of holotype of *Bradysaurus baini*) and there is no anterodorsal constriction of the proximal ulna (which is present in specimens of *Nochelesaurus*).

Instead of a projecting olecranon process above the articular surface, the holotype ulnae of *Embrithosaurus* have two raised medial and lateral olecranon crests, with a groove between them. Proximal medial and lateral crests on the olecranon processes have been reported in *Bunostegos* as autapomorphies of that taxon (Turner *et al.* 2015). In *Bunostegos*, the olecranon crests or "folds" are reported as folding and pointing towards each other, nearly touching in the largest of three specimens studied (Turner *et al.* 2015), with the medial crest being larger than the lateral one. In the holotype of *Embrithosaurus*, the crests are lower, wider apart, point proximally, do not fold to point towards each other, and never touch. Turner *et al.* (2015) suggest that an extensor tendon was present in the groove between the olecranon crests of *Bunostegos*, which is probably also the case in the holotype of *Embrithosaurus.*

Individual specimens of *Scutosaurus karpenskii* also show great morphological differences in the proximal ulna. For example specimen NHMUK PV R 4027, a cast of a very complete individual, has a large prominent olecranon process, whereas the mounted exhibited *Scutosaurus* skeleton at the American Museum of Natural History, New York, has no olecranon process and instead has two high, sharp, and distinct medial and lateral olecranon crests (as in *Bunostegos*).

Referred *Embrithosaurus* specimens FMNH UR 2443 and CGP CBT 112 have large and prominent olecranon processes. *Embrithosaurus* therefore appears to show great levels of variation of the ulna, from no olecranon process (sub-adult holotype) to a large olecranon processes above an enclosed articular surface (FMNH UR 2443, CGP CBT 112). An explanation is offered by Lee (1997b:239)

who maintains that the olecranon process is absent in juvenile specimens and ossifies late in ontogeny. The holotype of *Embrithosaurus* is a sub-adult individual as explained earlier. Broom (1935:39) also hypothesised that the lack of an olecranon in *Embrithosaurus* may be due to age. Accordingly, the absence of the olecranon process in the holotype of *Embrithosaurus* is most probably related to ontogeny.

It is interesting to note that *Nochelesaurus* specimen SAM-PK-6238 in turn has an olecranon process which is of an intermediate stage of ontogenetic development. The ulna is anterodorsally partially constricted (or pinched in) and therefore there is no anterodorsal limiting ridge, there are very low (5 mm high) lateral and medial crests, positioned anteriorly only, above which a low olecranon process exists (20 mm high).

The ontogenetic sequence of the development of the olecranon process thus appears to be:

- Stage 1: no olecranon process, short ulna, no anterodorsal limiting ridge, ulna not constricted or pinched anterodorsally, the articular surface passes over smoothly from anterior, to proximal to posterior in the form of a groove, flanked by raised olecranon lateral and medial crests (e.g. sub-adult holotype of *Embrithosaurus schwarzi*: SAM-PK-8034, Figs. 4.9, 4.10, 4.11 and three *Bunostegos* specimens: Turner *et al.* 2015);
- Stage 2: a low, small olecranon process, longer ulna, ulna somewhat constricted above the articular surface, still no anterodorsal limiting ridge, the articular surface passes over smoothly from anterior, to proximal in the form of a shallow groove, flanked by low olecranon lateral and medial crests (*Nochelesaurus* specimen SAM-PK-6238, Figs. 5.13, 5.14, 5.15);
- Stage 3: high prominent olecranon process, long ulna, ulna severely constricted above the articular surface from both sides (anterodorsal limiting ridge) creating an enclosed socket that stops the articular surface

(*Embrithosaurus* specimen FMNH UR 2443, Figs. 4.9, 4.10, holotype of *Bradysaurus baini*, Figs. 6.6, 6.7, 6.8).

As the presence and morphology of an olecranon process appears to be variable between specimens of the same species at different ontogenetic stages the use of olecranon processes and/or crest for species identification (such as in the diagnosis of *Bunostegos*) is probably unreliable and should be used with caution.

7.3.4 Humeral torsion differences

Lee (1997a) noted torsion in the proximal and distal expansions of the humerus of *Embrithosaurus* at approximately 45^0, which is not accurate as both humeri of the holotype show torsion of $70\text{-}80^0$ and are nearly perpendicular to each other (Fig. 4.7), and referred *Embrithosaurus* specimen FMNH UR 2443 has torsion of about 60^0. The right humerus of the holotype of *Embrithosaurus* had been broken at the shaft and the proximal and distal ends were reattached for this project where they best fitted tightly together, and we can be certain of an accurate reconstruction on the right as the unbroken shaft of the left humerus confirms torsion of $70\text{-}80^0$. This contrasts sharply with *Nochelesaurus*, which has very flat expansions, the flattest in the group, almost on the same plane ($20\text{-}40^0$ in most specimens, Fig. 5.8). It is not possible to determine the degree of torsion of the expansions in the humeri of the holotype of *Bradysaurus baini* as both humeri were broken and questionably reconnected at the mid shaft on the same plane with very flat expansions (Seeley 1892: 360), and so only referred specimens are useful. Broom (1903: 131) suggested that Seeley (1892) was in error when he reconstructed the proximal and distal expansions in nearly the same plane on the humeri of the holotype of *Bradysaurus baini*, and I agree with Broom as referred *Bradysaurus baini* specimens, such as the mounted skeleton at the Iziko South African Museum (SAM-PK-5624) have torsion of $70\text{-}80^0$, and specimen SAM-PK-3718 shows a torsion of 70^0. The important and well preserved sub-adult *Bradysaurus baini* specimen SAM-PK-5002 preserved no humerus. Both *Bradysaurus* and *Embrithosaurus* therefore have high degrees of

humeral torsion (60-80^0) and *Nochelesaurus* is the only species in the group with significantly less torsion (20-40^0).

Lee (1994, 1997a) also notes the smallest angle he defined in this group, 45^0, for *Nochelesaurus* (and *Embrithosaurus*), and a larger angle of 60^0 for *Bradysaurus.* Flatter expansions of the humerus therefore distinguishes *Nochelesaurus* specimens from the very twisted, almost perpendicular or right angled expansions of *Embrithosaurus* and *Bradysaurus.*

Turner *el al.* (2015) discussed the degree of offset between the planes of the proximal and distal expansions of the humerus and the implications for the forelimb posture of *Bunostegos.* They suggest a more upright (and less sprawling) posture for *Bunostegos* where the humerus has proximal and distal expansions that are untwisted and are in line with each other (flat) and note that most pareiasaurs have a value around 45^0, inferring a sprawling posture. Assuming this is correct, it implies that *Nochelesaurus*, which has the flattest expansions, may have had a more upright posture than *Embrithosaurus* and *Bradysaurus*.

7.3.5 Osteoderm ornamentation differences

The number and arrangement of osteoderms on the body of the *Tapinocephalus* AZ pareiasaurs has been known to be restricted to a narrow region above the vertebral column since Seeley's (1888, 1892) descriptions of *Bradysaurus* and was one of the most important features that Watson (1914b) emphasised in his separation of South African pareiasaurs into genera with few osteoderms (*Bradysaurus*, *Embrithosaurus*) and those with many osteoderms (*Pareiasaurus, Propappus*). Osteoderms are seldom preserved with the pareiasaurian material recovered from the middle Permian of South Africa. Where preserved, they are usually in the form of a few isolated scutes, scattered and articulated to dorsal surfaces of vertebrae. The holotypes of *Embrithosaurus schwarzi* and *Bradysaurus baini* preserve osteoderms in this manner, and the holotype of

Nochelesaurus preserves an isolated flat plate comprising a few articulated scutes.

Boonstra (1934b) in describing the ornamentation of the osteoderms of *Embrithosaurus* was the first to note the central boss of irregular shape on the largest scutes and also the disc-like or very thin nature of most scutes. Boonstra (1934b) also noted that in the three *Bradysaurus* species recognised at that time, the scutes are all relatively smooth, with practically no ornamentation, convex with a thickened centre that creates an incipient central boss in some scutes. Lee (1994, 1997a) also highlighted the boss on each osteoderm of *Embrithosaurus* as different from the unornamented osteoderms of *Bradysaurus* and *Nochelesaurus.*

These early descriptions are accurate, as regards the differences between the scutes of *Embrithosaurus* and *Bradysaurus*. My research has revealed more anatomical differences. In particular, the dorsal scutes of *Bradysaurus* have been further differentiated morphologically between three morphotypes: anterior, posterior and small stud-like scutes (see chapter 6). *Embrithosaurus* presents two morphotypes and has the most distinct osteoderms in the group of basal South African pareiasaurs. Osteoderm morphology has recently become more useful for pareiasaurian taxonomy, for example, Maisch and Matzke (2019) have shown *Anthodon? haughtoni* (v. Huene, 1944) to be a valid taxon based on autapomorphies of the osteoderm morphology. Boyarinova *et al.* (2019) showed that the morphology of the osteoderms in the East European pareiasaurs (*Scutosaurus* and *Deltavjatia*) are species specific. In *Deltavjatia* two morphotypes are developed, and in *Scutosaurus* there are four morphotypes. These studies demonstrate the high potential of osteoderm morphology for taxonomic differentiation.

Nochelesaurus has been historically neglected in this regard. Preparation of the scutes of the holotype reveal ornamentation different from that of *Bradysaurus* and *Embrithosaurus*. The osteoderms have a distinct, wide, roughly round central

boss (*Bradysaurus* has an incipient central boss or no boss and *Embrithosaurus* has a small, distinct, E or L shaped, rugose central boss) , and a periphery that is much higher or thicker than in *Embrithosaurus* and with none of the radiating ridges of *Embrithosaurus*.

These differences between the osteoderms of the three taxa are important distinguishing features which have been included in the updatd species level diagnoses.

7.3.6 Femoral differences

Lee (1994, 1997a) distinguished *Embrithosaurus* based on the presence of a curved, s-shaped, internal trochanter on the femur, not visible in dorsal view which he contrasted with the straight internal trochanters of *Bradysaurus* and *Nochelesaurus*.

Although the internal trochanter is not preserved in the holotype of *Embrithosaurus,* historic figures record it as gently curved and s-shaped in agreement with Lee (see chapter 4, Figs. 4.12, 4.13). This is further supported by referred *Embrithosaurus* specimens (FMNH UR 2443, CGP CBT 112) which have gently curved internal trochanters. However, the holotype of *Bradysaurus baini* also has a curved internal trochanter on the femur, which is larger, rounder and more severely curved than that of *Embrithosaurus* specimens. *Nochelesaurus* is the only pareiasaur in this group with a straight internal trochanter (as present on the holotype and several referred specimens) with *Embrithosaurus* possessing a gently curved trochanter, and *Bradysaurus* having a massively curved and rounded trochanter. Several related differences between the internal trochanters of these three taxa are explained in the diagnoses (see chapter 8). Therefore the morphology of the internal trochanter is a reliable morphological feature to identify the different middle Permian pareiasaur species.

Lee (1997b:246: character 109) noted a weakly developed external major trochanter as the primitive pareiasaurian condition, and proposed

Embrithosaurus as the only basal South African pareiasaur with a well-developed major trochanter, and therefore as more derived. Lee argues that the weaker (smaller) major trochanters of *Bradysaurus* and *Nochelesaurus* are caused by only a very slight thickening of the postaxial flange. However, measurements show that in dorsoventral thickness, the major trochanters are about 35-40 mm thick (and the postaxial flange about 20 mm thick) in all basal South African pareiasaur species. Only in specimens of *Embrithosaurus* however, does the major trochanter protrude posteriorly far (20-30 mm) beyond the general level of the postaxial flange of the femur. The major trochanters of the other middle Permian pareiasaurs from South Africa, protrude only 5-10 mm posteriorly. These differences in size of the posterior extend of the major trochanter in different species but have been used extensively for specimen identifications in this project, but should be cautioned as the differences are often minor.

A final feature proposed by Lee (1997a:253) is the narrower femur of *Embrithosaurus*, which creates a slightly concave postaxial edge, in dorsal or ventral view (Lee 1997b: 247: character 112). My research shows that the femora of the holotype of *Embrithosaurus* are slightly narrower in the way Lee describes, anteroposteriorly by 10 mm, than the femur of the holotype *Nochelesaurus* and 20-25 mm narrower than the femora of the holotype of *Bradysaurus baini,* supporting Lee's contention. However, the holotype femur of *Bradysaurus baini* is severely dorsoventrally crushed which may account for the anteroposteriorly wider femur. The size differences between *Embrithosaurus* and *Nochelesaurus* are minor and not reliable indicators for species separation. Furthermore, the postaxial edge of the femur in *Embrithosaurus* is straight to slightly convex (not concave) as in all middle Permian South African pareiasaurian taxa, especially in *Embrithosaurus* and *Bradysaurus*. The narrower femur of *Embrithosaurus* proposed by Lee has been removed as a character by which to identify the species.

7.3.7 Subscapular fossa considerations

Lee proposed that the subscapular fossa of *Nochelesaurus* is located "very close to the anterior margin of the scapula blade" (Lee 1997a:249) and that in all other pareiasaurs the groove is located more in the centre of the blade.

As the anterior border of the right scapulocoracoid of the holotype of *Nochelesaurus* is not preserved below the acromion processes, it is challenging to accurately determine the position of the subscapular fossa in relation to this missing anterior border. However, just above the subscapular fossa, a section of the swollen, cylindrical, bar-like anterior border of the scapulocoracoid is preserved where it is 40 mm in anteroposterior width. In all large middle Permian South African pareiasaur specimens studied, this anterior border of the scapulocoracoid extends dorsoventrally immediately anterior to the subscapular fossa and over its dorsoventral extent it does not vary in anteroposterior width. This provides good evidence that the subscapular fossa of the holotype of *Nochelesaurus* is positioned 40 mm behind the anterior border of the scapulocoracoid. In referred *Nochelesaurus* specimen SAM-PK-6238, the anterior border of the scapulocoracoid below the acromion process is also not preserved, but can be estimated based on typical morphology for the group, at about 40 mm behind the anterior border. My observations suggest that the subscapular fossa is positioned similarly in the holotypes of *Embrithosaurus* (at 45 mm) and the larger holotype of *Bradysaurus baini* (at 55 mm) from the anterior border.

Possibly Lee did not recognise that the anterior borders of the scapulocoracoids of the holotype of *Nochelesaurus* and referred specimen SAM-PK-6238 are not preserved, creating the misleading appearance of more anteriorly positioned subscapular fossa.

Measurements of the position of the subscapular fossa in relation to the posterior edge of the scapulocoracoid are complicated by the fact that the posterior edge of the scapulocoracoid is oblique, while the fossa is vertical, so

the dorsal and ventral portions of the fossa are located at different distances from the oblique posterior border. Nevertheless, measurements show the subscapular groove of the holotype of *Nochelesaurus* and referred *Nochelesaurus* specimen SAM-PK-6238 to be positioned between a range of 90-135 mm from the posterior border, which is similar to the position found in the holotypes of *Embrithosaurus* (60-150 mm), and the larger holotype of *Bradysaurus* (110-175 mm) (Table 4.1). There is no convincing evidence that the subscapular fossa is positioned more anteriorly on the scapulocoracoid in *Nochelesaurus* than in the other closely related species of large middle Permian South African pareiasaurs. As such, the anteriorly positioned subscapular fossa proposed by Lee has been removed as an autapomorphy and as a character by which to identify the species *Nochelesaurus alexanderi*.

7.3.8 Does *Nochelesaurus* possess a humeral tubercle?

Lee (1997a) proposed the presence of a distinct tubercle on the centre of the dorsal surface of the entepicondyle in both the holotype of *Nochelesaurus alexanderi* and in referred *Nochelesaurus* specimen SAM-PK-6238 (holotype of *Dolichopareia angusta*) as an autapomorphy of the genus. A clear and distinct tubercle is undeniably present on the humerus of SAM-PK-6238 (Figs. 5.9, 5.10) and is fully ossified and does not appear to be pathological. On the holotype, identification of a distinct tubercle is not as certain (Fig. 5.7), as explained in chapter 5. Boonstra's (1932c: 471, Fig 27) illustration of the right humerus of SAM-PK-6238 included the roughly circular tubercle, but he did not mention it in his brief systematic description, implying that he did not consider this feature significant. Referred *Nochelesaurus* specimens FMNH UR 2436, and FMNH UR 2480, both appear to show a humeral tubercle. I tentatively retain this feature as diagnostic of *Nochelesaurus*, but not as an autapomorphy as this feature is not present in all specimens of *Nochelesaurus*. As explained in chapter 5, the postaxial border of the intercondylar fossa of the humerus forms a swollen ridge

in all large middle Permian South African pareiasaurs, which could be misinterpreted as a tubercle.

7.3.9 Does *Nochelesaurus* possess a distal femoral flange?

Lee (1994, 1997a) stated that *Nochelesaurus* has an autapomorphy on the dorsal surface of the femur, which he termed a "distal femoral flange", being a flange that projects distally beyond the postaxial tibial facet. Close inspection of the femur of the holotype reveals no such obvious flange. However, the lateral (postaxial) condyle does extend distally far, 70 mm, beyond the distal edge of the medial condyle, further than the 30–40 mm extension of the holotype of *Embrithosaurus schwarzi* and the 20-30 mm estimated for the holotype of *Bradysaurus baini*. Therefore, this expansion is much longer in the holotype of *Nochelesaurus* and many, but not all referred specimens, and Lee's distal femoral flange is tentatively retained as a feature of *Nochelesaurus*, but not as an autapomophy as it is not present in all specimens, but is present in most.

7.4 Taxonomic discussion

7.4.1 Prioritization of important features

The holotypes of *Bradysaurus baini*, *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi* reveal obvious autapomorphies and morphological differences between the individual specimens, such as the shape of the pelvis of *Embrithosaurus schwarzi* or the inwardly pointing upper jaw teeth of *Bradysaurus baini*. The majority (65% or 157 specimens) of the 240 middle Permian South African pareiasaurs studied in this project, have been identified to species level. However, accessing such a large sample set of over 200 pareiasaurs a high proportion of which preserve relatively complete skeletons, this study found that the discrete diagnostic features or combination of features of the holotypes are sometimes not found in particular specimens. When using the diagnostic features of the holotypes to identify a particular specimen, it becomes apparent that some specimens have a combination of characters from more than

one species, or are intermediate between two or more species. In these few instances, I have noted these specimens as unidentifiable (see Appendix A, Unidentifiable section, 60 specimens), for example, specimen SAM-PK-9168 is unidentified in this project as it has several features of *Bradysaurus*, *Nochelesaurus* and *Embrithosaurus*. When a specimen exhibits a combination of features from more than one species, making positive identification challenging, I have also sometimes only been able to identify a specimen to a duel species level, i.e. either of two possible species (see Appendix A, Duel species identification section, 23 specimens). For example, in some instances the skull points to a particular species and the postcrania to another, for example specimens FMNH UC 1533 and BP/1/7165.

Note that most of the 60 unidentifiable specimens and the 23 specimens identified to one of two species, are the result of poor preservation, poor preparation or too few or no diagnostic parts preserved.

To avoid the scenario whereby a diagnostic model cannot securely identify a specimen, early workers created many species (reaching a maximum of 13 species in the *Tapinocephalus* AZ alone, Kuhn (1969)) each with slightly different features. This lead to a generally agreed inflated number of species historically, which Lee (1994, 1997a) reduced. To avoid an inflated number of very similar species, I have had to:

- prioritise certain diagnostic features as more important than others , based on major morphological differences (e.g. the orientation of the upper jaw teeth, the shapes of the postfrontal, postparietal, premaxilla and maxilla, the morphology of the posterior cheek bosses and the overall cranial ornamentation, the overall shape of the pelvis, features of the femur, the twisting of the humerus and the ornamentation of the osteoderms),
- accept the species identification of the majority of the features of a specimen (e.g. when analysis of a specimen identifies the specimen as

80% likely belonging to one species and 20% likely belonging to another, I have tentatively accepted the 80% majority identification), and

- increased the intraspecific character variation within each species (see below).

7.4.2 Increased intraspecific variability

Direct study of a large set of 240 pareiasaurs for this project, with assignment of specimens into only three species, has resulted in an increase in the variability within each species. Cranial variability is documented per species at a specimen level in Appendix E, Tables 1 to 6, and reveals the character ranges in individual species.

The variability of the numbers of cusps on the teeth of all three middle Permian South African species has been increased and now covers a range of seven to nine (*Embrithosaurus* and *Bradysaurus*) and seven to ten (*Nochelesaurus*) whereas previously *Embrithosaurus* was the only species to have more than seven cusps. *Embrithosaurus schwarzi* has either seven or nine cusped upper jaw teeth, *Nochelesaurus alexanderi* has seven or eight cusped upper jaw teeth (with one outlier specimen having five and seven cusped teeth) and *Bradysaurus baini* seven, eight or nine cusped upper jaw teeth. *Embrithosaurus* may have either dorsoventrally shortened maxillary teeth, lacking a long central trident (nine cusped teeth) or dorsoventrally elongated maxillary teeth, with a long central trident (seven cusped teeth) where as both *Bradysaurus* and *Nochelesaurus* only have dorsoventrally elongated maxillary teeth.

Lower jaw teeth show even more variability in all three species. *Embrithosaurus schwarzi* shows the least variability with seven or nine cusped lower jaw teeth, shortened teeth, symmetrical cusp arrangements, no medial cusps, a low lingual bulge, and no lingual cingulum. *Nochelesaurus alexanderi* is highly variable with seven to ten cusped lower jaw teeth, elongated teeth, non-symmetrical cusp arrangements, an incipient cingulum ridge on certain teeth, medial cusps

sometimes present, and one to three vertical lingual ridges. The lower jaw teeth of *Bradysaurus baini* are also highly variable with elongated or shortened teeth, seven to nine marginal cusps, symmetrical or non- symmetrical cusp arrangements, medial cusps sometimes present, and a bulged or vertically ridged lingual surface.

Maxillary teeth are always vertically oriented in *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi* specimens, but vary from obliquely posteroventrally to horizontally backwardly oriented in *Bradysaurus baini.* As explained earlier, these major differences do not appear to be the result of distortion and are probably real anatomical differences between the species.

Both *Bradysaurus baini* and *Embrithosaurus schwarzi* develop a maxillary boss in ontogeny and juvenile specimens may lack this boss, sub-adults may have a low or small boss, and adults usually the largest bosses. *Nochelesaurus alexanderi* specimens never develop a maxillary boss, not even large, adult specimens.

For *Bradysaurus baini* the size of the cheek (expressed in degrees below the tooth row that the ventral surface of the quadratojugal reaches, Turner *et al.* 2015, character 44) is highly variable, the most variable in this group of middle Permian pareiasaurs. The cheek flange varies from small (20^{0}) to large (30^{0}) below the tooth row in *Bradysaurus baini*, and two specimens have cheeks larger than 30^{0}. *Embrithosaurus schwarzi* (30-40^{0}) and *Nochelesaurus alexanderi* (+-30^{0}) have more consistently sized, larger cheeks. These size differences and patterns are consistent enough to be reliably used to identify specimens.

The size and shape of the bosses on the posterior cheek of *Bradysaurus baini* is also extremely variable, varying from small or medium sized bosses, as wide as high, to very large, wide, low, indistinct bulbous bosses, as in the holotype. The posterior cheek bosses of *Nochelesaurus* are also variable: either horizontally flat and plate-like bosses or medium sized bosses, as wide as high. Only *Embrithosaurus* consistently shows wide, low, bulbous bosses.

The size and shape of the angular boss of the lower jaw is highly variable in all species. However, only one pattern emerges, the observation that many large specimens of *Bradysaurus baini* have relatively small angular bosses compared to equally large *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi* specimens. However, this pattern is not secure and it not included in the diagnosis of *Bradysaurus baini.*

Some *Bradysaurus baini* specimens have a frontal with a high, distinct central boss, but most specimens have a large, wide, low, irregular frontal central boss.

Nasal tab-like processes on the three holotypes exhibit clear differences, suggesting they may be useful for species separation. *Nochelesaurus* does not possess an anterolateral tab, while *Bradysaurus* and *Embrithosaurus* do. *Bunostegos* is diagnosed with a nasal that has a posterolateral tab-like process that reaches the frontal (Tsuji *et al.* 2013). However, these nasal tabs are highly variable across specimens of *Bradysaurus*, *Embrithosaurus* and *Nochelesaurus* (see Appendix E, Table 4) and no consistent patterns emerge.

Postcranially, the development of the olecranon process of the ulna is highly variable (see above). Some authors have used the morphology of the olecranon process to distinguish between taxa (Watson 1914b, Boonstra 1932c). However, I and other authors (Lee 1997b) have hypothesised (see above) that small olecranon processes are the result of early ontogenetic development and cannot be used to distinguish species.

The internal trochanter is consistently different between the species, and shows only slight variability within each species. It is large, projecting and curved in both *Bradysaurus* and *Embrithosaurus*, but is more curved in *Bradysaurus*. In *Nochelesaurus* it varies from straight to slightly curved proximally. In *Embrithosaurus,* proximally it may be narrow or thick and rugose.

The distal extension of the lateral condyle of the femur is longest in most specimens of *Nochelesaurus*, but not all, and shows high levels of variability.

Pelvic differences between *Embrithosaurus* and *Bradysaurus* are highly consistent with little variability and are therefore reliable species separators.

Differences in the torsion of the proximal and distal expansions of the humerus between the species, discussed earlier, are also consistently present and appear to be reliable species separators.

7.4.3 The effects of distortion

Many authors have recognised that the pareiasaur remains recovered from the *Tapinocephalus* AZ have been distorted, thus complicating taxonomic assessments. Despite acknowledging this, Haughton and Boonstra's (1929a) pareiasaurian classification scheme relied on cranial proportional differences (interorbital width compared to tabular width) for their sub-divisions, after the use of dental factors for their primary divisions. As later evaluated by Lee (1994, 1997a) and Van den Brandt (2016), most of these cranial proportions are contentious characters, and that it is more reliable to focus on the absence or presence of discrete and dental cranial features.

Van den Brandt (2016) briefly discussed the observation of two general cranial morphotypes: 1) wide, broad, dorsoventrally flattened skulls with splayed out lateral cheeks, and 2) narrow, high, mediolaterally compressed skulls with tall, thin external nares. Whilst it is often possible to identify clear signs of distortion (e.g. buckled or displaced cranial bones), it is also true that often the wider or the narrower skulls appear to be well preserved and relatively unaffected by distortion. Interpreting the true skull shape is therefore often challenging. Overall, most skulls from this AZ are naturally dorsoventrally flat and wider than high (phylogenetic character 33: snout dimensions, Turner *et al.* 2015) apart from *Nochelesaurus*, which appears to be taller, more square, almost as high as wide, and has been phylogenetically scored as such in this project. It is tempting to classify the pareiasaurs from the *Tapinocephalus* AZ in these two broad

categories (wide or tall), but this approach would classify specimens based on deformation and distortion, and not on cranial features

7.4.4 Are differences due to sexual dimorphism?

Very little has been published on the subject of sexual dimorphism in pareiasaurs. Broom (1935) briefly documented some thoughts when discussing the variation between the holotypes of *Embrithosaurus schwarzi* and *Bradysaurus baini*. He emphasised that the obvious pelvic differences between these two taxa, documented by Watson (1914b), may be the result of sexual dimorphism. I disagree with Broom as these pelvic differences occur consistently with other characters that separate *Bradysaurus* and *Embrithosaurus* to distinguish between species and not genders. Broom went on to highlight the great difficulty in pareiasaurian systematics, explaining that nearly every specimen shows some differences compared to others, and that without knowing which characters vary as a result of ontogenetic age or sex, it is impossible to arrive at systematic finality.

Tsuji (2010, 2013) demonstrated the underdeveloped pareiasaurian angular boss as a juvenile character.The current study has shown the lack of a distinct maxillary boss in *B. seeleyi* to be an early stage in ontogenetic development, supported by the overall smaller and more gracile condition of the preserved postcranial elements.

As in many other reptile groups, female pareiasaurs were probably smaller and more gracile than the males. My research shows that *Bradysaurus baini* exhibits a large variation in cheek size. I suggest that: 1) the small cheeks (20^0) may belong to female individuals and, 2) larger cheeks (30^0) to males. Similarly, the bosses of the posterior cheek appear in two morphotypes: 1) small to medium, round, as wide as high bosses may be the female condition and, 2) large, low, wider than high, bulbous bosses may be the male condition.

7.4.5 Implications of a severe lack of bilateral symmetry

Van den Brandt (2016) and Van den Brandt *et al.* (2019) was the first to identify two distinctly different arrangement patterns of the posterior cheek bosses on the quadratojugal in basal South African pareiasaurs: one pattern has one small boss above the corner boss and the other pattern has two small bosses above the corner boss. Van den Brandt (2016) found these two different arrangement patterns present on specimens of *Bradysaurus baini*, *Bradysaurus seleeyi* and *Nochelesaurus alexanderi*, but not in any specimens of *Embrithosaurus schwarzi*. Accordingly he proposed the pattern of only one small boss above the corner boss as diagnostic for *Embrithosaurus*. However this arrangement pattern cannot be diagnostic of *Embrithosaurus* as specimens (SAM-PK-5624: *Bradysaurus baini*, and CGP CBT 112: *Embrithosaurus schwarzi*) have been found to have both arrangement patterns, a different one on either cheek. The fact that one individual can have both arrangement patterns shows that bilateral asymmetry exists in the size and placement of the posterior cheek bosses of the middle Permian South African pareiasaurs. This brings into question the diagnostic validity of the size and arrangement pattern of the posterior cheek bosses in very similar pareiasaurian species.

There is also large variation and asymmetry within a single individual: the ulnae of the holotype of *Bradysaurus baini*, show extreme size differences of the olecranon process on the left, which is short (15 mm dorsoventrally high) compared to the right, which is three times as high (45 mm dorsoventrally high) and if found not found together, these two ulna are different enough to be reasonably assigned to two different individuals and two different species. Similarly, the femur of *Nochelesaurus alexanderi* specimen SAM-PK-9137 shows asymmetry with both a straight (left femur) and a slightly curved (right femur) internal trochanter.

These examples and findings of severe bilateral asymmetry in the features of these middle Permian pareiasaurs, which would identify individual elements as a

different species when using only the right or left sides, should caution workers against emphasis of minor morphological differences to separate species.

7.4.6 One species or many?

A robust taxonomy and reliable distinguishing diagnostic characters to differentiate between pareiasaur species from the *Tapinocephalus* AZ of the Karoo, has been historically challenging and despite all the recent work done by Lee (1994, 1997a), Van den Brandt (2016), and this project, it remains challenging.

This project has synonymised *Bradysaurus seeleyi* with *Bradysaurus baini* on the basis that *B. seeleyi* was named using juvenile characteristics (see chapter 8). I have decreased the number of recognised species from the *Tapinocephalus AZ* from four to three, retaining the three very different holotypes, as each of these holotypes exhibit unambiguous autapomorphies or discrete diagnostic features, as documented by Van den Brandt (2016), Van den Brandt *et al.*(2019) and by this study (see chapter 8: Diagnostic features).

As explained in this discussion chapter, major morphological differences between the three species exist in the orientation of the upper jaw teeth, the shapes of the postfrontal, postparietal, the posterior cheek bosses, the shape of the pelvis, the internal trochanter of the femur, the twisting of the humerus and the ornamentation of the osteoderms.

However, due to the high degree of intraspecific variability within each species (see above) and some overlapping or shared features now evident from this study, the possibility exists that only one, extremely diverse, pareiasaurian taxon existed during the middle Permian of South Africa, with the documented differences the result of ontogeny and distortion.

8. CHAPTER EIGHT: TAXONOMIC REVIEW AND DIAGNOSES

8.1 Introduction

This chapter presents a taxonomic reassessment of the valid middle Permian pareiasaur species from South Africa. Tables 8.1 and Table 8.2 provide summaries of previous taxonomic schemes relating to middle Permian South African pareiasaurs and includes the changes proposed in this study.

For each valid species, the systematic palaeontology is presented (definition and revised diagnosis). Deltran optimization on the majority consensus tree of the updated phylogenetic analysis (see chapter nine) was used to extract diagnostic characters and synapomorphies for taxa and groups and these were incorporated into the revised diagnoses. Synonyms are listed, including a brief taxonomic history with comments or remarks for these important historic specimens and a justification for synonymising each taxon. Indeterminate material is listed last.

Appendix E contains six tables (Tables 1 to 6) which detail cranio-dental diagnostic features and differences between the three middle Permian South African pareaiasaurs, *Bradysaurus*, *Embrithosaurus* and *Nochelesaurus*, and also shows the intraspecific variability within each species (specimen numbers are included).

Appendix F contains key comparative cranial and postcranial diagnostic features between the three middle Permian South African pareaiasaurs, *Bradysaurus*, *Embrithosaurus* and *Nochelesaurus*, listed in bulleted points per region or element.

Table 8.1 Specimen number flow chart

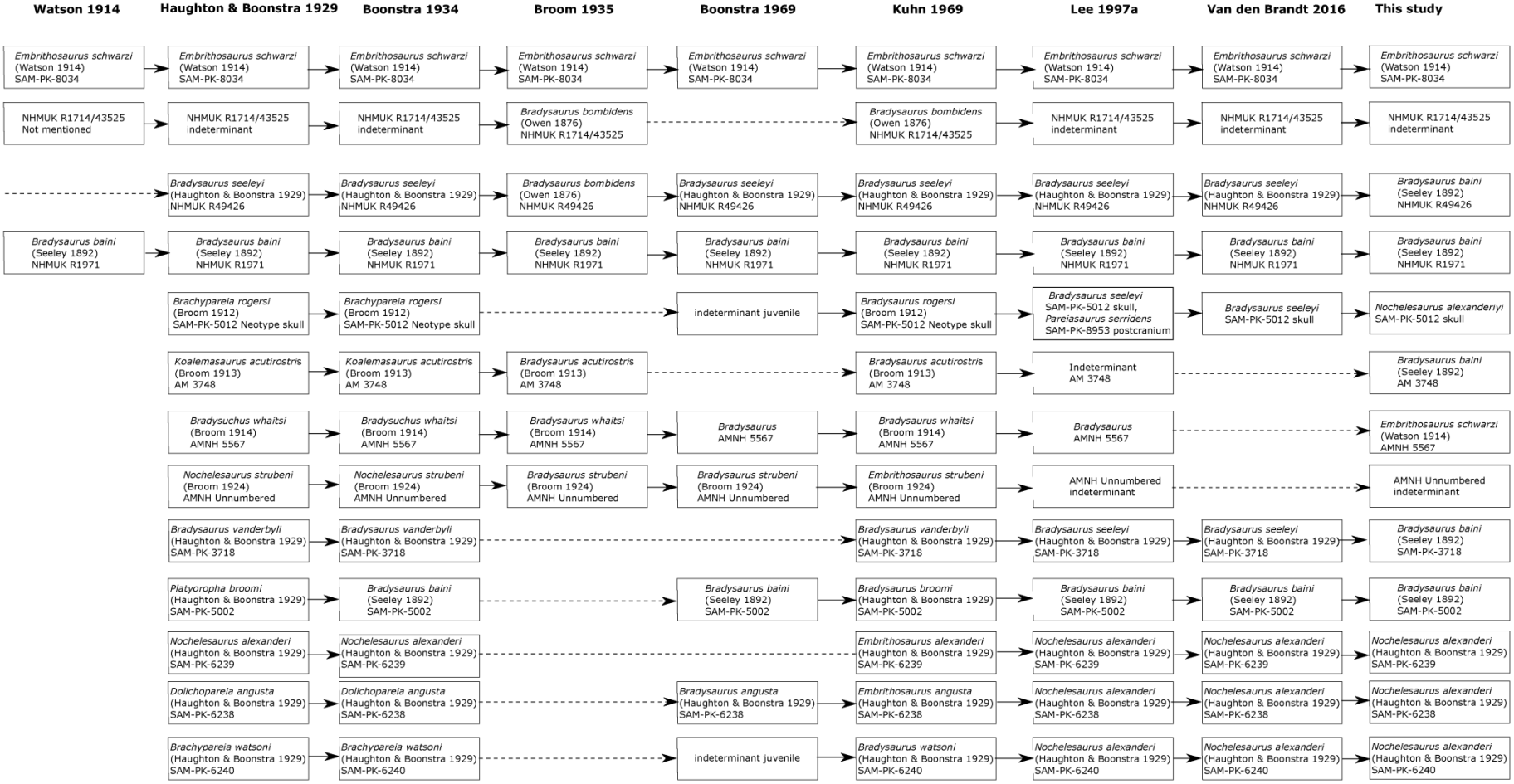
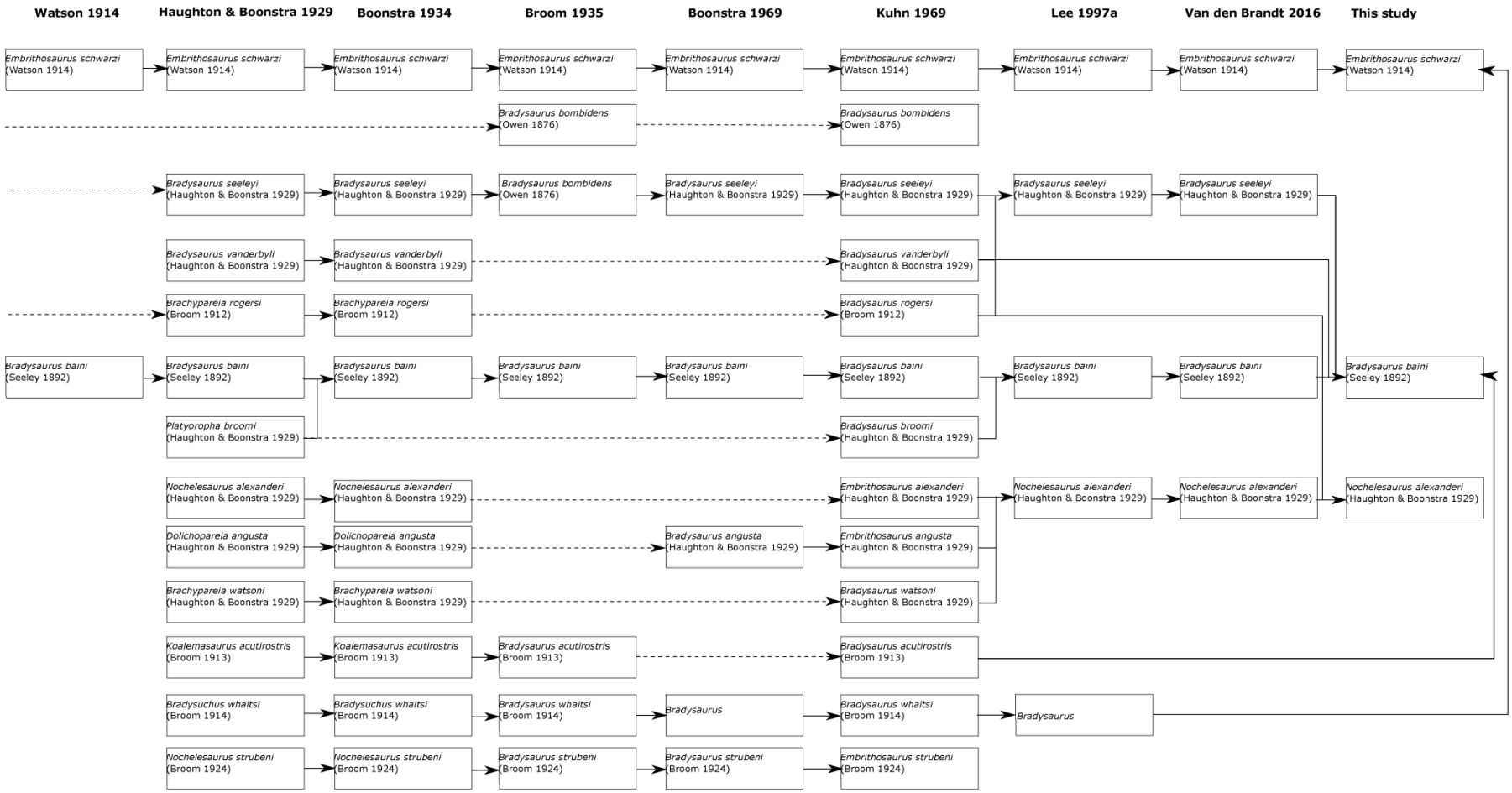


Table 8.2 Species flow chart



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Table 8.1: Specimen number flow chart showing a summary of previous taxonomic revisions of middle Permian South African pareiasaurs and the changes proposed in this study. Each row represents the same holotype specimen, and shows the species assigned by each author to that specimen. Dotted lines indicate where a specimen was not considered by an author.

Table 8.2: Species flow chart showing a summary of previous taxonomic revisions of middle Permian South African pareiasaurs and the changes proposed in this study. Each row represents the same species. Dotted lines indicate where a species was not recognised by an author. Solid lines indicate where a species was synonymised with another. All authors apart from Haughton and Boonstra (1929) and Kuhn (1969) consider *Platyoropha broomi* (SAM-PK-5002) a synonym of *Bradysaurus baini*. Lee (1997a) synonymised several taxa (holotype specimens) into only four species, which were retained by Van den Brandt (2016). This study proposes synonymising *Bradysaurus seeleyi*, *Bradysaurus vanderbyli* and *Bradysaurus acutirostris* with *Bradysaurus baini*, *Bradysaurus whaitsi* with *Embrithosaurus schwarzi*, and *Dolichopareia angusta*, *Brachypareia rogersi* and *Brachypareia watsoni* with *Nochelesaurus alexanderi.*

8.2 Systematic Palaeontology

REPTILIA Laurenti, 1768

PARAREPTILIA Olsen, 1947

PAREIASAURIA Seeley, 1888

PAREIASAURIDAE Cope, 1896

BRADYSAURIA Van den Brandt, 2019

8.2.1 Definition

The clade that includes *Bradysaurus baini*, *Nochelesaurus alexanderi*, *Embrithosaurus schwarzi* and their common ancestor.

8.2.2 Diagnosis

Clade of large-bodied pareiasaurs diagnosed by six synapomorphies: (1) character 21, presence of regular radiating ridges on the skull roof from the centre of the dermal skull roof bones (also the condition in two advanced pareiasaurians: *Scutosaurus* and *Provelosaurus*); (2) character 39, absence of supernumerary bones on the skull (unambiguous within pareiasauria, also the condition in *Owenetta*); (3) character 70, mandibular teeth, cusp number, seven

to nine cusps (unambiguous); (4) character 77, medial rows of palatal denticles widely separated, converging anteriorly (unambiguous); (5) character 79: pleurocentrum of the atlas separated from the axial intercentrum (unambiguous); and (6) character 115: notched anterior acetabulum (also the condition in *Pareiasuchus nasicornis* and *P. peringueyi*).

The Bradysauria are the only pareiasaurs to exhibit: character 13, basisphenoid, body, wide, strongly constricted, giving it an hourglass shape in ventral view; character 104, humerus, ulnar fossa (intercondylar depression), width, ulnar fossa is much wider than the olecranon process; character 129, pes, fifth digit, reduced, slender, shorter than the first pedal digit; and the condition of an absence of a central boss or bosses on the lateral squamosal (personal observation, not a listed phylogenetic character).

Additional phylogenetic features common to all known members of the Bradysauria, and up to three other pareiasaurs:

Character 7, paroccipital process, orientation, is U-shaped in occipital view, also the condition in *Bunostegos*; character 17, basal tubera, position, situated posteriorly, closer to the occipital condyle than the basipterygoid process, also the conditition in *Bunostegos* and *Elginia wuyongae;* character 25, interpterygoid vacuity, anterior shape, transversely-oriented, also the condition in *Bunostegos;* character 48, quadratojugal, ventral margin, ornamentation (bosses), absent, no ornamentation (bosses) on the ventral margin of the quadratojugal, also the condition in *Parasaurus*; character 49, junction of skull table and cheek, both flat surfaces, form a distinct angle where they meet, particularly behind the orbits, also the condition in *Deltavjatia*, *Bunostegos* and *E. wuyongae;* character 66, teeth, cusp arrangement, three central cusps close together, more lateral cusps farther apart and spaced farther apart from each other than these central three, also the condition in *Honania*; character 69, maxillary teeth, cusp number, seven to nine cusps, also the condition in *Bunostegos;* character 83, caudal vertebrae, number (tail length), long, with more than 25 caudal vertebrae, also the

condition in *Deltavjatia;* character 90, posterior coracoid, dorsal edge, almost horizontal, meets the posterior border of the scapula at an angle of less than 135^0, and character 91, cleithrum, present, also the conditions in *Shihtienfenia* and *Bunostegos*; character 99, entepicondyle and ectepicondyle relative size, equal, also the condition in *Shihtienfenia* and *Anthodon;* character 124, femur, postaxial flange, width, consistently wide, appearing straight, also the condition in *Deltavjatia* and *Honania;* character 133, osteoderms, body coverage, extent, osteoderms form only a longitudinal band closely overlying the vertebral column, and character 134, osteoderms, appendages, no osteoderms over the appendages, character 138, osteoderm, position, osteoderms do not touch, separated by a space, also the conditions in *Deltavjatia;* character 137, osteoderm, dimension, round and small, with a dimension no larger than diameter of the centra of the dorsal vertebrae, also the condition in *Deltavjatia, Shihtienfenia* and *Bunostegos;*

8.2.3 Type species

Bradysaurus baini Seeley, 1892

8.3 *Bradysaurus baini* (Seeley 1892) NHMUK R1971

8.3.1 Genus/Species type

GENUS: *BRADYSAURUS* Watson, 1914

TYPE SPECIES: *Bradysaurus baini* (Seeley, 1892)

8.3.2 Revised generic diagnosis

Same as for species.

8.3.3 Revised species diagnosis

One unambiguous cranial autapomorphy: Distal paroccipital process of the opisthotic anteroposteriorly expanded and with a large, distinct, dorsomedially

oriented posterior process on the posterior side. Regarding Lee's two other cranial autapomorphies: 1) the huge, rounded lump on the maxilla (a distinct maxillary boss) is shared with *Embrithosaurus*, *Sanchuansaurus*, *Pareiasaurus*, *Scutosaurus*, and *E. mirabilis* (character 31), and; 2) the ventromedially oriented upper jaw teeth (character 67) are shared with *Pareiasuchus nasicornis* and *Sanchuansaurus.* Since these occur in more than one taxon, these two features are removed as autapomorphies of *Bradysaurus baini*, but are retained as valid diagnostic features of the taxon.

One unambiguous postcranial autapomorphy: dorsal surface of the osteoderms smooth, convex, without a central boss (character 135).

Bradysaurus differs from co-occurring pareiasaurs in having: maxilla with a large and distinct rugose posterodorsal maxillary boss in adult specimens, lower or absent in juveniles (character 31); mediolaterally wide and curved ventral premaxilla and maxilla (20 mm wider than the tooth row), accommodating horizontally to ventromedially oriented, backwards pointing upper jaw teeth that are not visible in lateral view (character 67); maxilla with a wide, swollen maxillary-lacrimal ridge continuous with the swollen lacrimal boss complex; mandibular teeth with symmetrical or non-symmetrical mesial and distal marginal cusp arrangement; lateral quadratojugal ventrally covered with irregular rugose ridges and not flat, sometimes swollen and bulging forming a shelf in adults; smallest cheek flange amongst co-occurring pareiasaurs, extending as little as only 20^0 below the tooth row and size of cheek flange variable, between 20^0 and 30^0 (character44); bosses on the posterior margin of the quadratojugal either large, low, bulbous, wider than high and indistinct, or medium sized, as wide as high, more distinct and pointed; epicondyles of the humerus project distally far beyond the radial and ulnar articulation surfaces, appearing "forked" (character 98); proximal internal trochanter of the femur wide and strongly curved, with a perpendicular edge, and extending far ventrally; anterior dorsal osteoderms strongly convex, with incipient central boss, and very

light ornamentation; posterior dorsal osteoderms with shallow circular hollow and very light ornamentation.

Bradysaurus differs from *Embrithosaurus* in having: certain mandibular teeth with medial cusps; mandibular teeth with bulged or ridged lingual surface(character 71); mandibular teeth with non-symmetrically arranged marginal cusps, due to a very low and small cusp at the base of the distal margin of each tooth; posterior projection of major trochanter of the femur short; distal tibia ventromedially expanded and mediolaterally wide; anterior iliac blades not vertical but laterally upturned or everted (+- 45^0) and strongly curved (character 111); iliac shaft oriented anterodorsally, 30^0 above the horizontal plane (character 113); anterior iliac blades oriented 45^0 off the sagittal plane, posterior iliac blades dorsoventrally flat, oriented parallel to sagittal plane and with dorsal margins medially curved; puboischiatic plate wide, long, dorsally and ventrally flat; pelvis symphysis dorsoventrally thin; thin and narrow ventral keel on the puboischiatic plate; median pubic process small, square shaped with sharp edges, extending a short distance ventrally; second sacral rib is the largest; frontal central boss variable, small and flat or large and distinct.

Bradysaurus differs from *Nochelesaurus* in having: maxillary teeth with symmetrical mesial and distal marginal cusp arrangement; maxillary teeth lingual surface with a low, smooth bulge; mandibular teeth without horizontal cingulum; proximal and distal expansions of the humerus twisted 60^0-80^0 apart and almost perpendicular.

Bradysaurus and *Nochelesaurus* share small cheek flanges (character 44), and ridged lingual surface on the mandibular teeth (character 71).

8.3.4 Synonyms

8.3.4.1 *Platyoropha broomi* (Haughton and Boonstra 1929) SAM-PK-5002

SAM-PK-5002, sub-adult specimen of *Bradysaurus baini* (holotype of *Platyoropha broomi*) preserving the skull without lower jaw, shoulder girdle, most of the

pelvic girdle and the puboischaitic plate, both clavicles, interclavicle, both femora, four presacral vertebra (the 15^{th} -19^{th} vertebrae) with six-eight articulated osteoderms, first three sacral vertebrae, four caudal vertebrae, several unidentified postcranial fragments, and a few rib fragments.

Platyoropha broomi was erected by Haughton and Boonstra (1929a) based on SAM-PK-5002, mistakenly noting the interorbital width as greater than the supratemporal width and the orbits as posteriorly positioned. The cheek is narrow, but this is the result of the individual not being fully grown and therefore not diagnostic. The cheek is not "deep" (large) but actually quite small as it extends only 22.5^{0} below the tooth row. As later admitted by Boonstra (1934a) and agreed to by Lee (1994, 1997a) and Van den Brandt (2016), *Platyoropha broomi* is a sub-adult specimen of *Bradysaurus baini* as there are no morphological features to separate this specimen from the holotype of *Bradysaurus baini.*

Cranially, SAM-PK-5002 is consistent with all several diagnostic features of *Bradysaurus baini*, specifically the large knob-like posterior projecting process on the paroccipital process; a curved maxilla with inward pointing horizontally flat maxillary teeth (somewhat dorsoventrally crushed and therefore even more horizontally exaggerated to point backwards and slightly upwards); a wide, low, maxillary boss formed by a swollen, distinct, maxillary-lacrimal ridge; a swollen quadratojugal with curved rugose ridges laterally underneath a horizontal embayment (in exact agreement with the morphology of the holotype of *B. baini*, NHMUK R1971); and indistinct, low cranial ornamentation.

The postcranium is also consistent with diagnostic features of *Bradysaurus baini* especially the morphology of the iliac blades of the pelvis, the wide, proximally curved internal trochanter, the shape of the external trochanter, and the ornamentation of the osteoderms.

8.3.4.2 *Bradysaurus seeleyi* (Haughton and Boonstra 1929) NHMUK R49426

NHMUK R49426, skull, lower jaw, and partial postcranial elements (holotype of *Bradysaurus seeleyi*) comprising a left iliac blade with attached partial lateral sacral ribs and supraacetabular buttress, a clavicular fragment, a vertebral block containing the first 8 vertebrae, a very large vertebral block containing 10 partial dorsal vertebrae (9^{th} to 18^{th} vertebrae), with three partial osteoderms preserved, a sacral block containing four vertebrae (19^{th} -22^{nd} vertebrae), anterior caudal block containing four vertebrae (23^{rd} to 26^{th} vertebrae) that occludes well with the posterior end of the sacral vertebral block; posterior caudal vertebral block containing four vertebrae (27^{th}-30^{th} vertebrae) that articulates well with the posterior end of the anterior caudal block.

NHMUK R49426 was described as a new specimen of *Pareiasaurus bombidens*, by Seeley (1888). Haughton and Boonstra (1929a) did not recognise *P. bombidens* as valid and assigned NHMUK R49426 as the holotype of a new species, *Bradysaurus seeleyi*, on the basis of broad, (labio-lingually) flattened teeth, to accommodate this specimen in their classification scheme, and added a second specimen (SAM-PK-5624). They also added a third specimen (NHMUK R1970) which had also been referred by Seeley (1892) to Owen's *P. bombidens*. Haughton and Boonstra (1929a) noted the posterior border of the cheek with "relatively well defined bosses" (noting they are not as distinct or well defined as in *Nochelesaurus alexanderi*) as characteristic of *Bradysaurus seeleyi* specimens.

Lee (1994, 1997a) noted *Bradysaurus seeleyi* as exhibiting no obvious cranial or postcranial autapomorphies and that it differed from the very similar *Bradysaurus baini* in lacking the three cranial autapomorphies of that taxon (i.e. the large maxillary boss, the backwards pointing upper jaw teeth and the swollen paroccipital process of the opisthotic).

Lee (1994, 1997a) went on to justify *Bradysaurus seeleyi* as the most basal pareiasaur as a result of possessing: 1) the weakest (smallest) cheek flanges, and 2) a smooth anterior pelvic rim, lacking the median and lateral pubic processes

present in all other pareiasaurs. However, the holotype of *Bradysaurus seeleyi*, NHMUK R49426, possesses large cheek flanges (see below) and preserves no puboischiatic plate. Lee (1997a: 262: Fig 13A) illustrated the smooth pelvic rim using a specimen referred to *Bradysaurus seeleyi* (SAM-PK-3718). However, SAM-PK-3718 possesses a median pubic process and two lateral processes (see Appendix A: SAM-PK-3718) as is the case in all pareiasaurs. Van den Brandt (2016) retained *Bradysaurus seeleyi* as valid, and in his conclusion noted it as the least secure taxon in the group of middle Permian South African pareiasaurs, as he found the taxon to exhibit no clear autapomorphies. Van den Brandt (2016) found the species to be only identifiable through possessing a small cheek flange (also noted by Lee 1994, 1997a) in combination with the absence of the three cranial autapomorphies of *Bradysaurus baini*. Interestingly, Van den Brandt (2016) noted small cheek flanges are also present on some specimens of *B. baini*. Van den Brandt (2016:191-192) further concluded that *Bradysaurus seeleyi* shared at least two features with *B. baini*: the transversely narrow postparietal with all specimens of *B. baini* and the medium sized, relatively distinct, posterior cheek bosses with some specimens of *B. baini.*

Recent study of the holotype of *Bradysaurus seeleyi* (NHMUK R49426) reveals the specimen to be a sub-adult *Bradysaurus baini*, sharing all significant features of the holotype of *B. baini* except for one: the lack of a distinct maxillary boss, which is here ascribed to ontogenetic development, with this sub-adult individual lacking a distinct maxillary boss as it is not yet fully grown. In addition to the skull being small (see Table 7.2) the vertebrae of NHMUK R49426 and neural spines are noticeably small (the largest dorsal neural spines on the anterior sacrals are only 45 mm long and 40 mm wide) compared to the larger holotype of *Bradysaurus baini* (NHMUK R1971, 65 mm long, 70 mm wide), confirming this specimen as juvenile.

Since *Bradysaurus seeleyi* (NHMUK R49426) has been considered a valid taxon by most previous authors, a detailed justification for synonymising *Bradysaurus seeleyi* (NHMUK R49426) with *Bradysaurus baini* is necessary.

Justification for identification of NHMUK R49426 as a sub-adult *Bradysaurus baini*:

- The proposed distinguishing small cheeks of the holotype of *Bradysaurus seeleyi* (NHMUK R49426) are actually large and in the size range of *Bradysaurus baini*. Lee (1994, 1997a) indicated that *B. seeleyi* has the smallest cheek flanges amongst the *Tapinocephalus* AZ pareiasaurs, but did not provide measurements (e.g. the size of the angles formed by the cheek below the tooth row). Van den Brandt (2016, Van den Brandt *et al.* 2019) agreed and documented the size of the angle formed by the cheek below the tooth row as 20^0 (Van den Brandt 2016: 210: and here Appendix E, Table 5, 22^0 left cheek, 18^0 right cheek, average 20^0). This is significantly smaller than the holotypes of *Embrithosaurus schwarzi* (SAM-PK-8034: left cheek 24^0, right cheek $34^{0,}$ average 29^0), *Nochelesaurus alexanderi* (SAM-PK-6239: right cheek 33^0), and *Bradysaurus baini* (NHMUK R1971: left cheek 35^0, right cheek 25^0 average 30^0) (Van den Brandt 2016) or left cheek 35^0, right cheek 20^0, average $27.5^{\ 0}$ (Van den Brandt *et al.* 2019). Pareiasaurian cheek size is challenging to measure accurately as noted by Lee (1994, 1997a). The cheeks of the holotype of *B. seeleyi* (NHMUK R49426) do appear to be relatively small upon a superficial inspection, as they appear to extend only slightly below the level of the maxillary tooth row, especially on the right side. New, more accurate measurements show the left cheek to be larger, with its ventral border directed at an angle of 30^0 below the horizontal tooth row, and the right cheek to be relatively small at 20^0. The right cheek however, has been detached and was reattached with plaster approximately 30 mm too high, as shown by misalignment and mismatch of the right supratemporal bone breaks. Correctly aligned and attached, the right cheek would extend

roughly 30^0 below the tooth row, matching the left, which is very similar to the larger cheek flanges (average of 27.5^0) of the holotype of *Bradysaurus baini*. Furthermore, it is important to note that this project (and Van den Brandt 2016) determined that *Bradysaurus baini* specimens have the most variable cheek flanges of all pareiasaurian taxa in the group, ranging from smaller (20^0) to larger (30^0) (see Appendix E, Table 5). Phylogenetic character 44 (Turner *et al.* 2015, Van den Brandt 2016) notes cheek flanges that create an angle of less than 40^0 below the tooth row as small. By this definition *Bradysaurus baini* (20-30^0) and *Nochelesaurus* (30^0) cheek flanges are small and only *Embrithosaurus* (30-$40^{0)}$ has large cheek flanges in this group of pareiasaurs.

- The upper jaw teeth of NHMUK R49426 point posteroventrally backwards, a definitive characteristic of *B. baini*. Van den Brandt (2016) noted the upper jaw teeth of NHMUK R49426 as inwards or backwards pointing, but ascribed this to severe dorsoventral crushing of the skull, interpreting the actual morphology of the teeth as pointing straight down or slightly inwards. Re-examination of this specimen shows that the horizontally oriented upper jaw teeth (which are not visible in lateral view) are accompanied by a strongly convex premaxilla and maxilla (characteristic of *B. baini*) that is up to 15 mm mediolaterally wider than the tooth row and the inwards pointing teeth are probably not the result of dorsoventral crushing.
- Lack of a distinct maxillary boss on NHMUK R49426 is the result of the specimen being a sub-adult. A distinct maxillary boss is absent, but a swollen, low and wide, maxillary-lacrimal ridge is present. Lee (1994, 1997a) and Van den Brandt (2016) indicated that *B. seeleyi* lacked the large maxillary boss of *B. baini*. This is correct as NHMUK R49426 has no protruding, distinct maxillary boss, but it does have a bulbous, swollen, maxillary-lacrimal ridge originating low on the maxilla, which extends posterodorsally to the swollen lacrimal boss complex. A “bulging” maxilla and lacrimal, of differing sizes, as noted by Boonstra (1934:26) is present on most pareiasaurs. The length,

width, and placement of this swollen maxillary-lacrimal ridge on NHMUK R49426 is identical to the holotype of *B. baini*, and the entire region is simply lower in height and not as well developed. Since NHMUK R49426 is a relatively small skull and a sub-adult individual (see Table 7.2) it appears that the maxillary boss developed late in ontogeny. Evidence to support this hypothesis can be found in the juvenile CGP/1/2269 pareiasaur specimen, identified as *B. baini* as result of its backwards pointing, horizontally oriented, upper jaw teeth; low cranial ornamentation; narrow postparietal; smooth osteoderms; and partial large, process on the posterior distal paroccipital process of the opisthotic. The juvenile *B. baini* specimen CGP/1/2269 has a swollen posterodorsal maxillary-lacrimal ridge, no distinct maxillary boss yet developed and the specimen shows that the maxillary boss develops late in ontogeny in *B. baini*.

- The paroccipital process of the opisthotic of NHMUK R49426 has a large posterior, dorsomedial, "knob-like" process, a definitive characteristic of *B. baini*. Lee (1994, 1997a) and Van den Brandt (2016) noted the distal end of the paroccipital process of the opisthotic of NHMUK R49426 as not swollen and not possessing the posterior knob-like process seen in specimens of *B. baini.* Re-examination of NHMUK R49426 shows that the top half of paroccipital process of the opisthotic is not preserved on left side. On the right side, the area that was previously interpreted by Van den Brandt (2016) as part of the dorsal skull roof is actually part of the paroccipital process of the opisthotic and it shows a large knob-like process (40 mm mediolaterally wide, 30 mm dorsoventrally high, 20 mm projecting posteriorly). The previous misinterpretation of this process for the dorsal skull roof, is the result of not recognising that the right cheek has been reattached too high on the skull by about 30 mm.
- The smaller, more distinct posterior cheek bosses of NHMUK R49426 are within the size range of *B. baini*. The bosses on the posterior margins of the cheeks of NHMUK R49426 are medium sized, rounded, as high as wide and

therefore more distinct than the bulbous bosses of the holotype of *B. baini.* It is important to note that this project (and Van den Brandt 2016) have determined that *Bradysaurus baini* specimens show a wide range of variability in the morphology of the posterior cheek bosses, varying from large, wide, bulbous and indistinct to smaller, medium sized, relatively pointed, as round as high (see Appendix E, Table 5).

- The morphology of the pelvis of NHMUK R49426 is consistent with that of *B. baini*. The iliac blade is not vertical as the anterior process is turned upwards (everted). Posteriorly, the blade is oriented parallel to the midline and anteriorly it diverges outwards laterally at about 45^0 off the midline.
- The morphology of the sacral ribs of NHMUK R49426 is consistent with that of *B. baini*. The second sacral (20th vertebra) is the most massive sacral rib, and first sacral (19th vertebra) is smaller.
- The three partial scutes preserved on NHMUK R49426 have ornamentation consistent with the anterior dorsal osteoderms of the holotype of *Bradysaurus baini*. Each osteoderm has an indistinct raised, central region and no other obvious ornamentation.
- Lee (1994, 1997a) refers specimen SAM-PK-3718 (holotype of *Bradysaurus vanderbyli*) to *B. seeleyi* and used SAM-PK-3718 to illustrate a smooth anterior pelvic rim to differentiate *B. seeleyi* (Lee 1997a:262, Figure 13A). However, SAM-PK-3718 preserves a median pubic process and separate lateral pubic processes and is considered here a specimen of *B. baini* (see *Bradysaurus vanderbyli* below).
- The clavicle fragment of NHMUK R49426 has the small anterior process, as in the holotype of *B. baini.*

In light of all of these arguments, I consider *Bradysaurus seeleyi* a junior synonym of *Bradysaurus baini*.

8.3.4.3 *Bradysaurus vanderbyli* (Haughton and Boonstra 1929) SAM-PK-3718

SAM-PK-3718, holotype specimen of *Bradysaurus vanderbyli*, comprising a severely weathered and severely mediolateral crushed, very large skull and lower jaw, most of the dorsal vertebral column, both iliac blades, both acetabula , partial, severely weathered puboischiatic plate of the pelvis, proximal right femur, partial left scapulocoracoid, almost complete right scapulocoracoid, distal right humerus with articulated proximal radius and ulna, three unprepared dorsal vertebrae with four osteoderms, distal femora, left scapula blade, partial tibia, twelve anterior caudal vertebrae with one osteoderm.

Bradysaurus vanderbyli was erected by Haughton and Boonstra (1929a) based on SAM-PK-3718 with generic *Bradysaurus* features (less than nine cusps on the teeth, interorbital width much less than the supratemporal width) and with a very smooth posterior cheek border as diagnostic of this species. I concur with Lee (1994, 1997a) who recognised the border of the cheeks of SAMPK-3718 as severely weathered and that the posterior cheek bosses are actually large, low and bulbous, as in the holotype of *Bradysaurus baini*.

Lee (1994, 1997a) referred SAM-PK-3718 to *Bradysaurus seeleyi* based on the absence of three cranial autpomorphies of *Bradysaurus baini*, the presence of seven cusped teeth (thus not *Embrithosaurus* according to Lee) and the presence of small cheeks accompanied by the absence of discrete cheek bosses (thus not *Nochelesaurus* according to Lee). My research shows that SAM-PK-3718 possesses at least two of the three cranial autapomorphies of *Bradysaurus baini*: the maxillary teeth are inwards pointing and the distal paroccipital process is swollen and has a posteriorly projecting knob-like process. The specimen does not preserve a large maxillary boss, but as is the case with the flattened and eroded posterior edges of the cheeks of this specimen, the maxillary boss appears to be weathered-off on the left. On the right a partial maxillary boss remains (ventrally) and it appears that a large amount of bone is sheared-off

dorsally where spongy trabecular bone is visible. The cheeks of SAM-PK-3718 do appear to be small but measurements show them to be relatively large, extending an average of 28^0 below the tooth row. Cranially, SAM-PK-3718 is consistent only with *Bradysaurus baini*.

My study of SAM-PK-3718 shows the partially preserved puboischiatic plate to be severely damaged and eroded, and anteriorly preserves the remnant eroded core of a small (60 mm wide) median pubic process, separated by a notch from the lateral processes. Therefore the anterior pelvic rim is not smooth as previously considered (Haughton and Boonstra 1930b, Lee 1994, 1997a) and there is a median pubic process and two lateral processes, as seen in all other pareiasaurs.

Because of the lack of distinguishing features, SAM-PK-3718 is here considered to be a specimen of *Bradysaurus baini* identified by: large, bulbous and indistinct bosses on the posterior edge of the cheek (quadratojugal); a transversely narrow postparietal (as a result of deep weathering, some cranial sutures are discernible); an anteroposteriorly long distal paroccipital process of the opisthotic with a large knob-like posterior process; large cheek flanges; a curved maxilla with backwards pointing seven cusped upper jaw teeth; a roughly square postfrontal, slightly longitudinally elongated, and posteriorly curved medially; and a low, swollen maxillary-lacrimal ridge continuous with the lacrimal boss complex. The angular boss is remarkably small for such a relatively large skull (consistent with the generally smaller angular bosses of specimens of *Bradysaurus baini*), thin, narrow, slender, short, with a slightly swollen rim proximally and a very blunt, flattened tip.

Postcranially, SAM-PK-3718 is also consistent with *Bradysaurus baini:* both lilac blades are aligned longitudinally (estimated), with the anterior process or anterior-most quarter of the blade laterally curved outwards (about 40^0 on the right, 20-30^0 on the left) and slightly everted upwards (about 20-30^0 on the right); the first lateral sacral rib is only medium sized on both sides and the second is

massive and the largest (as in *Bradysaurus baini*); the puboischiatic plate is flat and low and anteroposteriorly long (+-320 mm) and the midline keel is not very deep (75 mm); dorsoventrally low acetabulum; anteroposteriorly long (200 mm) glenoid fossa; the internal trochanter of the femur has its ventral tip eroded but clearly is proximally strongly curved (concave preaxially, convex postaxially); the lateral condyle of the femur reaches 40 mm distally beyond the medial condyle (so not as far as in *Nochelesaurus*); the distal humerus lacks the tubercle of *Nochelesaurus*, the ulna has a 40 mm long olecranon process with an enclosed hooked socket for the reception of the humerus; the proximal and distal planes of the right humerus are about 70^0 apart (as in *Embrithosaurus* and *Bradysaurus* and contrasting with the flatter expansions of *Nochelesaurus*); the dorsal osteoderms comprise at least one small, as wide as high (25 mm), stud like osteoderm (as in *Embrithosaurus* and *Bradysaurus baini*) and three larger (55-60 mm wide) osteoderms that are 20-25 mm thick (lacking the thin periphery of the osteoderms of *Embrithosaurus*) and are evenly and smoothly convex dorsally. Interestingly, the ornamentation of these three large osteoderms are heavier than the anterior or posterior dorsal osteoderms of the holotype of *Bradysaurus baini* and more similar to the anterior dorsal osteoderms of the holotype of *Embrithosaurus*, in that they have a very rugose surface comprising thickened tab-like radial processes and large circular pits. The single osteoderm on an anterior caudal vertebra is small (40 mm wide) very thin, very flat and low and disc-like with very light ornamentation or ridges. The right scapula blade is very long (500 mm including the acromion process), probably due to the fact that this is a very large individual, and narrow at its midpoint (115 mm), both features more commonly found on specimens of *Nochelesaurus* The distal right scapula blade is damaged but is at least 180 to 190 mm wide, so quite flared as in *Bradysaurus* specimens.

8.3.4.4 *Pareiasaurus acutirostris* (Broom 1913) AM 3748

This specimen comprises a reconstructed skull, a dozen small cranial fragments, lower jaw, twenty one weathered dorsal vertebrae, a weathered distal radius, and an additional right cheek piece from another individual.

The skull of AM 3748 has been reconstructed from a few large cranial fragments held together with copious amounts of grey plaster obscuring much of the actual bone. The braincase and palate are unprepared, however, typical pareiasaurian palatal tooth rows of small denticles are identifiable. This specimen was used to justify the erection of a new species by Broom (1913a) *Pareiasaurus acutirostris* based on it being only roughly two-thirds the size of *Pareiasaurus (Bradysaurus) baini* and in having a very narrow snout.

Haughton and Boonstra (1929a) assigned AM 3748 as the holotype of a new genus, *Koalemasaurus,* based on the interorbital width being much greater than the tabular width and with the orbit being in the anterior half of the skull. However, the interorbital width is slightly less than the tabular width, as in all pareiasaurs, and the orbits are positioned slightly anterior of the middle of the skull. Subsequent authors retained this specimen as distinct: *Koalemasaurus acutirostris* (Boonstra 1934a); and *Bradysaurus acutirostris* (Broom 1935) and Kuhn (1969) until Lee (1994, 1997a) declared the taxon invalid and indeterminate, noting the holotype as a juvenile, laterally compressed skull of a large *Tapinocephalus* zone pareiasaur.

The specimen is certainly a juvenile specimen, as suggested by Lee (1994, 1997a). Juvenile characteristics include a small skull measuring only 328 mm from the tip of the snout to the most posterior edge of the supratemporal corner bosses (on a perpendicular plane), the small occipital condyle of only 46 mm in mediolateral width, the very small and low left angular boss (only 20 mm long), and the low numbers of teeth as there are only 14 to 15 alveoli preserved on each side of the lower and upper jaws. In addition, the supposed narrow snout and skull is the result of mediolaterally compression (also stated by Lee (1994,

1997a)) which is supported by observing the unnatural lateral compression and distorted shape of the external naris, which is very narrow and high.

Identified as a juvenile *Bradysaurus baini* as the premaxilla and maxilla are somewhat curved and bent horizontally and the maxillary teeth emerge obliquely posteroventrally (not vertically) from the maxilla. The maxilla is mediolaterally wide. The cranial ornamentation is low, bulbous and indistinct in general, including the bosses on the posterior edge of the cheek, a feature of *Bradysaurus baini*. The preserved right cheek extends far below the maxillary tooth row (about 35^0). The lateral surface of the quadratojugal (cheek) has no distinct bosses, so probably does not belong to a specimen of *Nochelesaurus* or *Embrithosaurus.* The cheeks are mediolaterally relatively thick, matching *Bradysaurus baini.* The paroccipital process of the opisthotic is complete on the right and is fairly thick and robust and has a fairly large (larger than in *Embrithosaurus*) oblique, dorsomedially oriented, knob-like, posteriorly projecting process, matching the morphology of a juvenile *Bradysaurus baini*. The maxilla behind the external naris is not preserved on either side. Similar to the sub-adult *Bradysaurus baini* specimen SAM-PK-5002, on the lateral cheeks, there is a vertically aligned, shallow depression, immediately in front of the posterior cheek bosses of the quadratojugal and squamosal, and these posterior cheek bosses are bent forwards, creating a sort of overhang.

8.4 *Embrithosaurus schwarzi* (Watson 1914) SAM-PK-8034

8.4.1 Genus/Species type

GENUS: *EMBRITHOSAURUS* Watson, 1914

TYPE SPECIES: *Embrithosaurus schwarzi* Watson, 1914

8.4.2 Revised generic diagnosis

Same as for species.

8.4.3 Revised species diagnosis

No cranial autapomorphies. The three unambiguous pelvic postcranial autapomorphies of Lee (1995, 1997a) are confirmed: 1) anterior iliac blades flat and vertical/dorsoventral (not everted or upturned) (character 111); 2) iliac blades not parallel but diverge anteriorly, oriented 45-60^0 off the sagittal plane, and; 3) pelvic symphysis dorsoventrally very thick (character 119).

Embrithosaurus differs from co-occurring pareiasaurs in: nine cusped maxillary teeth are dorsoventrally short and mesiodistally wide, lacking an elongated, central, three cusped trident at the apex of the crown, and with marginal cusps arranged more regularly around the tooth crown than in co-occurring taxa; mandibular teeth lacking medial cusps; small, distinct maxillary boss (character 31); prefrontal with a central, shallow, wide depression on some specimens; frontal with very small, low, central boss; postfrontal mediolaterally elongated; largest cheek flange in the group of co-occurring taxa, extending 30-40^0 below the tooth row; large, low, indistinct bulbous bosses (wider than high) on the posterior edge of the quadratojugal; small, distinct, dorsomedially oriented posterior process on the posterior side of the distal paroccipital process of the opisthotic. deep notch medial to the posteroventral process of the clavicle in some specimens; humerus with shallow intercondylar fossa (character 103); humerus lacking a short, curved insertion ridge on the shaft of the dorsal proximal humerus; narrow delto-pectoral crest; long posterior projection of the major trochanter of the femur (character 122); notch proximal and distal of the major trochanter; proximal internal trochanter with a perpendicular edge, gently curved and extending far ventrally and variable from narrow to wide and rugose; distal internal trochanter wide and rugose; large 60^0 angle between medial and lateral facets of the proximal articulation surface of the tibia; high, anterior dorsal osteoderms with distinct, small, central boss, made of rugose tab-like (L or E shaped) ridges, with thin, flat peripheries (character 136).

Embrithosaurus differs from *Bradysaurus* in having: vertical and narrow premaxilla and maxilla (< 5 mm wider than the tooth row), accommodating vertically oriented upper jaw teeth; 18 upper jaw teeth (character 68); iliac shaft oriented anterodorsally 30^0 off the vertical plane; pelvic symphysis anteroposteriorly short (character 118); puboischiatic plate narrow, short and dorsally concave; thick and wide ventral keel with oblique lateral sides; median pubic process large, tongue shaped with rounded edges, extending far anteroventrally; first sacral rib is the largest; caudal vertebrae with almost straight, lateral projections (character 85).

Embrithosaurus differs from *Nochelesaurus* in: absence of gap (vertical separation) on the posterior edge of the cheek between the dorsal-most quadratojugal boss and the large squamosal boss; proximal and distal expansions of the humerus twisted 60^0-80^0 apart and almost perpendicular.

8.4.4 Synonyms

8.4.4.1 *Pareiasaurus* (*Bradysaurus*) *whaitsi* (Broom 1914) AMNH FARB 5567

AMNH FARB 5567 comprises a large skull (410 mm long at the midline) and lower jaw. Reasonably well prepared, apart from the palate which is obscured with matrix. Nearly half of the surface area of the dorsal skull roof is damaged and filled in with plaster. The upper and lower jaw teeth are all severely damaged, most are not preserved (sheared-off) with a minority preserved but obscured with matrix.

The skull is severely mediolaterally compressed such that the snout appears pointed and the external naris appears narrow and tall, especially the right naris. Overall the skull is obliquely dorsoventrally crushed such that the left side of the skull is ventrally displaced compared to the right and the orbits are flattened.

Pareiasaurus whaitsi was founded on AMNH FARB 5567 (Broom 1914) with the diagnostic characters being a large orbit and the presence of two angular bosses instead of one. Haughton and Boonstra (1929a) made this specimen the

holotype of the new genus *Bradysuchus*, primarily based on the two bosses on the angular. *Bradysuchus whaitsi* was retained by Boonstra (1934). Broom (1935), citing a re-examination he performed in 1928 on the holotype, proposed that the smaller of the two angular bosses is actually a displayed osteoderm. Accordingly Broom (1935) synonymised the species with *Bradysaurus*, an identification retained by subsequent authors (Boonstra 1969, Kuhn 1969, Lee 1994, 1997a). Lee (1994, 1997a) examined the holotype, noting the extra lateral angular boss as possibly pathological (formed by a healed fracture) as suggested by Boonstra (1969) or an osteoderm. He concluded that the feature is taxonomically insignificant and was able to identify AMNH FARB 5567 only as *Bradysaurus*.

My examination of AMNH FARB 5567 notes the ventral angular boss on the right lower jaw as very long (80 mm), slender, pointed, directed posteroventrally, and curving strongly medially. It has a thickened rim about half way down the boss, after which it narrows to quite a sharp tip. The second boss is formed by a large osteological growth on the lateral surface of the dorsal portion of the right angular boss, 70 mm anteroposteriorly long, 45 mm in dorsoventral height, and 25 mm in lateral extent. It is very rugose and uneven, with two deep cavities: one dorsally and one posteriorly. The left mandible has part of the corresponding region preserved and there is no indication of any lateral projecting growth or pathology. Another pareiasaur specimen (SAM-PK- K11272: *Pareiasaurus serridens*) also manifests an additional pathological lateral boss on the lower jaw.

The cheeks are relatively large with both cheeks extending about 30^0 below the tooth row and mediolaterally narrow (posterior portions of the quadratojugal and squamosal measure 38-42 mm at their widest). The maxilla has no maxillary boss, but is swollen to form a low, wide, bulging posterolateral maxillary-lacrimal ridge. The premaxilla and maxilla lateral to each tooth crown is narrow (<5 mm) and therefore the upper jaw teeth were pointing straight downwards in life, as seen in *Embrithosaurus* and *Nochelesaurus* specimens The distal portion of the

paroccipital process of the opisthotic is anteroposteriorly expanded (70 mm long) and forms a low (only 5 mm high) but distinct, oblique, dorsomedially oriented, posteriorly projecting, sharp ridge, very similar to those of specimens of *Embrithosaurus*.

The cranial ornamentation is relatively low and indistinct and the bosses on the margin of the orbit on the prefrontal, postfrontal and postorbital are low and indistinct, as in *Embrithosaurus* and *Bradysaurus baini*. The bosses of the posterior edge of the cheek are not similar to those of *Nochelesaurus*, and are small to medium sized, but low and bulbous. Despite the lack of a distinct maxillary boss, this skull is most similar to *Embrithosaurus schwarzi* and is assigned to that taxon.

8.5 *Nochelesaurus alexanderi* (Haughton and Boonstra 1929) SAM-PK-6239

8.5.1 Genus/Species type

GENUS: *NOCHELESAURUS* Haughton and Boonstra, 1929

TYPE SPECIES: *Nochelesaurus alexanderi* Haughton and Boonstra, 1929

8.5.2 Revised generic diagnosis

Same as for species

8.5.3 Revised species diagnosis

No cranial autapomorphies.

No postcranial autapomorphies. Concerning Lee's three postcranial autapomorphies: 1) the subscapular fossa is not located close to the anterior margin of the scapula blade and is not diagnostic or an autapomorphy; 2) the tubercle on the humerus is not present on all specimens of *Nochelesaurus* and so is removed as an autapomorphy, but is retained as part of the diagnosis; and 3)

the flange on the dorsal femur that projects distally far beyond the postaxial tibial facet, does not consist of any obvious flange but rather a distal extension of the femur and is not present on all specimens of *Nochelesaurus* and so is removed as an autapomorphy, but is retained it as part of the diagnosis.

Nochelesaurus differs from co-occurring pareiasaurs in having: maxillary teeth with non-symmetrical cusp arrangements the result of a very low, very small, basal cusp on the mesial margin; maxillary teeth with three to five vertical ridges on the lingual surface; up to ten cusps on mandibular teeth; snout relatively narrow, only slightly wider than high or as high as wide (character 33); transversely wide rectangular postparietal; maxilla without a maxillary boss; more distinct overall cranial ornamentation than *Bradysaurus* or *Embrithosaurus* (especially on the prefrontal, postfrontal and postorbital) (character 50); frontal central boss large and distinct; corner cheek boss large and elongated, proximal narrow neck, raised distal rim, pointed tip, and sometimes covered with rugose ridges; posterior edge of the quadratojugal (cheek flange) with distinct bosses that vary from horizontally flat and plate-like to medium sized, round (as wide as high) pointed bosses (character 50); presence of a gap (vertical separation) on the posterior edge of the cheek between the dorsal-most quadratojugal boss and the large squamosal boss; cheek flange extending approximately 30^0 below the tooth row; distal portion of the paroccipital process of the opisthotic lacking the dorsomedially elongated, posterior process of *Bradysaurus* and *Embrithosaurus*, and is low and smooth or with a dorsolaterally elongated and gently swollen posteroventral edge; basisphenoid, ventral surface, tubercles present on the ventral surface of the neurocranium just behind the basipterygoid processes (character 14); most specimens with a long and narrow scapula blade with little distal flaring, preaxial and postaxial margins expand gradually (character 88); proximal and distal expansions of the humerus very flat, only 20^0-40^0 apart and almost on the same plane (character 92); some specimens with a distinct tubercle on the postaxial margin of the intercondylar fossa of the humerus; ventrolaterally expanded distal radius creating a non-symmetrical radius;

postaxial shaft of the femur straight; lateral condyle of the femur extends distally far beyond the medial condyle in most specimens; narrow distal femur; posterior projection of major trochanter short (< 5 mm); proximal internal trochanter straight or slightly curved, dorsoventrally low, with an oblique proximal edge (character 125); osteoderms with a high and wide central boss covering most of the scute, comprising roughly five or six rugose, flattened, radial, tab-like processes, with a high and thick periphery.

Nochelesaurus differs from *Bradysaurus* in having: vertical and narrow premaxilla and maxilla (< 5 mm wider than the tooth row), accommodating vertically oriented upper jaw teeth; 18 upper jaw teeth (character 68); maxillary-lacrimal ridge low, not reaching the lacrimal boss complex; narrow cheek flange (posterior portions of the quadratojugal and squamosal).

Nochelesaurus differs from *Embrithosaurus* in having: lingual surface of some mandibular teeth with an incipient horizontal cingulum carrying medially placed cusp(s); lingual surface of mandibular teeth with one to three distinct vertical ridges (character 72); distal tibia ventromedially expanded and mediolaterally wide.

Bradysaurus and *Nochelesaurus* share small cheek flanges (character 44), and ridged lingual surface on the mandibular teeth (character 71).

8.5.4 Synonyms

8.5.4.1 *Dolichopareia angusta* (Haughton and Boonstra 1929) SAM-PK-6238

SAM-PK-6238, partial skull with lower jaw, postcranial material comprises a partial right scapulocoracoid, left distal scapula blade fragment, partial interclavicle and clavicles, both humeri, a right radius and ulna, a right fibula, the second (axis) to sixteenth vertebrae, several dozen ribs and rib fragments. This specimen is the holotype of *Dolichopareia angusta* (Haughton and Boonstra 1929a) from the same locality as the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239). Identified as *Nochelesaurus alexanderi* by Lee (1994, 1997a),

who made *Dolichopareia angusta* a junior synonym of *Nochelesaurus alexanderi*. Van den Brandt (2016) agreed with Lee. This specimen I identify as a referred *Nochelesaurus alexanderi* based on several characters (vertical upper jaw teeth, the absence of a maxillary boss, a roughly square longitudinally elongated postfrontal, a rectangular and wide postparietal, and features of the mandibular teeth) extensively referred to in chapters three and five of this project (cranial and postcranial descriptions of *Nochelesaurus alexanderi*). Many of the cranial features listed by Haughton and Boonstra (1929a) to distinguish *Dolichopareia angusta* are shared with *Nochelesaurus alexanderi*, such as the deep (large) cheek and heavy skull ornamentation. The very pointed snout and median boss are taphonomic and both the result of severe mediolateral compression. The relatively low and indistinct bosses on the posterior border of the cheeks are the result of severe weathering and over preparation affecting the entire skull.

Lee (1994, 1997a) also recognised two of the three autapomorphies of *Nochelesaurus alexanderi* on SAM-PK-6238: the anterior location of the subscapular fossa, and the presence of the tubercle on the entepicondyle of the humerus. A large humeral tubercle is present. Lee's autapomorphy of an anteriorly positioned subscapular fossa as diagnostic of *Nochelesaurus alexanderi* is not valid as there is no conclusive evidence to support its presence in the holotype or referred specimens.

8.5.4.2 *Brachypareia watsoni* (Haughton and Boonstra 1929) SAM-PK-6240

SAM-PK-6240, holotype of *Brachypareia watsoni*, comprising a small, juvenile skull and lower jaw (see Table 7.2) and unprepared atlas and axis. the specimen has dorsoventrally flattened orbits, but the poorly preserved anterior right quarter of the skull (25 % of the skull) comprises plaster, and the posterior portions of the right cheek and most of the palate are not preserved. Most of the upper and lower teeth are not preserved and only one lower tooth crown is anatomically useful.

Erected by Haughton and Boonstra (1929a), based on SAM-PK-6240, *Brachypareia watsoni* was described as having the orbit in the posterior half of the skull, a broad low (small) cheek, marked posterior cheek bosses, and a pointed snout. Lee (1994, 1997a) made *Brachypareia watsoni* a junior synonym of *Nochelesaurus alexanderi*, a conclusion supported by Van den Brandt (2016).

The cheeks of SAM-PK-6240 are large (average of 29^0) as they are in *Nochelesaurus.* The angular boss is short and small (confirming the juvenile age of this skull) and terminates with a thicker than normally seen, swollen, thickly rimmed, blunt, square to slightly rounded knob-like end (the unusual bluntness is probably the result of the dorsoventrally crushing that affects the skull). One preserved dentary tooth shows 7 cusps, with a central isolated elongated trident of three cusps and two lateral cusps either side with large spaces between these cusps. Diagnostically, the lingual surface shows a swollen vertical central ridge extending down from the central three-cusped complex, clearly and deeply separated from the two lateral cusps.

Cranial ornamentation is very high, discrete and distinct. The bosses on the posterior edge of the cheek (quadratojugal) are distinct and pointed, horizontally flat and plate-like (as in the holotype of *Nochelesaurus*), the corner boss is relatively large with a thin neck and a thickened distal rim, the two to three bosses on the lateral quadratojugal are distinct and high, the boss on the squamosal has a dorsal and ventral anterior extension on the lateral cheek. The maxilla has a low, swollen maxillary-lacrimal ridge, lacking a maxillary boss, the cheeks are large, there is a small posterior process on the paroccipital process of the opisthotic. The cheeks are each mediolaterally wide for such a small growing juvenile skull. The premaxilla and maxilla are vertical, but ventrally curved inwards due to the dorsoventral crushing of the skull, and the anterior teeth are vertical and the posterior teeth more inwards pointing due to the dorsoventral crushing. The skull is most consistent with *Nochelesaurus alexanderi*, although not perfectly so.

8.5.4.3 *Brachypareia rogersi* (Haughton and Boonstra 1929) SAM-PK-5012

SAM-PK-5012, mediolaterally compressed (buckled at the midline) and poorly prepared right half of a small skull with an isolated left cheek flange and posterior left lower jaw, five unprepared dorsal vertebrae with several weathered osteoderms, small right humerus, small right femur with articulated tibia, small left radius, proximal right ulna, distal fibula, eight to ten unprepared dorsal and caudal vertebrae, and other unprepared fragments. The manus is in a plaster jacket, with some isolated digits.

Haughton and Boonstra (1929a) erected *Brachypareia rogersi* based on SAM-PK-8953, a specimen comprising only a partial postcranium and lacking a skull. In the same paper, they assigned specimen SAM-PK-5012 to *Brachypareia rogersi* based on similarities in the limb bones and vertebrae which they said "agree very closely with those of the type" and declared SAM-PK-5012 the neotype (Haughton and Boonstra 1929a: 84). Kuhn (1969) assigned *Brachypareia rogersi* to *Bradysaurus*. According to Lee (1994, 1997a) *Brachypareia rogersi* (SAM-PK-8953) is invalid as the taxon comprises postcranial elements of a specimen of *Pareisaurus serridens*, SAM-PK-8953, and the skull of SAM-PK-5012. SAM-PK-8953 was collected from the Hoedemaker Member of the Beaufort Group on the farm Hoedemaker 239, Beaufort West district, Western Cape. Lee (1994, 1997a) found SAM-PK-5012 (skull and postcranium) to be identical to *Bradysaurus seeleyi* in lacking the cranial autapomorphies of *Bradysaurus baini* and the larger cheeks of *Embrithosaurus* and *Nochelesaurus*. Van den Brandt (2016), considering only cranial anatomy, agreed with Lee's identification for SAM-PK-5012 as *Bradysaurus seeleyi.*

Haughton and Boonstra (1929a) noted the interorbital width as greater than the distance between the supratemporals and a more posteriorly positioned orbit, a rounded snout, and a broad and low cheek with a smooth posterior edge. However, as in all middle Permian South African pariasaurs, the interorbital width of SAM-PK-5012 is slightly less than the width between the

supratemporals and the orbit is positioned slightly in front of the middle of the skull. The snout is rounded (as it lacks a maxillary boss) and the cheeks are large. Lee (1994, 1997a) considered that SAM-PK-5012 lacks the three cranial autapomorphies of *Bradysaurus baini* (maxillary boss, inwards pointed upper jaw teeth and a swollen distal paroccipital process of the opisthotic), and placed it in *Bradysaurs seeleyi*.

SAM-PK-5012 is a very small skull (see Table 7.2) of a very young, juvenile individual. Cranially, the upper jaw teeth point straight downwards and the maxilla is vertical and thin. The cheeks are large. There is no maxillary boss but there is a low, swollen maxillary-lacrimal ridge. The cranial ornamentation is distinct and heavy. The bosses on the posterior cheek are partly broken off but are quite distinct, the dorsal-most quadratojugal boss being plate-like with and dorsal and ventral anterior projection on the lateral cheek, as is the boss on the posterior squamosal. The worn off central frontal boss appears to have been high. The lateral cheek is very flat and the bosses are worn off. These features of the skull and postcrania (see below) are most consistent with an identification as *Nochelesaurus*.

The right femur is very small (only 290 mm long), and has a straight internal trochanter (as in the holotype of *Nochelesaurus*) that emerges gradually, obliquely (not perpendicularly) from the femur and protrudes only 10 mm ventrally beyond the femur. There is no anterior projection on the distal portion of the internal trochanter. The major trochanter is very small (<5 mm) posteriorly, the notch above it is shallow, the tubercle on the proximal-postaxial corner of the femur is worn, but present. The lateral condyle reaches distally far beyond the level of the medial condyle, 30 mm, on a small 290 mm long femur. The femur is anteroposteriorly narrow across the distal condyles at 95 mm.

The distal and proximal expansions of the right humerus are not very twisted and are only 40^0 off the same plane. No tubercle is present on the rim of the intercondylar fossa. The small ulna has a large, convex, 25 mm high olecranon

process (very similar to referred *Nochelesaurus* specimen SAM-PK-6238) above an articular surface that is relatively well demarcated, with rough, low, anterolateral rim.

8.6 Indeterminate material

8.6.1 *Pareiasaurus bombidens* (Owen 1876) NHMUK R1714 (43525)

Pareiasaurus bombidens was erected by Owen (1876) based on very poor material (NHMUK R1714/43525). This specimen comprises the unprepared anterior portion of a skull (fragmentary maxilla and lower jaw) and an unprepared articulated vertebral column containing nine dorsal vertebrae. Subsequently the poor quality holotype of *P. bombidens* was not even mentioned by Watson (1914b) and was noted as indeterminate and unclassifiable in the taxonomic reassessments of Haughton and Boonstra (1929a), Boonstra (1934a), Lee (1994, 1997a) and Van den Brandt (2016) (Table 8.1). Only Broom (1935) and Kuhn (1969) explicitly retained *P. bombidens* (in the form of *Bradysaurus bombidens*) in their taxonomic classifications. This specimen offers few anatomical details. The fragmentary maxillary teeth are elongated and appear to have seven cusps with three central cusps on an isolated trident and these teeth are posteroventrally obliquely directed. The vertebrae are relatively small and otherwise typical for the group, showing convex, lightly rugose, diamond-shaped, dorsal neural spines. This material is Pareiasauridae indet.

8.6.2 *Pareiasaurus strubeni* (Broom 1924) AMNH FARB unknown specimen number

Pareiasaurus strubeni was named by Broom (1924) in a short addendum at the end of a generalised pareiasaurian cranial and mandibular descriptive paper that included several unnumbered adult and juvenile pareiasaur specimens. Broom (1924) based the taxon on a lower jaw from Abrahamskraal, with only 14 or 15, large teeth, with broad overlapping crowns, but did not provide a specimen

number. Broom provided figures of the lower jaw (Broom 1924: 508: Text-figure 5) and for the 5th tooth of the right mandible (Broom 1924: 508: Text-figure 6A) indicating eight marginal cusps.

When Haughton and Boonstra (1929a) erected *Nochelesaurus* as new genus based on massive 6-8 cusped teeth, pointed snouts and deep cheeks, they described Broom's (1924) unnumbered lower jaw as the holotype of *N. strubeni*, with the species defined by a single median nasal boss and a lack of bosses on the posterior border of the cheek. They also assigned two more cranial specimens (SAM-PK-5019 and SAM-PK-5590) to the taxon. Boonstra (1934a) added three more specimens and a few diagnostic cranial characters to *Nochelesaurus strubeni*.

Broom (1935) referred to his figured lower jaw and tooth of the holotype of (*Bradysaurus*) *strubeni* (Broom 1924: 508: Text-figures 5, 6A) noting the individual as probably juvenile as there were only 15 lower jaw teeth. He declared the holotype, much of it dug out by himself, as "perhaps the most perfect pareiasaur skeleton ever discovered" (Broom 1935:45) and noted the smooth skull and a single boss above the snout behind the nostrils. Lee (1994, 1997a) noted the diagnostic characters of the lower jaw of *Pareiasaurus strubeni* as being the result of the immature status of the individual (fewer, larger teeth and shorter jaws) and concluded that the specimen is an indeterminate juvenile of a large *Tapinocephalus* Zone pareiasaur.

I have not been able to confirm the specimen number of the holotype of *Pareiasaurus strubeni* from the literature. However, the AMNH museum catalogue records specimen AMNH FARB 2232 (partial lower jaw) as "*Pareiasaurus strubeni*" and refers to Broom's publication (Broom 1924). AMNH FARB 2232 is fragmentary lower jaw with sheared-off teeth, lacking angular bosses, and I could not match this specimen to Broom's (1924) illustration of the lower jaw of the holotype.

Additionally, the most complete middle Permian South African pareiasaur curated at the AMNH (AMNH FARB 3897), was purchased in 1924 from Robert Broom and is recorded as from the same locality as the lower jaw holotype of *Pareiasaurus strubeni* (Abrahamskraal, Prince Albert). Currently considered *Bradysaurus* sp, this specimen comprises an unprepared postcranium, with a partial skull and fragmentary lower jaw. The lower jaw of AMNH FARB 3897 does not match Broom's lower jaw figure of the holotype of *Pareiasaurus strubeni* (Broom 1924: 508: Text-figure 5). The postcranium of AMNH FARB 3897 is too fragmentary and poorly preserved for identification. Therefore *Pareiasaurus strubeni* is considered Pareiasauridae indet.

9. CHAPTER NINE: PHYLOGENETIC ANALYSIS

9.1 Introduction

This chapter provides an updated pareiasaurian phylogenetic analysis. Several dozen character score updates were introduced for the middle Permian pareiasaur taxa (see Appendix B) and the resulting updated phylogenetic analysis is discussed for all pareiasaurs.

9.2 Brief history of previous pareiasaurian phylogenetic analyses

Below follows a brief summary and progression of all pareiasaurian phylogenetic analysis performed. Lee (1997b) produced the first cladistic phylogenetic analysis of the relationships among pareiasaur taxa, using knowledge gained from his earlier work on the relationships between parareptiles (Lee 1993, 1994, 1997a). Lee (1997b) included pareiasaurs, turtles, *Owenetta*, *Barasaurus*, *Sclerosaurus*, procolophonids, lanthanosuchids, nyctiphruretids and nycteroleterids in the analysis and defined 128 characters (66 cranial, 62 postcranial). This analysis found pareiasaurs and turtles to form a robust clade. It is important to note that Lee designed this character analysis to investigate pareiasaur-turtle relationships.

Jalil and Janvier (2005) named and described a new Moroccan pareiasaur *Arganaceras vacanti* based on an almost complete skull and two additional new forms based on postcrania, provisionally referred to as “Pareiasauria gen. et sp. indet. 1” and “Pareiasauria gen. et sp. indet 2”. They retained the 128 characters and conditional states defined by Lee (1997b) and the 31 taxa used and added Millerettidae. They performed a very thorough phylogenetic analysis on their three new taxa, which also included the newly named *Bunostegos akokanensis* from Niger (Sidor *et al.* 2003).

Tsuji and Muller (2008) re-described the first named, enigmatic and poorly studied pareiasaur *Parasaurus geinitzi*, and in their phylogenetic analysis also relied heavily on the work of Lee (1997b), making only minor modifications to some of the character scores. Significantly, these authors excluded several outgroup taxa, namely *Sclerosaurus*, *Lanthanosuchus*, *Nyctiphruretus* and Testudines. They replaced Nycteroleteridae with *Macroleter poezicus* and retained Millerettidae and Procolophonidae as the other two outgroups. Noting a lack of anatomical data, they removed the pareiasaurs *Sanchuansaurus pygmaeus*, the 'Welgevonden' pareiasaur and the two unnamed Argana pareiasaurs, resulting in only 22 taxa being analysed. They found that many of the 128 characters became uninformative once certain taxa (especially Testudines) were excluded and so analysed only 97 of the 128 characters. Their phylogenetic analysis was poorly resolved which they attributed to the fact that "many characters traditionally used in studies on pareiasaurian phylogeny were originally defined only for investigating turtle relationships, but not for deciphering the ingroup relationships of pareiasaurs" (Tsuji and Muller 2008:1111). Tsuji and Muller (2009) produced a new modern phylogenetic definition of Parareptilia (see chapter one, Fig. 1.1) and retained the Pareiasauria within Parareptilia.

Tsuji (2010, 2013) published a detailed study on the anatomy, cranial ontogeny and phylogenetic relationships of the Russian pareiasaur *Deltavjatia rossicus*. The character definitions used in her phylogenetic analysis were largely based on the work of Lee (1997b) and Jalil and Janvier (2005), and included a few new characters designed to represent the variation within pareiasaurs, resulting in 125 informative characters. Tsuji (2013) excluded *Lanthanosuchus* and Testudines, and as per Tsuji and Muller (2008) reiterated that the exclusion of turtles resulted in several characters becoming uninformative as these characters were designed as synapomorphies to unite the derived pareiasaur *Anthodon* with turtles. She also excluded all procolophonids from the analysis

and included six nycteroletids, Millerettidae and *Owenetta* as the outgroups, resulting in a total of 29 taxa used.

Tsuji *et al.* (2013) described the cranium of *Bunostegos akokanensis* and updated the phylogenetic analysis using 127 characters, and retained the ingroups and outgroups recently defined by Tsuji (2013).

Xu *et al.* (2015) in their reestablishment of the Chinese pareiasaur *Honania complicidentata*, applied their revised coding for *Honania* to the matrix of Tsuji *et al.* (2013). They modified two characters and excluded *Sanchuansaurus*.

Turner *et al.* (2015) in their postcranial description of *Bunostegos akokanensis* used the matrix of Tsuji *et al.* (2013) as their starting point and incorporated the character codings and taxonomic revisions of Xu *et al.* (2015). It is important to note that Turner *et al.* (2015) made significant modifications to the character states. They added four new characters, split several existing characters, and redefined others for the 21 pareiasaurian taxa and the eight outgroups (29 taxa in total). This resulted in Turner *et al.* (2015) listing 139 characters (78 cranial, 61 postcranial) noting that they excluded four from their analysis (characters 2, 3, 11 and 79) as they were uninformative.

Benton (2016) performed an alpha-taxonomic review of the Chinese pareiasaurs and coded the specimens into the data matrix of Turner *et al.* (2015). He rescored four of the five Chinese pareiasaurian taxa (retaining the existing scores for *Honania*) and used 31 taxa and 139 characters. Liu and Bever (2018) retained the 139 characters of the matrix of Turner *et al.* (2015) to score a new Chinese elginid taxon. They revised four character statements (13, 37, 44 and 51) through rewording characters 44 and 51, and through adding more states to characters 13 and 37.

Most recently, Van den Brandt *et al.* (2019) described the cranium of *Embrithosaurus schwarzi* in detail for the first time and rescored the cranial characters (characters 1-78) using the matrix of Liu and Bever (2018). Characters

related to postcrania (characters 79-139) were excluded. They retained all 30 taxa used by Liu and Bever (2018), i.e. the 22 pareiasaurian species and the eight parareptilian outgroups. In order to remove ambiguity in the language used, Van den Brandt *et al.* (2019) reworded five character statements and states (characters 44, 48, 50, 51 and 68). Changes in scoring for *Embrithosaurus schwarzi* were introduced in characters 4, 5, 23, 31, 41 and 68; for *Bradysaurus baini* in character 31; for *Bradysaurus seeleyi* in character 41; for *Nochelesaurus alexanderi* in character 39; and for *Bunostegos akokanensis* in character 66.

9.3 Previous phylogenetic positions of the middle Permian South African pareiasaurs

Lee's (1997b) first cladistic analysis of pareiasaurs found numerous most parsimonious trees (MPTs) in which the consensus tree shows *Bradysaurus seeleyi* as the most basal pareiasaur, followed by a polytomy including *B. baini*, *Nochelesaurus alexanderi* and a clade including *Embrithosaurus schwarzi* and all remaining pareiasaurs (Fig. 9.1). *Embrithosaurus schwarzi* thus was the most derived of the four taxa from the middle Permian of South Africa and Lee did not recover a monophyletic *Bradysaurus*. Derived features of *Embrithosaurus schwarzi* included a higher number of marginal cusps on the teeth (seven to nine); straight lateral projections on the caudal vertebrae; a shorter and thicker pubic symphysis; a large major trochanter on the femur; postaxial flange of the femur that narrows in the middle; a proximally curved internal trochanter; and a central boss on the osteoderms. My research shows that a higher number of marginal cusps can be found in all basal South African pareiasaurian taxa, the postaxial flange of the femur of *Embrithosaurus* does not narrow in the middle, and a proximally curved internal trochanter also applies to *Bradysaurus baini*.

The initial character scores assigned to these four basal taxa by Lee (1997b) have received very little revision, especially from direct study of the material. As a result, the phylogenetic position of the four basal-most South African pareiasaurs

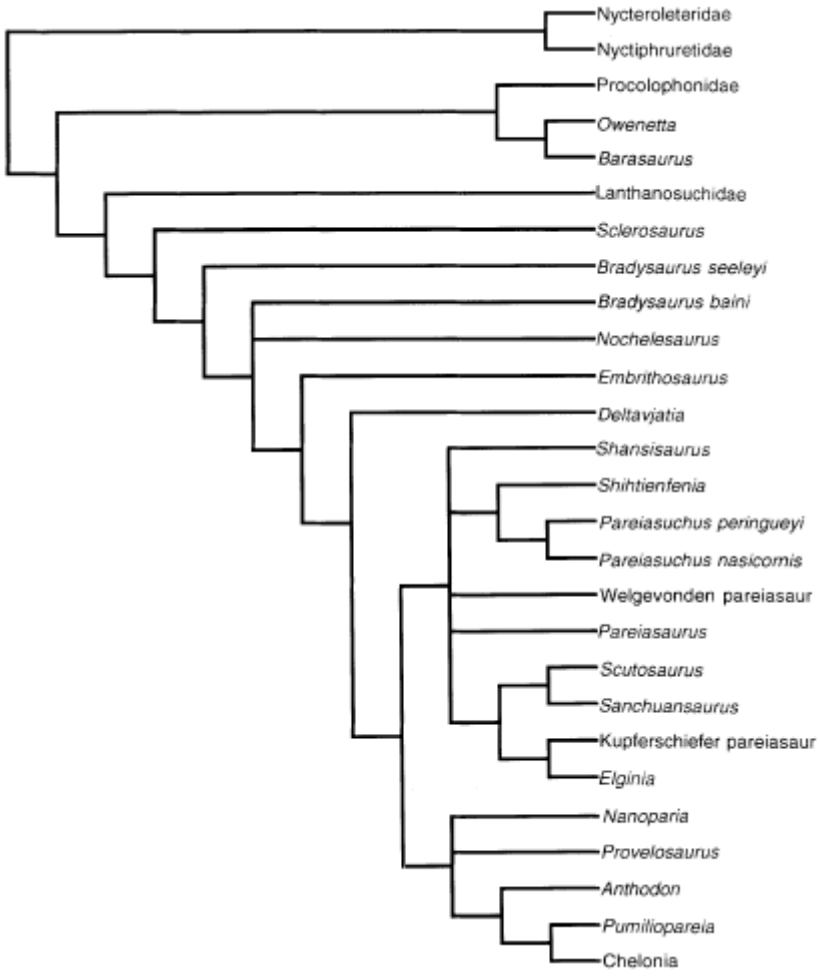


Figure 9.1: Strict consensus tree of 54 most parsimonious trees found in the analysis of Lee (1997b), including all taxa, taken from Lee (1997b:255, Fig.21B). The single, fully resolved tree of Lee (Lee 1997b:256, Fig. 22) excluded *Bradysaurus baini* and so is not shown here.

have been virtually unchanged across all analyses (Lee 1997b; Jalil and Janvier 2005; Tsuji and Muller 2008; Tsuji 2013; Tsuji *et al.* 2013; Turner *et al.* 2015; Xu *et al.* 2015; Benton 2016, Liu and Bever 2018). The pareiasaurs from the *Tapinocephalus* Assemblage Zone of South Africa have always been recovered as the most basal genera, suggesting a Gondwanan origin for the group. Subsequent studies (e.g. Liu and Bever 2018) continued to recover *B. seeleyi* as the most basal pareiasaur, followed by a polytomy including *B. baini* and *Nochelesaurus* and a clade including *Embrithosaurus* and all remaining pareiasaurs (Fig. 9.2). In all analyses *Embrithosaurus* is recovered as the most derived pareiasaur of the basal group of the four taxa from the middle Permian of South Africa.

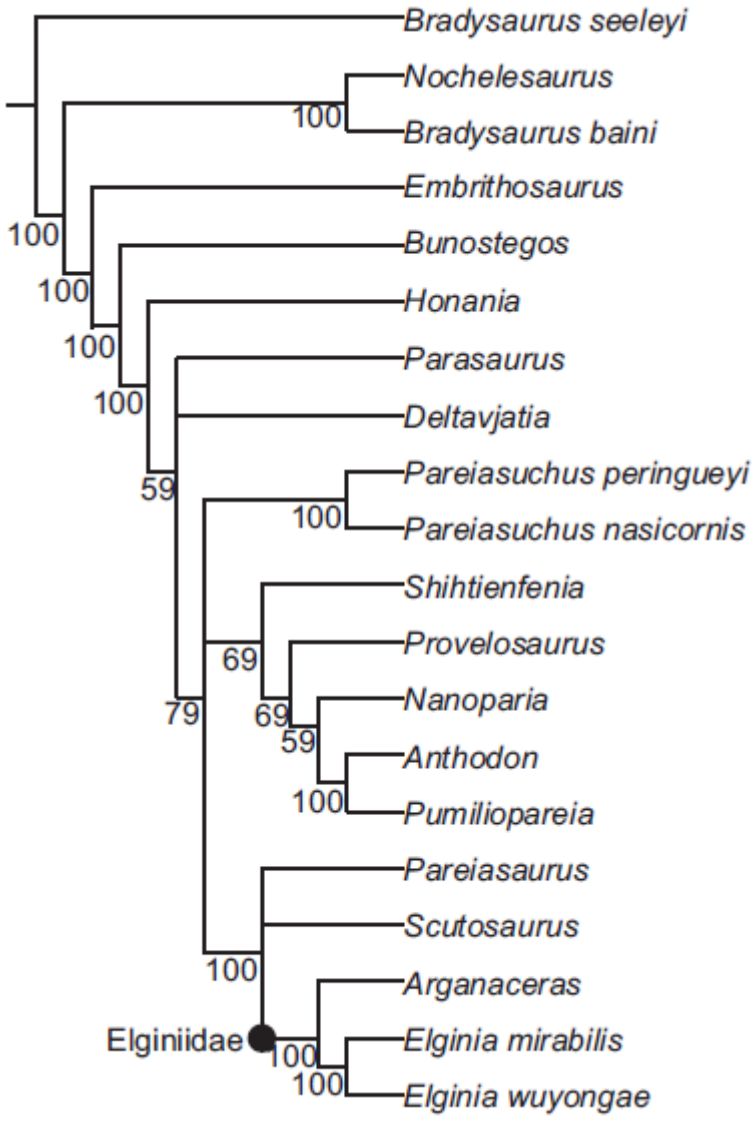


Figure 9.2: Majority rule consensus tree of 100 most parsimonious trees, excluding *Obirkovia* and *Sanchuansaurus* (taken from Liu and Bever 2018:9: Fig. 5B).

Van den Brandt *et al.* (2019) introduced changes to the cranial character scores for the middle Permian South African pareiasaurs based on personal observations. This phylogenetic analysis recovered the four basal middle Permian South African as a monophyletic group for the first time, a different result compared to all previous authors. Van den Brandt *et al.* (2019) named the basal monophyletic group Bradysauria, in which *Nochelesaurus alexanderi* and *B. seeleyi* formed a polytomy, and *Embrithosaurus schwarzi* and *Bradysaurus baini* form a monophyletic clade. However, as in all previous hypotheses, they did not recover a monophyletic *Bradysaurus*.

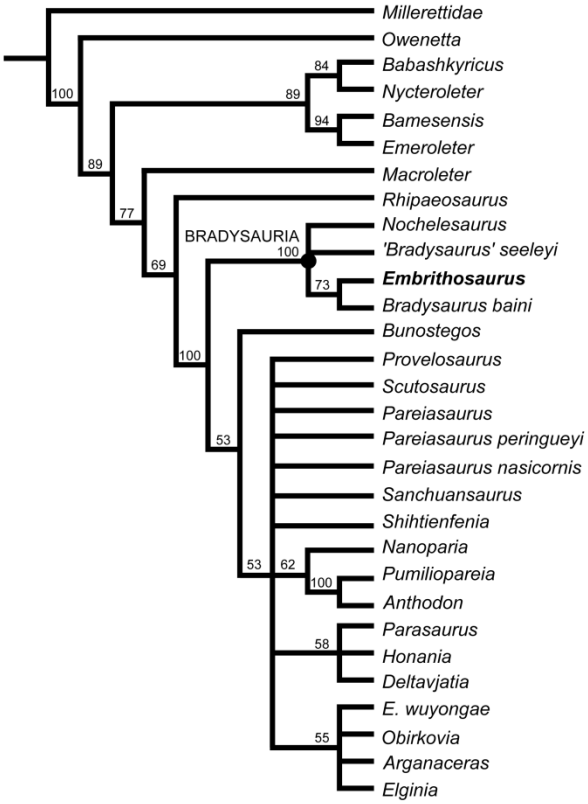


Figure 9.3: Cladistic relationship of *Embrithosaurus* within Pareiasauria, 50% majority-rule consensus tree of 1763 most parsimonious trees (mpt) of length 140. Numbers at each nodes indicates the frequency of clades in the fundamental trees (taken from Van den Brandt *et al.* 2019, Fig. 18).

9.4 Updated phylogenetic positions of the middle Permian South African pareiasaurs

9.4.1 Methods

Following the revised descriptions undertaken for this thesis, the cranial and postcranial characters for all valid middle Permian South African species have been scored (see Appendix B), based on direct studies of the holotypes and important referred specimens. Character statements and states for three characters (14, 74 and 102, see Appendix B) were reworded to remove errors and ambiguity in the language used without changing the meaning or intention of the statements.

The matrix of Van den Brandt *et al.* (2019) was used for initial cranial character scores (characters 1-78) and the matrix of Liu and Bever (2018) for the initial postcranial character scores (characters 79-139). Characters 2, 3, 11, 117, and 129 were excluded from the analysis as they are uninformative. *Bradysaurus seeleyi* was deleted from the 30 taxa used by Van den Brandt *et al.* (2019) and Liu and Bever (2018) resulting in 21 pareiasaurian species and eight parareptilian outgroups. All of the modified statements and conditional states for characters 44, 48, 50, 51 and 68, proposed by Van den Brandt *et al.* (2019) were retained. A significant number of changes in the scoring were introduced: changes in scoring for *Embrithosaurus* were introduced in characters 76, 79, 80, 92, 99, 113, 115, 124, 136, 139; for *Bradysaurus* in characters 38, 39, 44, 69, 70, 71, 79, 80, 92, 98, 102, 107, 111, 113, 115, 125; and for *Nochelesaurus* in characters 3, 4, 5, 14, 19, 23, 33, 42, 43, 44, 64, 68, 69, 70, 71, 72, 76, 79, 81, 82, 83, 88, 99, 102, 103, 107, 108, 110, 112, 114, 116, 117, 122, 127, 135, and 136 (see Appendix B).

The program TNT (Tree Analysis Using New Technology) version 1.5 was used to find the most parsimonious trees (Goloboff *et al.* 2008; Goloboff and Catalano 2016). Considering the relatively large size of the data matrix (29 taxa and 139 characters) the search strategy for the most parsimonious trees (mpt) entailed a heuristic search of 10 random addition sequences with TBR (tree bisection reconnection), saving 10 trees per replication, and an additional search using the trees from RAM as the starting point and implementing TBR on those trees. The default setting for branch collapsing in TNT, rule 1 (minimum length = 0), which collapses branches if the support is ambiguous was used (Goloboff *et al.* 2008). Millerettidae was selected as the root and all characters were run as unordered and equally weighted.

9.4.2 Results and discussion

The TNT analyses found 1065 most parsimonious trees (mpt) of length 258. The strict consensus tree (Fig. 9.4A) shows the Pareiasauria recovered as a monophyletic group, comprising an extended basal polytomy of twelve terminal

taxa and three monophyletic groups: *Pareiasuchus nasicornis* and *P. peringueyi*, the middle Permian pareiasaurs from the Karoo (*Embrithosaurus* + *Nochelesaurus* + *Bradysaurus*) and the dwarf South African pareisaurians (*Nanopareia* + *Pumiliopareia* + *Anthodon*) with *Provelosaurus*, in which *Nanopareia* and *Provelosaurus* are in a polytomy, and *Pumiliopareia* and *Anthodon* form a clade.

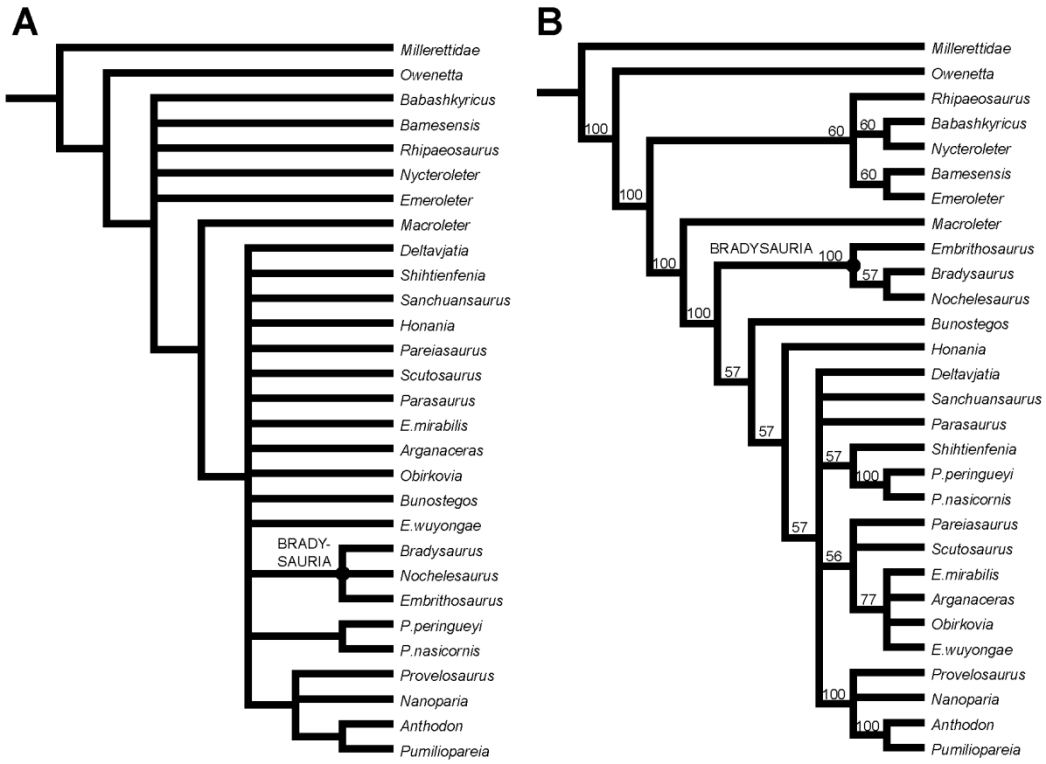


Figure 9.4: Cladistic relationships of the Bradysauria within Pareiasauria, A, strict consensus tree, B, 50% majority-rule consensus tree of 1065 most parsimonious trees (mpt) of length 258. Numbers at each node indicate the frequency of clades in the fundamental trees. Retention Index (RI) = 0.609, Consistency Index (CI)= 0.784.

In agreement with Van den Brandt *et al.* (2019), the majority rule tree shows the South African middle Permian pareiasaurs (*Embrithosaurus* + *Nochelesaurus* + *Bradysaurus*) forming a basal monophyletic group which Van den Brandt *et al.* (2019) termed Bradysauria.

Van den Brandt *et al.* (2019) found the Bradysauria to be supported by three synapomorphies: character 21, presence of regular radiating ridges on the skull roof from the centre of the dermal skull roof bones (also the condition in two

advanced pareiasaurians: *Scutosaurus* and *Provelosaurus*); character 39, absence of supernumerary bone on the skull (unambiguous within pareiasaurian, also the condition in *Owenetta*); and character 77, medial rows of palatal denticles widely separated, converging anteriorly (unambiguous).

The most recent analysis (Fig. 9.4B) finds Bradysauria to be supported by six synapomorphies: characters 21, 39 and 77; and three additional characters (70, 79 and 115): character 70, mandibular teeth, cusp number, seven to nine cusps (unambiguous); character 79, pleurocentrum of the atlas separate from the axial intercentrum (unambiguous); and character 115, notched anterior acetabulum (also the condition in in *P. nasicornis* and *P. peringueyi*). The condition of character 79 is unknown in most pareiasaurs, but has now been updated in the basal South African forms.

In Bradysauria, *Nochelesaurus* and *Bradysaurus* from a monophyletic group supported by two synapomorphies (characters 44 and 71): character 44, quadratojugal (cheek) flange small, extending $0\text{-}40^{0}$ below the level of the maxillary tooth row; and character 71, lingual surface of the mandibular teeth with a distinct, triangular ridge, narrowing towards the crown of the tooth. *Embrithosaurus* is the sister taxon of the monophyletic group. The two elginid taxa also have small cheeks and several derived pareiasaurs have a triangular ridge on the inner surface of the mandibular teeth.

After the Bradysauria, *Bunostegos* and then *Honania* form a grade between the basal pareiasaurs and the more derived forms (Fig. 9.4B). *Bunostegos* and all remaining pareiasaurs are united by four synapomorphies: characters 13, 48, 50 and 66, which is the same result found by Van den Brandt *et al.* (2019): character 13, wide, not strongly laterally constricted basisphenoid; character 48, presence of bosses on the ventral margin of the quadratojugal; character 50, cheek ornamentation present on the posterior or ventral margins of the cheek in the form of well-developed, more distinct, taller, more pointed bosses; and character 66, cusps regularly spaced along the tooth crown.

The members of Bradysauria do not exhibit the more derived characters as their basisphenoids are wide, and strongly laterally constricted, giving an hourglass shape in ventral view; bosses are not present on the ventral margin of the quadratojugal; cheek ornamentation consists of low, rounded bosses (except for *Nochelesaurus* which has more distinct, taller, more pointed bosses); and cusps are irregularly spaced along the tooth crown. These basal features of the Bradysauria are well known and are established in the literature.

The group formed by *Honania* and all remaining pareiasaurs (Fig. 9.4B) is united by four synapomorphies (characters 69, 90, 91 and 92): character 69, 9–11 or more cusps on the maxillary teeth; character 90, dorsal edge of the posterior coracoid oriented posteroventrally forming an angle of more than 135^0 with the posterior border of the scapula; character 91, absence of the cleithrum; and character 92, the torsion of the humerus being less than or equal to 45^0. The Bradysauria and *Bunostegos* have fewer cusps (7-9) on the maxillary teeth, the posterior coracoid is more horizontal, meeting the posterior border of the scapula at an angle of less than 135^0, the cleithrum is present, and the torsion of the humerus is greater than or equal to 60^0 (except in *Nochelesaurus*).

After *Honania* there is a polytomy formed by three terminal taxa (*Parasaurus*, *Sanchuansaurus* and *Deltavjatia,* Fig. 9.4B) and three monophyletic groups, all united by two synapomorphies (characters 122 and 124): characters 122, larger, more distinct major trochanter; and character 124, femur with a narrow postaxial flange at the midpoint of the femur.

The first monophyletic group comprises the Chinese *Shihtienfenia* and a monophyletic *Pareiasuchus* from southern African comprising *P. nasicornis* and *P. peringueyi* all united by four synapomorphies (characters 71, 87, 95 and 111): character 71, lingual surface of the mandibular teeth with a distinct, triangular ridge, narrowing towards the crown of the tooth; character 87, length of the scapula blade greater than or equal to three times the glenoid fossa diameter; character 95, narrow and rounded postaxial flange of the entepicondyle; and

character 111, strongly everted, almost horizontal anterior margin of the ilium. Character 71 is also a synapomorphy uniting *Nochelesaurus* and *Bradysaurus* (see above).

P. nasicornis and *P. peringueyi* are united by six synapomorphies (characters 72, 93, 108, 113, 115 and 120): character 72, absence of horizontal cingulum on the lingual surface of the marginal teeth; character 93, narrow and rounded postaxial flange of the ectepicondyle; character 108, strong and sheet-like second and third sacral ribs; character 113, Ilium, shaft inclined far anteriorly, forming an angle of more than 45^0 with the vertical; character 115, notched anterior acetabulum; and character 120, strong preaxial expansion of the head of the femur. The conditional states of characters 72 and 93 in this group are also present in the three South African dwarf pareiasaurs.

The second monophyletic group in the majority rule (Fig. 9.4B) and the strict consensus (Fig. 9.4A) comprises the three dwarf South African pareiasaurs (*Nanopareia*, *Pumiliopareia*, and *Anthodon*) and the South American taxa *Provelosaurus*. *Pumiliopareia* and *Anthodon* are monophyletic and *Nanopareia* and *Provelosaurus* are in a polytomy. The three South African dwarf forms and *Provelosaurus* share ten synapomorphies (characters 25, 72, 92, 93, 97, 100, 101, 110, 113 and 136): character 25, v-shaped anterior interpterygoid vacuity; character 72, absence of a horizontal cingulum on the lingual surface of the marginal teeth; character 92, torsion of the humerus less than or equal to 20^0; character 93, narrow and rounded preaxial flange of the ectepicondyle; character 97, entepicondylar foramen exposed in ventral (flexor) view; character 100, radial condyle of the humerus located terminally, encroaching onto the distal end of the humerus; character 101, ulnar articulation surface of the humerus forms a groove bordered posteriorly by a prominent tubercle; character 110, no or only slight anterior expansion of the iliac blade; character 113, shaft of the Ilium orientated vertical or posterodorsally; and character 136, osteoderms

ornamented with fine, straight, regularly spaced ridges radiating out from a central boss to the edge.

The third monophyletic group (Fig. 9.4B) comprises *Scutosaurus*, *Pareiasaurus*, and a monophyletic Elginiidae (*Elginia wuyongae*, *Obirkovia*, *Arganaceras*, and *Elginia mirabilis*) all united by the presence of five synapomorphies (characters 14, 15, 31, 33 and 111): character 14, tubercles present on the ventral surface of each basipterygoid process (basisphenoid), immediately behind the interpterygoid vacuity and the transverse suture with the pterygoid; character 15, presence of a central boss on the ventral surface of the basioccipital; character 31, prominent boss or horn present on the maxilla immediately behind the external naris; character 33, snout as high as wide; and character 111, strongly everted, almost horizontal anterior margin of the ilium.

The four elginid taxa are united by five synapomorphies (characters 13, 35, 41, 50 and 58): character 13, basisphenoid narrow with relatively straight margin; character 35, presence of a postfrontal "horn"; character 41, tabular (supernumerary element), contact, well-developed, making contact posteriorly, excluding the postparietals from the posterior edge of the skull table; character 50, ornamentation present on the posterior or ventral margins of the cheek in the form of prominent, conical horns with sharp, pointed tips; and character 58, dermal bosses of cranial bones have a central long, pointed horn.

9.4.2.1 Resampling and bootstrapping

Van den Brandt *et al.* (2019) found values of support for the monophyletic groups in the strict consensus low, all of them with Bremer support of 1, whereas bootstrapping values were 69 for Pareiasauria, 67 for the dwarf South African pareiasaurians and 58 for the Bradysauria.

In this new phylogeny, the bootstrapping values are 78 for Pareiasauria, 54 for the two *Pareiasuchus* taxa, 61 for *Pumiliopareia* and *Anthodon,* and below 50 for the Bradysauria, the group of *Pumiliopareia*, *Anthodon, Nanopareia* and

Provelosaurus, and the four elginids plus *Scutosaurus* and *Pareiasaurus*. The Bradysauria have a Bremer support of 2, and all other monophyletic groups 1.

The updated phylogenetic analysis of the middle Permian South African pareiasaurs from the *Tapinocephalus* Assemblage Zone of the Beaufort Group, show them to be the most basal pareiasaurs, forming a monophyletic group, and confirming support for the Gondwanan origin for the Pareiasauria. Unlike all previous analysis, *Embrithosaurus* is not found as the most derived basal pareiasaur from the middle Permian of South Africa but rather the most basal bradysaurian pareiasaur. This is the result of significant changes made to several character scores. This new phylogenetic result contradicts the stratigraphic ranges, which shows *Embrithosaurus* as the last genus of middle Permian South African pareiasaurs to appear in the stratigraphic sequence (see chapter 10), possibly indicating a long ghost linage for the genus.

10. CHAPTER TEN: STRATIGRAPHIC RANGES OF PAREIASAURS

10.1 Introduction

This chapter describes the stratigraphic ranges for pareiasaurian species from the *Tapinocephalus* Assemblage Zone which have been recognised as valid.

10.2 Previous stratigraphic range determination of pareiasaurids

Seeley (1892) briefly described Karoo stratigraphy as comprising five zones, the lowest Mesosaurian rocks, with his second zone being that of the Pareiasaurians, followed by the higher zones of the Dicynodonts, the specialised group of Theriodonts and the Zanclodonts. After renaming the genera of pareiasaurs from the lower zones, Watson (1914b) realised that *Pareiasaurus* occurs only in higher zones, and thus renamed the low Pareiasaurus zone the *Tapinocephalus* zone, after the abundance of dinocephalians from this stratigraphic horizon.

Boonstra (1932) briefly described and charted that the large bodied, comparatively primitive pareisaurs, first encountered very near the base of the *Tapinocephalus* Assemblage Zone, undergo few changes and die out near the top of the zone. Later, he (Boonstra 1969) assigned the majority of pareiasaur specimens (189 out of 215) referred to in his paper on the fauna of the *Tapinocephalus* AZ, to the “lower subdivision” of the Zone, and all of the rest to the “middle subdivision”, apart from one specimen in the “upper subdivision”. He considered the only two valid genera (*Bradysaurus* and *Embrithosaurus*) as fully developed from near the base of the zone and perhaps surviving into the middle parts of the zone.

In their new vertebrate biozonation of the Westren Karoo Basin, Keyser and Smith (1979) proposed renaming the lower and middle *Tapinocephalus* AZ the Dinocephalian zone and charted one large pareiasaur, *Embrithosaurus*, as ocurring throughout the zone and into the overlying *Pristerognathus/Diictodon* Assemblage Zone.

In their stratigraphic study of a small area of the Lower Beaufort of the South Western Karoo, north of Laingsberg, Loock *et al.* (1994) concentrated mostly on the distribution of dinocephalians and dicynodonts and found pareiasaurs to occur from the upper Leeuvlei Member to the lower Moordenaars Member of the Abrahamskraal Formation.

Smith and Keyser (1995a) produced a more detailed chart for *Bradysaurus* and *Embrithosaurus*, illustrating all occurences as from the base of the *Tapinocephalus* AZ (approximately 650 meters above the base of the Abrahamskraal Formation) into the lower part of the overlying *Pristerognathus* AZ (lower Teekloof Formation or Poortjie Member).

Day (2013, Day *et al.* 2015) produced the most accurate and up to date stratigraphic ranges for most of the terrestrial tetrapod fauna of the middle Permian, including the Pareiasauria, from the *Eodicynodon*, *Tapinocephalus* and *Pristerognathus* assemblage zones of the lowermost Beaufort Group. Day completed several years of field work, produced new stratigraphic sections and analysed others. He covered a large proportion of the farms of the south western Karoo in order to assign stratigraphic interval ranges to the deposits from each farm related to the height above the base of the Abrahamskraal Formation and therefore the lithostratigraphic members present. In this way, Day (2013) assigned all fossil specimens, recovered from a particular farm, a stratigraphic range and produced his updated stratigraphic ranges of pareiasaur genera in the middle Permian Beaufort Group (Fig. 10.1).

Van den Brandt (2016) re-identified 39 out of 108 cranial pareiasaur specimens (36%) and ascribed the low percentage of positive identifictions to be the result of the study being restricted to crania and also the poor condition of most of the material. On the basis of his cranial taxonomic identifications Van den Brandt (2016) produced a new chart of middle Permian South African pareiasaurian stratigraphic ranges using the range intervals compiled by Day (2013) for individual farm localities (Fig. 10.1).

10.3 This study

For this project 240 pareiasur specimens were directly re-examined for re-identification, using the updated diagnoses provided by this project. The method used by Van den Brandt (2016) was followed using the stratigraphic range intervals compiled by Day (2013) for individual farm localities to determine the stratigraphic ranges for the re-identifed pareiasaur specimens. All the pareiasaur specimens studied were recovered west of 24^0 East longitude, where the Abrahamskraal Formation comprises six lithostratigraphic members (Day 2013). Table 10.1 shows the numbers of identified middle Permian pareiasaur specimens per museum collection, and table 10.2 the number of specimens of individual species.

Institution	Identified	Unidentified/Duel Id	Total	% Identified
TUBINGEN	1	0	1	100%
CGP	16	10	26	62%
SAM	84	25	109	77%
ESI	24	27	51	47%
NHMUK	5	1	6	83%
AM	1	2	3	33%
AMNH	7	13	20	35%
FMNH	19	5	24	79%
TOTAL	**157**	**83**	**240**	**65%**

Table 10.1: Specimen identification per institution, with 157 positive re-identifications out of the 240 pareiasaur specimens recovered from the *Tapinocephalus* Assemblage Zone.

Genus	Species	Specimens
Bradysaurus	*baini*	74
Embrithosaurus	*schwarzi*	40
Nochelesaurus	*alexanderi*	43
Bradysaurus/Embrithosaurus		6
Bradysaurus/Nochelesaurus		7
Embrithosaurus/Nochelesaurus		10
Unidentified		60
TOTAL		**240**

Table 10.2: Specimen identification per species. 157 positive re-identifications (*Bradysaurus baini*, *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi*), 23 dual species identifications and 60 unidentified specimens of pareiasaur specimens recovered from the *Tapinocephalus* Assemblage Zone.

For each valid species, the stratigraphic ranges produced by 1) Day (2013, Day *et al.* 2015), 2) Van den Brandt (2016), and 3) this study are presented and discussed below.

10.4 *Bradysaurus* stratigraphic range

Bradysaurus has historically been assigned as a "waste basket" taxon for most large pareiasaurian specimens collected from the *Tapinocephalus* Assemblage Zone and as a result Day's (2013, Day *et al.* 2015) use of existing museum catalogue identifications resulted in the inclusion of 95 specimens of *Bradysaurus*.

Day (2013, Day *et al.* 2015) found the stratigraphically lowest occurence of *Bradysaurus* to be specimen SAM-PK-11940 (from the farm Vereniging, Laingsburg district) which was constrained to a broad interval of 1300-1650 m above the base of the Abrahamskraal Formation, upper Koornplaats Member. Day (2013) found the highest occurrence to be specimen SAM-PK-4999 (farm Grootfontein, Beaufort West district), stratigraphically at the boundary between the Abrahamskraal Formation (top of Karelskraal Member) and the Teekloof Formation. This wide stratigraphic range of *Bradysaurus* reaches the very top of the *Tapinocephalus* AZ and the majority of the specimens were found between the mid Swaerskraal and lower Moordenaars Members of the Abrahamskraal Formation (Fig. 10.1).

Van den Brandt (2016) used only eighteen *Bradysaurus baini* specimens (of which three had no locality information). He found the lowest occurence specimens to be SAM-PK-12048 and BP/1/347 (from the farms Dwars Rivier, Laingsburg district and Buffelsvlei, Beaufort West district respectively) which were not well constrained stratigraphically, situated between the upper Koornplaats, and Moordenaars Members of the Abrahamskraal Formation (Day 2013). The highest occurence was specimen BP/1/7213 (farm Witfontein 85, Sutherland district) well constrained to the the top of the Moordenaars Member

or the lower Karelskraal Member. The stratigraphic range of *Bradysaurus baini* was therefore found to extend from the upper Koornplaats Member to the lower Karelskraal Member, which was not as extensive as the range determined by Day (2013) (Fig. 10.1).

Van den Brandt (2016) included eight cranial specimens of *Bradysaurus seeleyi* in his study, ranging from the lowest occurrence specimen BP/1/7886 (Banksdrif, Lainsburg district) well constrained to the mid/upper Koornplaats Member (the lowest stratigraphic position for any *Tapinocephalus* AZ pareiasaur) and the highest occurrence the holotype specimen NHMUK R49426 (Palmietfontein Beaufort West district) mid Karelskraal Member, within 100 m of the top of the Abrahamskraal Formation (Fig. 10.1).

This study has used 74 reidentified *Bradysaurus baini* specimens. The lowest occuring specimen is BP/1/7886 (Banksdrif, Lainsburg district) well constrained to the mid/upper Koornplaats Member. The highest occurence are specimens NHMUK R49426 (Palmietfontein, Beaufort West district), mid Karelskraal Member, and several specimens from north of the Nuweveldberge. The stratigraphic range of *Bradysaurus baini* therefore extends from the mid/upper Koornplaats Member to the mid Karelskraal Member, which is a longer range than that reported for *B. baini* by Van den Brandt (2016), and the same as the range for *B. seeleyi* (Van den Brandt 2016) because *B. seeleyi* has been synonomised with *B. baini* in this study (Fig. 10.1).

10.5 *Embrithosaurus* stratigraphic range

Day (2013) used only the holotype and five referred specimens of *Embrithosaurus*. He found the lowest occurrences of *Embrithosaurus* to be the holotype specimen SAM-PK-8034 and referred specimen SAM-PK-K00324 (from Hogeveld and Seekoevallei respectively, both in the Beaufort West district) both constrained to the lower Moordenaars Member, being 2150-2250 m above the base of the Abrahamskraal Formation (Day 2013). Highest occurrences were

specimens NHMUK R7782 (Hottentotsrivier, Beaufort West district) and BP/1/7213 (Witfontein 85, Sutherland district), which Day (2013) assigned to 50-150 m below the base of the Poortjie Member, in the lower Karelskraal Member. Day therefore considered the stratigraphic range of *Embrithosaurus* to extend from the lower Moordenaars Member to the lower part of the Karelskraal Member of the Abrahamskraal Formation (Fig. 10.1).

Van den Brandt (2016) only used four specimens of *Embrithosaurus*. As per Day (2013) he found the lowest occurrence to be the holotype of *Embrithosaurus* (SAM-PK-8034) to be in the lower Moordenaars Member. The highest occurrence of *Embrithosaurus* was SAM-PK-9105 (from Melkboschfontein, Prince Albert district), constrained to the mid Moordenaars Member. *Embrithosaurus* therefore has a very narrow stratigraphic range within the lower to mid Moordenaars Member, which Van den Brandt (2016) explained as probably the result of a very small data set (Fig. 10.1)

This study used 40 re-identified *Embrithosaurus* specimens and found the lowest occuring specimen SAM-PK-9165 (from Van Der Byls Kraal, Beaufort West district) at the boundary of the Swaerskraal/Moordenaars Members. The highest occurence is specimen BP/1/7241 or SAM-PK-012252 (from Wolwehoek, Beaufort West district and Gannakraal, Fraserberg district respectively) in the lower to mid Karelskraal Member. The stratigraphic range of *Embrithosaurus* thus extends from the Swaerskraal/Moordenaars boundary to the mid Karelskraal Member of the Abrahamskraal Formation. The lower end of the range is thus virtually unchanged from the work of Day (2013) and Van den Brandt (2016), but the highest ocurance has increased significantly from the level found by Van den Brandt (2016), to the mid Karelskraal Member, near the top of the Abrahamskraal Formation (Fig. 10.1).

10.6 *Nochelesaurus* stratigraphic range

Day (2013) used only three specimens identified as *Nochelesaurus* by Lee (1994, 1997a): the holotype (SAM-PK-6239) and two referred specimens (SAM-PK-6238, SAM-PK-6240). The lowest stratigraphic occurrence was SAM-PK-6240 (from Abrahamskraal, Prince Albert district) stratigraphically not well constrained to the Moordenaars Member. The highest occurence was the holotype SAM-PK-6239 and SAM-PK-6238 (both from Boesmanskop, Beaufort West district) uppermost Karelskraal Member (Fig. 10.1).

Van den Brandt (2016) used nine specimens and found the stratigraphic range of *Nochelesaurus* unchanged from Day (2013) as specimen SAM-PK-6240 was still the lowest and SAM-PK-6239 and SAM-PK-6238 were still the highest specimens.

This study used 43 re-identified *Nochelesaurus* specimens. The lowest occuring specimen is BP/1/8011 (from De List, Laingsberg district) from the upper Koornplaats Member. The highest occurence remains the holotype SAM-PK-6239 and specimen SAM-PK-6238 (both from Boesmanskop, Beaufort West district), uppermost Karelskraal Member. The stratigraphic range of *Nochelesaurus* is therefore from the upper Koornplaats Member to the uppermost Karelskraal Member at the top of the Abrahamskraal Formation (Fig. 10.1).

Highest and lowest stratigraphic occurances from last three studies: Day 2013, Van den Brandt 2016, and this study									
Study	**Genus**	**Species**	**Lowest Specimen**	**Member**	**Biostrat**	**Highest Specimen**	**Member**	**Biostrat**	**Range**
This study	*Bradysaurus*	*baini*	BP/1/7886	mid/upper Koornplaats	lower Tap AZ	NHMUK R49426	mid Karelskraal	upper Tap AZ	from the upper part of the lower Tap AZ to the upper Tap AZ (presence lower down is uncertain due to poor sampling)
VdB 2016	*Bradysaurus*	*baini*	SAM-PK-12048, BP/I/347	upper Koornplaats	lower Tap AZ	BP/I/7213	lower Karelskraal	upper Tap AZ	Lower Tap to upper Tap
VdB 2016	*Bradysaurus*	*seeleyi*	BP/I/7886	mid/upper Koornplaats	lower Tap AZ	NHMUK R49426	mid Karelskraal	upper Tap AZ	Lower Tap to upper Tap
Day 2013	*Bradysaurus*		SAM-PK-11940	upper Koornplaats	lower Tap AZ	SAM-PK-4999	top of Karelskraal	top of Tap AZ	Lower Tap to Top of Tap
This study	*Embrithosaurus*	*schwarzi*	SAM-PK-009165	Swaerskraal/Moordenaars boundary	mid Tap ZA	BP/1/7241, SAM-PK-012252	lower/mid Karelskraal	upper Tap AZ	Throughout the upper Tap AZ
VdB 2016	*Embrithosaurus*	*schwarzi*	SAM-PK-8034	lower Moordenaars	mid Tap ZA	SAM-PK-9105	mid Moordenaars	upper Tap AZ	
Day 2013	*Embrithosaurus*	*schwarzi*	SAM-PK-8034, SAM-PK-K324	lower Moordenaars	mid Tap ZA	NHMUK R7782, BP/I/7213	lower Karelskraal	upper Tap AZ	
This study	*Nochelesaurus*	*alexanderi*	BP/1/8011	upper Koornplaats	lower Tap AZ	BP/1/7252	lower Karelskraal	upper Tap AZ	from the upper part of the lower Tap AZ to the upper Tap AZ (presence lower down is uncertain due to poor sampling)
VdB 2016	*Nochelesaurus*	*alexanderi*	SAM-PK-6240	Moordenaars	mid Tap ZA	SAM-PK-6239, SAM-PK-6238	uppermost Karelskraal	top of Tap AZ	
Day 2013	*Nochelesaurus*	*alexanderi*	SAM-PK-6240	Moordenaars	mid Tap ZA	SAM-PK-6239, SAM-PK-6238	uppermost Karelskraal	top of Tap AZ	

Table 10.3: Straigraphic ranges of *Bradysaurus*, *Embrithosaurus* and *Nochelesaurus*, from the most recent stratigraphic studies, Day (2013, Day *et al.* 2015), Van den Brandt (2016) and this study.

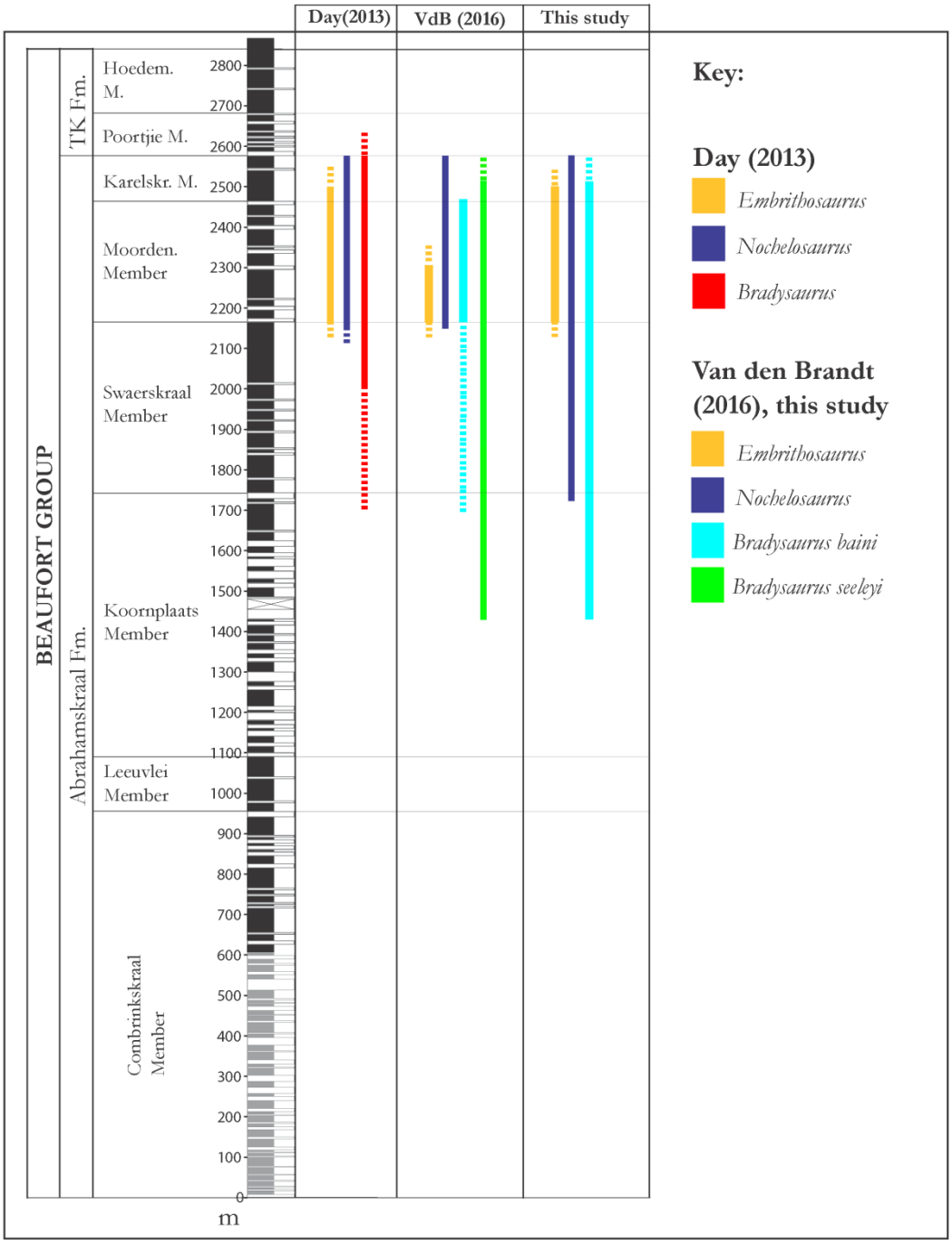


Figure 10.1: Composite stratigraphic ranges of pareiasaur genera in the middle Permian Beaufort Group, for positively identified specimens of each species, Day (2013), Van den Brandt (2016) and this study. Numerals denote meters above the base of the Abrahamskraal Formation. Solid lines indicate well constrained stratigraphic provenances, dotted lines indicate poorly constrained stratigraphic provenances with a wide range.

10.7 Geographic distribution of middle Permian pareiasaurs

Recently collected fossil material in museum collections have precise Global Positioning Satellite (GPS) latitude and longitude coordinate data. However, most of the specimens studied in this project are historic, with little more than the farm name recorded.

Nicolas (2007, and also van der Walt *et al.* 2011) created the Beaufort Fossil Vertebrate GIS database wherein she assigned centroid GPS coordinates (latitude and longitude co-ordinates calculated for a central geographic point assigned to a farm) to historic farm localities. Day (2013) built on this data and the current study plotted the geographic localities of 142 of the 157 re-identified pareiasaurs of this project (13 specimens lack locality information).

The database shows that the middle Permian pareiasaurs are restricted to a relatively small geographic region of the south western Karoo. The majority of the specimens are located in a rough triangle between Prince Albert in the south, Sutherland in the west, and Beaufort West in the east. A few specimens are scattered further north, just north of Fraserberg. In the north of the basin (e.g. Free State Province) outcrops from only the lower *Tapinocephalus* Assemblage Zone are preserved, and not the upper parts of the Zone (Groenewald *et al.* 2019), accounting for the lack of middle Permian pareiasaur specimens.

Strangely no *Tapinocephlaus* AZ pareiasaurs are known from the southeast of the basin. This may simply be the result of reltively little prospecting from this part of the basin, coupled with less outcrop area.

The geographic distribution map (Fig. 10.2) shows all three species are randomly scattered and no species is clustered in any one particular area, indicating that they occur throughout the outcrop area of the Abrahamskraal Formation in the southwestern part of the basin.

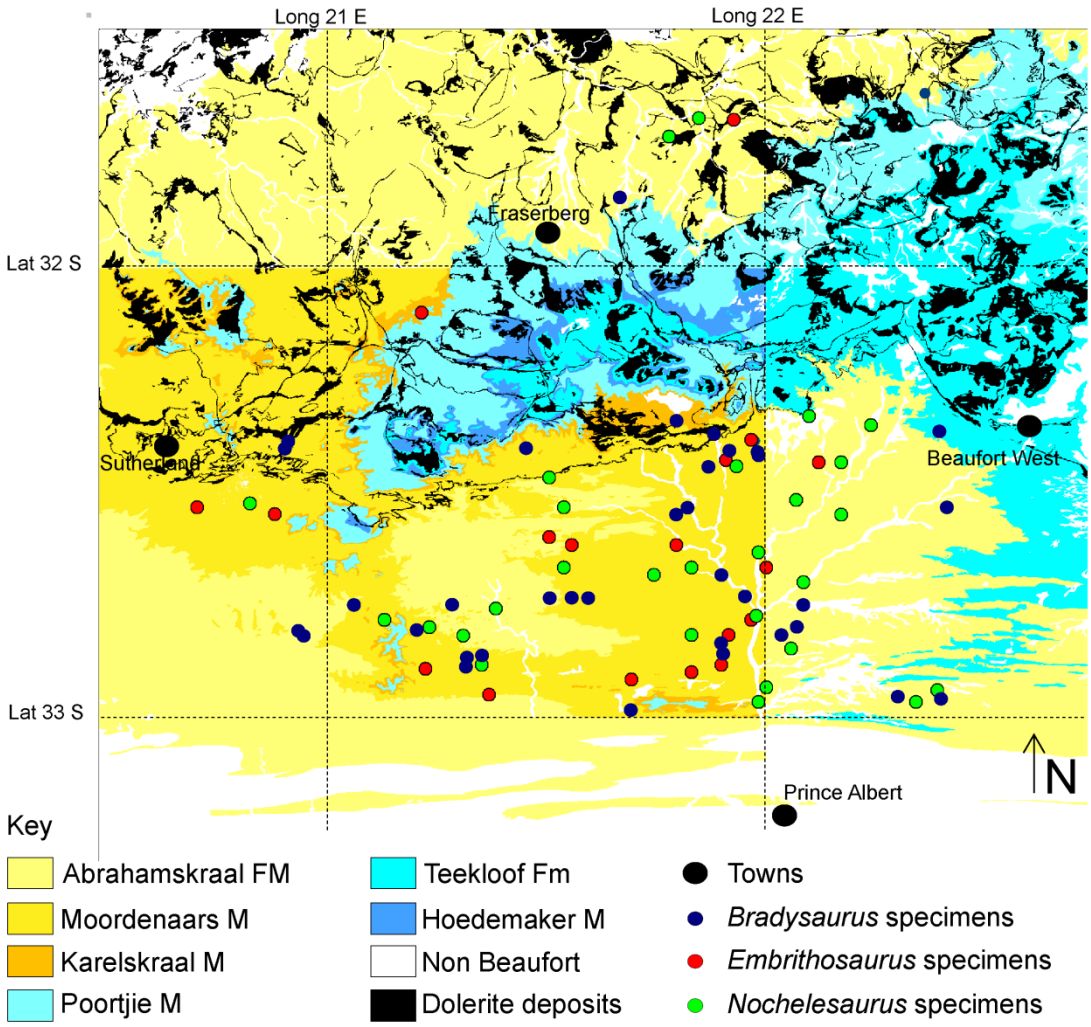


Figure 10.2: Geographic distribution of 142 pareiasaur specimens in the middle Permian Beaufort Group, superimposed on geological data. *Bradysaurus* in blue, *Embrithosaurus* in red and *Nochelesaurus* in green. The Moordenaars Member and Karelskraal Member are in the Abrahamskraal Formtion (*Tapinocephalus* Assemblage Zone). The Poortjie Member and Hoedemaker Member are in the overlying Teekloof Formation (*Pristerognathus* and *Tropidostoma* Assemblage Zone). Almost all specimens occur between 33 and 32 degrees South latitude. Figure created using the software Global Mapper version 15 and four maps: 3122 Victoria West (F G Le Roux and C H de Beer, Council for Geosciences, Pretoria 1:250 000 Geological Series, 1989); 3120 Williston (J H A Viljoen, Council for Geosciences, Pretoria 1:250 000 Geological Series, 1989); 3220 Sutherland (H de V Wickens and H P Siegfried, Council for Geosciences, Pretoria 1:250 000 Geological Series, 1983); 3222 Beaufort West (A Marsh, P W Leaman, and M R Johnson, Council for Geosciences, Pretoria 1:250 000 Geological Series, 1979).

10.8 Stratigraphic discussion

Stratigraphic data presented in this chapter shows *Bradysaurus* to appear first in the geological record, in the middle Koornplaats Member, followed by *Nochelesaurus* in the lower Swaerskraal Member, and *Embrithosaurus* in the lower Moordenaars Member. The upper range of each genus is in the middle Karelskraal Member, except for *Nochelesaurus*, which extends all the way through the Karelskraal Member.

It should be noted that collecting below the stratigraphic level of the mid Koornplaats Member is currently poorly sampled and there remains the possibility of discovering earlier pareiasaurs.

Compared to the ranges presented by Day (2013) and Van den Brandt (2016), the stratigraphic range of *Nochelesaurus* has been significantly extended downwards. *Embrithosaurus* remains stratigraphically the most constrained taxon with the shortest range, appearing only in the uppermost *Tapincephalus* AZ. The fact that *Embrithosaurus* is phylogenetically the most basal genus of the group, but stratigraphically the last to appear, suggests a long ghost lineage for the genus or may simply be the result of a lack of specimens from lower in the stratigraphy. None of the Bradysauria have been found in the overlying Poortjie Member of the Teekloof Formation, thus affirming that the Bradysauria became extinct during deposition of the Karelskraal Member of the Abrahamskraal Formation.

11. CHAPTER ELEVEN: CONCLUSION

This project on the osteological morphology and taxonomy of the pareiasaurs from the *Tapinocephalus* Assemblage Zone of the Beaufort Group forms part of the long term project of the Evolutionary Studies Institute to understand middle Permian terrestrial tetrapod biodiversity turnover. The study required investigating all pareiasaur material from the Abrahamskraal Formation of the Beaufort Group which is curated in different museums around the world, as well as field work to find additional material and better understand their stratigraphic context.

11.1 Cranial description

This work has produced the first detailed cranial description of *Nochelesaurus alexanderi*. This species is recognised by its more distinctive cranial ornamentation, especially the longer, larger, more pointed bosses on the posterior margins of the cheeks, unique features of the dentition (non-symmetrical marginal cusp arrangements, incipient horizontal cingulum with medially placed cusp) and a combination of other cranial features (e.g. wide postparietal, square postfrontal, large cheeks, vertical upper jaw teeth, lack of a maxillary boss, more gracile distal paroccipital process of the opisthotic).

Van den Brandt (2016) and Van den Brandt *et al.* (2019) documented the first detailed cranial description for *Embrithosaurus schwarzi* and this cranial diagnosis has been altered and updated here, based on more specimens and the inclusion of new cranial and postcranial features based on additional referred specimens. Cranially, most affected are aspects of the dentition, which have a wider range (seven to nine cusps) than the nine proposed by Van den Brandt (2016) and Van den Brandt *et al.* (2019). *Embrithosaurus* has the largest cheek flange of the group of middle Permian pareiasaurs, the only genus to approach and marginally exceed up

to a 40^0 angle below the tooth row; distinctive dentition, a narrow postparietal, a mediolaterally elongated postfrontal and a combination of other cranial features.

Lee (1994, 1997a) produced accurate detailed illustrations for *Bradysaurus baini* and an accurate diagnosis and this project has contributed an updated cranial diagnoses for the species. Maxillary teeth are posteroventrally or medially (horizontally) oriented, cranial ornamentation is low, the maxillary boss is large in adults, and the distal paraoccipital process of the opisthotic is distinctive. Interestingly, the range of variability in the sizes of the cheeks and in the sizes of the bosses on the posterior margin of the cheeks has increased significantly. Specimens of *Bradysaurus baini* may have smaller (20^0) to larger (30^0) cheek flanges, which may carry either large, wide, bulbous bosses on the posterior margins (such as in the holotype) or smaller, medium sized bosses, as high as wide (such as specimens previously referred to *Bradysaurus seeleyi*). Increased variability and new dental features have been found in specimens of *B. baini,* such as ridged labial surfaces of lower jaw teeth and a higher number of marginal cusps.

11.2 Postcranial description

The core of this project involved producing updated and detailed postcranial descriptions, recognising postcranial characters for diagnoses and illustrations for middle Permian South African pareiasaurian genera: *Embrithosaurus, Nochelesaurus* and *Bradysaurus.*

Embrithosaurus schwarzi is a distinct and valid species, most easily separated from the co-occurring species through features of the pelvis and the unique osteoderms within the group of pareiasaurs. The pelvis of *Embrithosaurus schwarzi* is very different to that of *Bradysaurus baini* on a number of features and measurements, as indicated by Lee (1994, 1997a) who noted three autapomorphies, and provides the most useful and unambiguous postcranial diagnostic information between these

otherwise similar taxa. Additional unpublished specimens were identified as members of this species. The three pelvic autapomorphies of Lee (1994a, 1997) have been confirmed and retained: the iliac blades are oriented obliquely from the longitudinal midline, they stand vertically, and the midline pelvic symphysis is the thickest. Additionally, the pelvis of *Embrithosaurus schwarzi* has been found to be higher, narrower, and shorter than those of co-occurring taxa, with a larger and longer median pubic process. The radius and tibia were found to be more symmetrical than those of the co-occurring taxa.

The postcranium of *Nochelesaurus alexanderi* has never been fully described, but Lee (1994a, 1997) did propose three autapomorphies, all of which have been discarded as a result of this PhD study. The subscapular fossa is not located anteriorly. The tubercle on the humerus and the distal femoral flange are present, but only in certain specimens, so cannot be autapomorphies, but are still useful in the diagnosis. From the new postcranial study, it is evident that *Nochelesaurus alexanderi* is a distinct species, most easily separated from the co-occurring species through the straight internal and the small external trochanters of the femur; the longer, thinner scapula blade; the relative less twisting of the humerus, sometimes with a tubercle; and relatively rugose osteoderms.

The postcranial skeleton of *Bradysaurus baini* was re-described in detail, and it is shown to be most easily separated from the other middle Permian South African pareiasaurs because of: the twisted humerus; the wide, low and long pelvis with parasagittal posterior iliac blades and anterior lateral and horizontal eversion; unornamented osteoderms; short and distally fared scapula blade; the large femur with a distinctive, curved and projecting internal trochanter and lack of a large external trochanter. Different from other pareiasaurs, the second sacral rib (on the 20^{th} vertebra) is the largest in the sacrum and not the first sacral rib.

11.3 Taxonomic conclusions

This project has built on the recent taxonomic work of Lee (1994, 1997a) and Van den Brandt (2016). From a maximum of thirteen described species (Kuhn 1969) the number of valid pareiasaurid species is now reduced to three: *Bradysaurus baini*, *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi* as *Bradysaurus seeleyi* has been synonymised with *Bradysaurus baini*. The list of distinguishing features between the three valid species has been enhanced and made more robust using both cranial and postcranial characters.

Despite the rigorous re-descriptions and analysis of both cranial and postcranial characters which lead to the recognition of three valid taxa, there are some specimens which exhibit characters of more than one taxon. This suggests greater morphological variation within a single species, or that there are a greater number of taxa. This problem can be addressed only by the discovery of more well preserved specimens.

11.4 Phylogenetic conclusions

This research has made substantial modifications to the scoring of characters, resulting in the most up to date cladistic analysis of middle Permian pareiasaurs. This study recovered the three basal middle Permian forms as a monophyletic group for the first time, supporting a first pulse of pareiasaurian diversification represented by the Bradysauria, which are currently restricted to the South African Karoo. *Nochelesaurus* and *Bradysaurus* are sister taxa and *Embrithosaurus* is the most basal member of the group.

11.5 Stratigraphic conclusions

This study has recognised the existence of three valid middle Permian pareiasaurian taxa and determined that they represent a distinct clade, the Bradysauria, restricted

to the *Tapinocephalus* Assemblage Zone of the Karoo Supergroup. Following taxonomic refinement and a better understanding of the cranial and postcranial morphology of pareiasaurs, all middle Permian South African material, 240 specimens, in museum collections curated worldwide were analysed through personal observation. A large proportion of these specimens comprise relatively complete skeletons, but many are poorly prepared and preserved. This study enabled identification of 157 specimens to species level and the stratigraphic provenance of 142 of these specimens were recorded to enable accurate recognition of the range of each species. *Bradysaurus baini* is the oldest pareiasaurian and has its first appearance datum (FAD) in the Koornplaats Member, followed by *Nochelesaurus* in the Swaerskraal Member and by *Embrithosaurus* in the Moordenaars Member. The LAD (last appearance datum) of all three taxa is at a similar stratigraphic level in the Karelskraal Member at the top of the Abrahamskraal Formation.

This study has greatly enhanced understanding of not only stratigraphic ranges of the basal-most pareiasaurs, but also the taxonomic diversity of these large parareptiles which, together with dinocephalians, were the largest terrestrial tetrapods of the middle Permian and were victims of the end Capitanian extinction event. *Bradysaurus*, *Embrithosaurus* and *Nochelesaurus* are the most basal pareiasaurs and all went extinct, afterwhich a wide diversity of Late Permian species, with Laurasian wide distribution, descended from the ancestor(s) of the Bradysauria.

This project has highlighted and increased the degree of morphological intraspecific variability of each valid species. However, overlapping of characters between the basal genera still exists and future studies to sort this out will require a greater number of well preserved and stratigraphically well provenanced specimens.

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APPENDIX A: SPECIMEN IDENTIFICATIONS

This appendix contains a list of all specimens directly studied during this project, organised per species. For each of the 240 pareiasaur specimens studied from the *Tapinocephalus* Assemblage Zone, the parts preserved are documented and a diagnostic justification is provided.

Embrithosaurus schwarzi specimens are listed first (40 specimens, numbered 1 to 40), followed by *Nochelesaurus alexanderi* (43 specimens, numbered 41 to 83) and *Bradysaurus baini* (74 specimens, numbered 84 to 158). Duel species identifications (23 specimens, numbered 158 to 180) and unidentifiable specimens (60 specimens, numbered 181 to 240) are included last.

Specimens are ordered per institution: AM, AMNH, CGP, ESI, FMNH, NHMUK, SAM, TUB.

Embrithosaurus schwarzi (1-40)

1. AMNH FARB 2450 (part of SAM-PK-9128): *Embrithosaurus schwarzi*

Articulated right tibia, fibula, tarsus and pes in a white plaster jacket. A physical paper note stored with this specimen indicates that it is part of specimen SAM-PK-9128 (which comprises both distal femora, both ulnae, left tibia and fibula, right radius and a distal left radius) and was collected by Boonstra in 1929 and loaned to C.Lang at the AMNH in 1939. This appears to be accurate as both AMNH FARB 2450 and SAM-PK-9128 are from the same locality, Voelfontein, Prince Albert district, and have consistent preservation style and colouring, and no parts are duplicated.The general size and morphology of the right tibia and fibula of AMNH FARB 2450 are an excellent match to the morphology of the right tibia and fibula of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034).

2. AMNH FARB 2451 (part of SAM-PK-9148): *Embrithosaurus schwarzi*

Articulated right forelimb comprising radius, ulna, carpals and manus in a white plaster jacket. A physical paper note stored with AMNH FARB 2451 indicates that it is part of specimen SAM-PK-9148 (which is a mounted right distal hindlimb comprising tibia, fibula, tarsal and pes) and was collected by Boonstra in 1929 and loaned to C.Lang at the AMNH in 1939. This appears to be accurate as both AMNH FARB 2451 and SAM-PK-9148 are from the same locality, Welgemoed, Prince Albert district, and have consistent preservation style and colouring. The right radius of AMNH FARB 2451 is similar to the radii of the holotype of *Embrithosaurus schwarzi* (SAM-PK-8034) in terms of the general gracile morphology.

The right ulna of AMNH FARB 2451 is longer (390 mm) than the ulnae of the holotype of *Embrithosaurus schwarzi* (290 mm) and also has a low, convex olecranon process (10-15 mm high) above the proximal edge of the proximal articulation surface, which differs from the lack of an olecranon process, the proximal shallow groove, and the presence of proximal medial and lateral crests of the sub-adult holotype ulna of *Embrithosaurus schwarzi.* Other larger specimens of *Embrithosaurus schwarzi* (e.g. CGP CBT 112) have longer ulnae with prominent, low olecranon processes. AMNH FARB 2451 (ulna) can also confidently be referred to *Embrithosaurus schwarzi* on the basis that it is is part of SAM-PK-9148, which is positively identified as *Embrithosaurus schwarzi* (see below, SAM-PK-9148).

3. AMNH FARB 5567: *Pareiasaurus whaitsi* (Broom 1914) (Holotype) = *Embrithosaurus schwarzi* (see chapter eight)

4. AMNH FARB 23880: *Embrithosaurus schwarzi*

Partial skull with several maxillary teeth preserved with much obscuring white plaster. The maxillary teeth are vertically oriented and appear to have nine marginal cusps, allowing for identification as *Embrithosaurus schwarzi.*

5. AK 90-1/CGP/1/853: *Embrithosaurus schwarzi*

Postcranium comprising a large block containing the pectoral girdle, blocks of articulated vertebrae with attached osteoderms, ribs, humeri, femora, partial pelvic girdle, tibia, fibula, distal femur, caudal vertebrae, proximal ulna, unidentified postcranial fragments and partial skull.

The humerus is relatively flat with the proximal and distal expansions only about 30 – 40^0 off the same plane. The internal trochanter of the femur is proximally gently curved as in *Embrithosaurus*. The vertebral osteoderms are flattened, and very rugose, with a distinct central boss and thick, distinct radial ridges on the periphery, most similar to *Embrithosaurus*. The proximal ulna has a large and high olecranon process.

The skull is small (sub-adult or juvenile) and severely mediolaterally crushed to appear very narrow. The cheeks are large, extending 30^0 or more below the rooth row, and there is a small, distinct maxillary boss on a vertical and narrow maxilla.

6. CGP CBT 112: *Embrithosaurus schwarzi*

Skull with articulated lower jaw and complete postcranium comprising most elements of the skeleton and most of the vertebral column. Identified as *Embrithosaurus schwarzi* by Lee (1994, 1997a) based on the presence of the three pelvic autapomorphies of this taxon and a skull consistent with all important features of the holotype, apart from the maxillary teeth which are only seven cusped and elongated. Based on the pelvis of this individual, I agree with Lee. The sixth, seventh and eighth vertebrae have a few osteoderms attached. These are large, very rugose, with tab-like processes and ridges, “L or “E” shaped covering most of each boss, beyond which the periphery of the scutes are very thin, flat and disc-like. These dorsal neural spines have a shallow longitudinal groove that extends the entire length of the dorsal spine, creating two flaps laterally.

7. GSP R338/CGP/1/796: *Embrithosaurus schwarzi*

Small juvenile skull with occluded lower jaw, missing most of the left side. The maxillary teeth have nine cusps and are wide and are vertically oriented. The right cheek is relatively large, but distorted. The angular boss is underdeveloped and small (juvenile sized). Identified as *Embrithosaurus schwarzi* by Lee (1994, 1997a) an identification with which I agree.

8. RMS 566/CGP/1/795: *Embrithosaurus schwarzi*

A very large skull, relatively unprepared, with partial occluded lower jaw, and with several hundred small unidentified postcranial fragments, partial fragmentary vertebrae, four large white plaster jackets containing partial unprepared vertebrae and rib fragments, partial puboischiatic plate and right acetabulum.

Postcranially, the puboischiatic plate is mediolaterally narrow (120 mm anteriorly) on the dorsal side between the iliac blades, and is concave. The midline pubis symphysis is thick and high, as in *Embrithosaurus*. Cranially, the posterior cheek bosses are all large and bulbous, indistinct and almost smooth, (not *Nochelesaurus)*. The cheek is narrow and relatively large. Since there is no large boss on the maxilla in this very large adult skull, and only a distinct low maxillary-lacrimal ridge, this specimen cannot belong to *B. baini*. The paroccipital process of the opisthotic has a small posterior process. The upper jaw teeth are damaged and unprepared and seem to be wide as in *Embrithosaurus schwarzi.*

9. BP/1/1777: *Embrithosaurus schwarzi* (tentative)

Large partial lower jaw fragment with five teeth, two of which are well preserved with almost complete crowns and partially exposed surfaces. These teeth are seven cusped and elongated with a low, smooth bulge on the lingual surface (as in *Embrithosaurus* and *Bradysaurus baini*) and no vertical ridges, cingulum or medial cusps (which are present in *Nochelesaurus*). Tentatively assigned to *Embrithosaurus schwarzi*, since some specimens of *Bradysaurus baini* sometimes have medial cusps and vertical ridges on the lingual surface. Further preparation of the two well preserved teeth would facilitate a more secure identification.

10. BP/1/7241: *Embrithosaurus schwarzi*

Subadult specimen comprising a proximal left femur, a more complete right femur, and a few small fragments of ribs, vertebrae and unidentified postcrania. The proximal left femur has a large, posteriorly projecting (20 mm) major trochanter, with a shallow notch proximal to it and deep notch distally. The proximal portion of the internal trochanter is gently curved, rough and rugose (as in *Embrithosaurus* specimen CGP CBT 112) and “s” shaped, with a concave preaxial (anterior) side and a convex postaxial (posterior) side. The internal trochanter is quite low (only 20 mm high), probably attributed to the fact that this is a still developing sub-adult specimen. Identified as *Embrithosaurus schwarzi*.

11. BP/1/8014: *Embrithosaurus schwarzi*

Seven cranial fragments, including a diagnostic right anterior maxillary fragment preserving a large, round to pointed and distinct maxillary boss with two maxillary

foramen below, a low swollen maxillary-lacrimal ridge, a vertical maxilla with downwards pointing teeth. This combination of features can only belong to a specimen of *Embrithosaurus schwarzi*. One dorsally damaged, 40 mm wide, very flat, disc-like osteoderm is preserved which seems to be evenly and smoothly convex (as in *Bradysaurus baini*) and lacking a distinct central tab-like boss. There is a large, wide, neural spine with a deep midline groove on the dorsal surface.

12. FMNH No data pareiasaur: *Embrithosaurus schwarzi*

Articulated juvenile radius and ulna (only 225 mm long), lacking an olecranon process proximally and instead has proximal lateral and medial crests with a shallow groove in betweeen and no limiting anterodorsal ridge to the proximal articular surface. Identified as *Embrithosauurs schwarzi*.

13. FMNH UR 2442: *Embrithosaurus schwarzi*

Unprepared ribs and vertebral fragments, and an extremely badly weathered snout. The upper jaw teeth are vertically directed and the bosses on the posterior edge of the left cheek are very large and bulbous, a combination of features that occurs only in *Embrithosaurus schwarzi*.

14. FMNH UR 2443: *Embrithosaurus schwarzi*

Partial lower jaws, partial left scapulocoracoid, left humerus, proximal end of articulated left radius and ulna, pelvis, right femur, a dorsal vertebra and some fragments.

Unquestionably *Embrithosaurus schwarzi* due to pelvic features: high and narrow pelvis, upright shaft, median pubic process lip shaped, rounded and anteriorly projecting, puboischiatic plate strongly dorsally concave between the iliac blades, flat and straight iliac blades oriented 45^0 off the midline anteriorly diverging, blades vertical and without horizontal eversion or turning. Interestingly, behind the acatabulum there is a relatively long horizontal plate reaching 80-90 mm posteriorly. Ulna with well defined proximal articular surface, delineated proximally, with a 30 mm high olecranon process, made of the two sides of the ulna which just meet above the articular surface. The right femur has large internal trochanter, curved, high and extending 50 mm above the femur. The left humerus has proximal and distal expansions about 60^0 apart and the distal condyles are only 225 mm wide. The intercondylar fossa of the humerus is shallow (20 mm deep) and the distal condyles extend only 25 mm distally beyond the articular surface.

15. FMNH UR 2486: ***Embrithosaurus schwarzi***

Left pelvis, unquestionably identified as *Embrithosaurus schwarzi* as a result of pelvic features: narrow pelvis: measuring 110 mm wide anteriorly between the iliac blades

and 160 mm wide posteriorly between the iliac blades; dorsal surface of the puboischiatic plate between the iliac blades is is not flat but is deeply concavely curved; ventral surface of the puboischiatic plate is not flat but comprises two straight obliquely plates either side of the midline keel, with a very deep or high midline keel (110 mm anteriorly); "lip" or “tongue” shaped anterior midline median pubic process which is rounded and evenly curved, convex and prominently projecting or anteriorly extending; thin, almost vertical iliac blades, anteriorly diverging by 50^0 from the midline and so not parallel aligned; iliac blades concavely curved (not straight); shaft of the iliac blades are almost vertical.

16. NHMUK R7782: *Embrithosaurus schwarzi* (tentative)

Partial skull (complete left side, incomplete right side) with sectioned braincase, atlas, axis, axial and atlantal arches, lower jaw.

Due to the presence of only seven cusps per tooth, this specimen was not positively identified as *Embrithosaurus* by Van den Brandt (2016, Van den Brandt *et al.* 2019). This is an important historic specimen, identified as *Embrithosaurus* by Watson (1914a) and provisionally assigned to *Embrithosaurus* by Lee (1994, 1997a).

I now conclude that this specimen should be tentatively assigned to *Embrithosaurus schwarzi* as a result of the following morphological features. It is a large skul of a presumably adult fully developed individual and has a small distinct (25 mm x 20 mm) posterodorsal maxillary boss on the maxillary-lacrimal ridge, as in the holotype of *Embrithosaurus.* The postfrontal is mediolaterally elongated and anteroposteriorly short, as in the holotype of *Embrithosaurus*. The paroccipital process of the opisthotic has a small but distint, knob-like, posterior process that extends 10 mm posteriorly and is oriented dorsomedially, as in the holotype of *Embrithosaurus.* The cheek is narrow, only 43-45 mm mediolaterally at its widest. Interestingly, the lower jaw is extremely high and has oversized, very long, very sharp and very pointed, conically horn-shaped, elongated angular bosses. It must be noted that the maxillary teeth are oriented posteroventrally, which must be the result of dorsoventral compression since *Embrithosaurus* has vertically oriented maxillary teeth. The bosses on the posterior edge of the cheek are relatively small, but are low and bulbous, and the corner boss is relatively long, conical and elongated.

17. SAM-PK-1207: *Embrithosaurus schwarzi* (tentative)

Partial left half of a skull, possibly including articulated atlas and axis. This large, extremely poorly prepared partial skull has a broken-off, medium sized, left angular boss, vertically oriented upper jaw teeth, large cheeks (extending 40^0 below the tooth row), features only found in *Embrithosauurs schwarzi* so I tentatively assign this specimen to *Embrithosaurus schwarzi.*

18. SAM-PK-1882: *Embrithosaurus schwarzi*

Partial puboischiatic plate. At first impression this large, partial puboischiatic plate, missing large anterior and posterior portions, appears very wide and flat when viewed ventrally (as in *Bradysaurus*). Measurements show that between the bases of the iliac blades the dorsal surface is narrow, only 110 mm wide anteriorly and 130 mm wide posteriorly, and strongly and deeply concavely curved, as seen in specimens of *Embrithosaurus schwarzi*. The midline pelvic symphysis is dorsoventrally very thick anteriorly (90 mm). The ventral keel is wide and covers a larger portion of the ventral surface than the condition found in specimens of *Bradysaurus baini*. Identified as most probably belonging to *Embrithosaurus schwarzi*.

19. SAM-PK-3030: *Embrithosaurus schwarzi*

Mediolaterally compressed, partial, juvenile lower jaw consisting of the left ramus, anterior right ramus, two lower jaw fragments with teeth and two other unidentified fragments.

The left angular boss is noticeably large on this small (juvenile) lower jaw, very different from the very tiny angular boss on the similarly sized lower jaw of CGP/1/2269 (juvenile) *Bradysaurus baini* specimen from the Council for Geosciences, Pretoria. This angular boss is distally very long (45 mm), but anteroposteriorly even longer and elongated (50 mm), resulting in a strange shape. It is also strange in that distal to the swollen rim midway along its length, it is severely swollen and thickened distally, bulging mediolaterally to 35 mm wide, forming a large, bulbous “tennis-ball” shape distally. A large, robust, rounded distal angular boss is most often seen in specimens of *Embrithosaurus*. SAM-PK-3030 has seven cusped mandibular teeth which could belong to any pareiasaurian species in this group. The lingual surfaces of the dentary teeth are partly exposed for two teeth on the anterior right ramus which show a smooth, bulged surface, as seen in *Embrithosaurus* and *Bradysaurus.* Tentatively referred to *Embrithosaurus schwarzi*.

20. SAM-PK-4345: *Embrithosaurus schwarzi*

Material comprising 35-40 cranial fragments making up most of a single, juvenile skull and a plate comprising six to eight articulated osteoderms. Features consistent with *Embrithosaurus schwarzi* include: small knob-like posterior process on the paraoccipital processes of the opisthotic, narrow postparietal that excludes the supratemporal, posterolateral swellings of the occipital flange; extremely low, bulbous, indistinct posterior cheek bosses on the right qudratojugal (partly worn off), nine cusped right posterior maxillary teeth that are wide, short and stubby; maxillary-lacrimal ridge with small, distinct maxillary boss and distinct lacrimal boss complex; vertical, thin maxilla with vertically oriented upper jaw teeth. The

osteoderms are weathered but are flat and disc-like, +-15 mm high, with distinct, high central bosses on most osteoderms, and with remnants of worn down, thick, rugose, tab-like ridges emanating radially beyond the central bosses. There are large and small circular pits present. Non typical *Embrithosaurus* features include a very low (only 10 mm high) right angular boss (partially worn off) and large and distinct central frontal bosses.

21. SAM-PK-4348: *Embrithosaurus schwarzi*

Extremely damaged, poorly conserved, broken specimen made of 100-200 fragments, preserving a partial pelvis, partial scapulocoracoid, partial clavicles and interclavicles, both proximal ulnae, partial radii, partial distal femora, three articulated dorsal vertebrae, and several dozen large unidentified postcranial fragments.

This specimen is in urgent need of reconstruction and basic conservation as most of the material preserved is too damaged, distorted, broken and fragmentary to be diagnostically useful. However, the partial puboischiatic plate reveals a very thick midline (100 mm), and a ventral puboischiatic plate that is directed steeply upwards at a 45-50^0 angle. The puboischiatic plate is also anteroposteriorly very short, estimated to be 230 mm as the very anterior edge is not preserved, and appears to be mediolaterally narrow, although it is only partially preserved. These features are consistent with only *Embrithosaurus schwarzi.*

22. SAM-PK-4352: *Embrithosaurus schwarzi*

Eight cranial fragments including three lower jaw fragments, cheek pieces and a partial snout, left femur, proximal right femur, partial left scapulocoracoid comprising dorsal glenoid, acromion process and scapula blade, distal ulna, carpal, tarsal, two vertebrae, distal fibula, and a radius.

The maxillary teeth are vertically oriented and each have at least seven marginal cusps. The angular bosses are long and slender with a swollen rim midway along their length, posteroventrally directed, more posteriorly directed distal to the swollen rim and are relatively small for the large size of the animal and end in a round, slightly pointed tip. The one well preserved boss on the posterior edge of the cheek is large and bulbous.

The complete left femur is identical to the femur of the holotype of *Embrithosaurus schwarzi* with: a major trochanter that projects posteriorly very far, 20-25 mm, a very slight notch proximal to the major trochanter on the postaxial side, a deep notch distally on the postaxial flange, separating the major trochanter from the postaxial shaft; the proximal region of internal trochanter is gently curved, with a concave preaxial (anterior) side and a convex postaxial (posterior) side*;* the proximal

region of internal trochanter extends far ventrally (30 mm) from the femur, the proximal edge of the internal trochanter emerges perpendicularly (at 90^0) out of the femur; moderately distally extended lateral condyle, beyond the distal edge of the medial condyle (45 mm); and a a wide femur across the distal condyles at 180 mm.

The distal ulna has a large olecranon process, extending 35 mm above the articulation surface, comprised of lateral and medial curves that meet above the hooked, well-defined, anterodorsal edge of the articulation surface. Identified as *Embrithosaurus schwarzi.*

23. SAM-PK-5000: *Embrithosaurus schwarzi*

Poorly preserved and prepared, large, partial skull preserving the snout and left side of the skull. Most of the right humerus is preserved in a large proximal and a large distal fragment with the entepicondyle preserved separately and few very small fragments preserved. Partial proximal left humerus.

The skull is large and longitudinally long (430 mm) with a large cheek, unquestionably vertically oriented maxillary teeth (so not *Bradysaurus*), with seven cusped teeth, with a swollen and distinct, wide but low, maxillary-lacrimal ridge, and very large cheeks ($30\text{-}40^0$), all features present in *Embrithosaurus.* On the humerus, the delto-pectoral crest is narrow, only 55-60 mm wide, the lateral and medial condyles reach only 20 mm distally beyond the radial and ulnar articular surfaces, the triangular intercondylar fossa is shallow at only 20 mm deep and the proximal and distal expansions are twisted to about $50\text{-}60^0$ apart, all features present in *Embrithosaurus.*

24. SAM-PK-5127: *Embrithosaurus schwarzi* (tentative)

Large pareiasaur specimen comprising a sectioned right fibula, two more distal fibulae, complete right femur, distal ulna, distal interclavicle, partial proximal right humerus, right tibia, vertebral neural spines, radius and distal radius, both astragalocalcania, proximal ulna, partial carpus and manus, a vertebral centrum, a few more postcranial fragments, partial skull preserved as several small to large fragments.

The left cheek is mediolaterally very narrow (only 35 mm wide) and gracile considering the large size of the femur. The posterior cheek bosses are small, low, and bulbous and not very distinct. The paroccipital process of the opisthotic has a moderately sized, posterior projection distally, matching *Embrithosaurus*. The maxillary teeth are sheared off but appear to be vertically aligned.

The right femur has a prominent major trochanter (so not *Nochelesaurus*), extending posteriorly 15 mm, with a deep notch proximal and a shallow notch distal to it on

the postaxial flange. The mid shaft, postaxial bulging of the femur is pronounced, as in *Bradysaurus* and *Embrithosaurus*. The internal trochanter is moderately high (30-35 mm) and is proximally gently curved, with a very short anterior process distally and rugose adductor ridge even more distal, all features of specimens of *Embrithosaurus*. The lateral distal condyle of the femur does not extend very far beyond the distal edge of the medial condyle (35-40 mm) which is consistent with *Bradysaurus* and *Embrithosaurus*.

The right tibia is not a good match to *Embrithosaurus* as it is wide with proximal articulation surfaces only about 45^0 apart, and with a ventomedially expanded distal portion, as in *Bradysaurus* and *Nochelesaurus.* The proximal ulna has a very large olecranon (50 mm high) process and enclosed articulation surface beneath it. Identified tentatively as *Embrithosaurus schwarzi* based on the skull and the femur.

25. SAM-PK-5590: *Embrithosaurus schwarzi* (tentative)

Large pareiasaur comprising approximately 150 partially prepared, broken and variously damaged fragments, in desperate need of repair and conservation as several dozen fragments show old plaster and glued surface breaks now broken and separated and scattered. Specimen preserves most of both scapulocoracoids, cranial fragments including the right cheek and partial lower jaws, isolated angular boss, damaged proximal left femur, tarsal, distal humerus, partial interclavicle, partial iliac blades, and large articulated vertebral blocks.

The two angular bosses are anteroposteriorly long (60 mm) and therefore very large and thick and stubby in appearance, reminiscent of a pareiasaurian terminal claw, as it is mediolaterally narrow and proximally very swollen, tapering distally to a pointed tip. A separate isolated broken off angular boss however is longer and thinner with a midway swollen rim and is rounded and fuller and not as mediolaterally compressed, more like the holotype of *Embrithosaurus*. The cheek bosses are large and bulbous (broken off), with a large corner boss, two small bosses above that, a last dorsal-most quadratojugal boss, and a large gap (30 mm high) dorsal to a large squamosal boss and cheek that is mediolaterally very thin or narrow, 40 mm, a combination that occurs only in *Embrithosaurus*.

The scapula blade is short and distally not very wide (170 mm) and the subscapular fossa is far behind the anterior border (60-70 mm). The proximal femur does not belong to a specimen of *Nochelesaurus*, as the adductor ridge and broken-off internal trochanter are not straight proximally and are positioned far away from the preaxial (anterior border) as in *Embrithosaurus* and *Bradysaurus*. The iliac blades are thin and very straight and flat with only a slight concave curvature and are therefore similar to *Embrithosaurus*. Identified as probably *Embrithosaurus schwarzi*.

26. SAM-PK-6242: *Embrithosaurus schwarzi*

Right femur, both partial scapulocoracoids including both distal scapula blades, both distal ulnae, right tibia, left iliac blade with acetabulum, right acetabulum, both distal humeri, partial clavicle and interclavicle, several isolated vertebrae and vertebral fragments, and an additional estimated 200-300 small to medium sized postcranial fragments. Note: this specimen is packed into eight large boxes and one small box, but even so, this specimen needs to be completely rearranged and repacked as the material in the boxes are packed far too densely and are very heavy to lift or manoeuvre, and it is not packed to allow for reasonable access to the specimen.

The scapula blades are distally extremely wide and flared to at least 190-200 mm, yet the mid section of each blade, at the level of the medial process, is very narrow and constricted to only 90 mm, giving the blades a noticeably strange, straight and sharp triangular shape as the anterior and posterior margins are very straight (not curved).

The damaged and crushed right femur has a perpendicular internal trochanter, high at 40 mm in height, which is gently curved proximally, with a short, sharp, anterior projection (5-8 mm) at the distal base of the proximal curve, followed by a rugose adductor ridge distally, all consistent with *Embrithosaurus*. The major trochanter is sheared-off, but is certainly dorsoventrally thick, at least 35 mm thick/wide.

The partial pelvis is a very good match to the anatomy of the holotype of *Embrithosaurus schwarzi*: the complete left iliac blade is massive, it is straight, strongly anteriorly diverging approximately 45-55^0 off the midline, flat to slight concave laterally, vertical, and anteriorly does not show the lateral bending or the upwards everted blade of specimens of *Bradysaurus*.

The proximal articulation surfaces of the right tibia are offset from each other by 50-60^0. The ulna has a high olecranon process (20-30 mm) above a well enclosed proximal articulation surfaces. Identified as *Embrithosaurus schwarzi.*

27. SAM-PK-6535: *Embrithosaurus schwarzi*

Clavicle fragment, lower jaw fragment, acetabulum, dorsal articulated vertebrae in a block, distal left femur, proximal right femur, both partial scapulocoracoids, partial right iliac blade, right humerus, distal left small humerus (belonging to a different individual), partial maxilla, partial interclavicle and right clavicle, proximal tibia, several large cranial fragments, partial right lower jaw ramus, partial anterior ramus, several dozen small to medium sized postcranial fragments and a dicynodont occiput.

The partial maxilla is vertical, narrow and with vertically oriented teeth (so can only belong to *Embrithosaurus* or *Nochelesaurus*). The cranial fragment of the right cheek shows three, small, round, very distinct lateral bosses on the quadratojugal, as in *Embrithosaurus* and *Nochelesaurus*, and very low, rugose ornamentation. A corner cheek fragment has large, round and distinct (not very bulbous) boss on it.

The scapula blade is very narrow (85 mm) at the level of the medial process or mid-cleithrum level, and distally remains narrow, flaring or widening only a little and very gently (the distal tip is not preserved) and is very similar to the scapula blade of *Nochelesaurus alexanderi* specien SAM-PK-6238 (Holotype of *Dolichopareia angusta*). This could be due to longitudinal compression though as the anterior and posterior portions of the blade are swollen and thickened, as if they have been crushed in.

The large right humerus is most similar to *Embrithosaurus* as the proximal and distal expansions are greatly twisted to 60-70^0 apart. As in the holotype humerus of *Embrithosaurus*, the intercondylar fossa of SAM-PK-6535 is relatively shallow (25-30 mm deep), the distal condyles do not reach distally very far beyond the articulation surface, only about 25 mm; and the delto-pectoral is narrow (65 mm).

The distal lateral condyle of the left femur does not extend far beyond the medial condyle, at approximately 30 mm. The proximal right femur preserves the internal trochanter as high (40 mm), strongly curved proximally, with a short anterior projection just distal to the proximal curvature and an adductor ridge that does not extend distally far. This strongly curved internal trochanter is more similar to *Bradysaurus* than to *Embrithosaurus,* which usually has a more gently curved internal trochanter, but this specimen could represent a very large or old *Embrithosaurus*, where the curvature has continued to increase with ontogeny. The right clavicle lacks the anterior notch seen on the holotype of *Embrithosaurus* and specimen CGP CBT 112. Identified as *Embrithosaurus schwarzi.*

28. SAM-PK-8034: *Embrithosaurus schwarzi* (Watson 1914) (Holotype) (see chapter eight)

29. SAM-PK-9098: ***Embrithosaurus schwarzi***

Juvenile specimen comprising partial skull with a large piece of the right cheek, large right maxilla with occluded lower jaw, small left cheek corner boss, partial right angular boss fragment, several smaller cranial fragments including a basal tubera. Postcranially a partial humerus, a right femur, and a few unidentified postcranial fragments are preserved. A much larger right proximal ulna with large olecranon process is preserved which is probably not part of SAM-PK-9098, as it is labelled “may be part of SAM-PK-9089” and has therefore been moved to SAM-PK-9089, which is a very large specimen.

Referred by Boonstra (1934a) to *Brachypareia rogersi*, Van den Brandt (2016, Van den Brandt *et al.* 2019) noted the diagnostic short and wide maxillary teeth, containing nine marginal cusps (identifiable on the first four right maxillary teeth preserved) and he identified this specimen as *Embrithosaurus schwarzi*, with which I concur as these maxillary teeth are identical to the maxillary teeth on the holotype of *Embrithosaurus*. Interestingly, the labial surfaces of these maxillary teeth have one vertical ridge for each marginal cusp. The posterior cheek edge bosses are large, wide, bulbous and indistinct. It is important to note that there is no maxillary boss (*Embrithosaurus* develops a small maxillary boss from the sub-adult stage and older. Since SAM-PK-9098 is a juvenile individual, the maxillary boss has probably not yet have developed). There is a low, swollen maxillary-lacrimal ridge, 40 mm wide. The angular boss is short and stubby (not long), round, as anteroposteriorly long as mediolaterally wide at the swollen proximal level, resemble a pareiasaurian "terminal claw", often seen in specimens of *Nochelesaurus*.

The femur is short (juvenile) only 340 mm long, and the internal trochanter is gently curved proximally and is positioned 30-40 mm posterior to the preaxial border of the femur. The major trochanter is eroded and not well preserved. The humerus is very poorly preserved and the twisting of the proximal and distal expansions are about 50-60^0 apart. Identified as *Embrithosaurus schwarzi.*

30. SAM-PK-9105: ***Embrithosaurus schwarzi*** **(tentative)**

A large skull with occluded lower jaw, and two partial mani in white plaster jackets. Referred to *B. baini* by Boonstra (1934a), and tentatively assigned to *Embrithosaurus* by Van den Brandt (2016, Van den Brandt *et al.* 2019) through a process of elimination. The skull is severely weathered and appears quite narrow. The cheek size cannot be determined and the maxilla is very poorly preserved, as is the entire skull. The occiput in inaccessible. The posterior cheek bosses appear to be large, bulbous and indistinct, and so cannot belong to *Nochelesaurus*, and belong to either *Bradysaurus* or *Embrithosaurus.* The maxillary teeth are relatively vertically oriented, and so probably do not belong to a specimen of *Bradysaurus*. I tentatively assign the identification as *Embrithosaurus schwarzi.*

31. SAM-PK-9116: ***Embrithosaurus schwarzi*** **(tentative)**

Distal left ulna, partial left femur, partial acetabulum, hindlimb in plaster jacket, forelimb in plaster jacket, portions of distal radii, ulnae, tibiae and fibulae, several large unidentified postcranial fragments.

The proximal left ulna shows identical morphology to the proximal ulna of referred *Nochelesaurus alexanderi* specimen SAM-PK-6238: there is no anterodorsal limiting ridge preventing the articulation surface from extending proximally, and the articulation surface extends proximally and curves convexly so; there is a low

olecranon process formed between and above two very short lateral and medial crests; on the olecranon process, anteriorly, the concave curvatures from the lateral and medial surfaces of the ulna are very short and incomplete; and there is a strong posterodorsal limiting ridge.

Importantly the partial left femur certainly does not belong to *Bradysaurus baini* as a result of the morphology of the internal trochanter, which is is identical to the morphology present in *Embrithosaurus* specimen CGP CBT 112. It is roughly straight but the proximal half is thickened and the postaxial (posterior) side is very slightly or gently convex and the preaxial (anterior) side very slightly concave, and there is a very short anterior projection (<5 mm) at the preaxial distal corner of the curvature. The internal trochanter is low (only projecting ventrally 10-15 mm from the proximal femur) with a perpendicular proximal edge. The distal half of the internal trochanter (adductor ridge) is notably rugose and irregular as in CGP CBT 112. The lateral condyle does not extend far past the distal edge of the medial condyle, only about 30 mm, as seen in *Bradysaurus* and *Embrithosaurus*.

The morphology of the ulna strongly suggests identification as *Nochelesaurus* (SAM-PK-6238) but since the morphology of the proximal ulna is highly variable within any one species (*Embrithosaurus* holotype SAM-PK-8034 compared to *Embrithosaurus* specimen CGP CBT 112) and even within the same individual (left and right sides of *Bradysaurus baini* holotype NHMUK R1971), and the femur strongly suggests *Embrithosaurus*, I tentatively retain the current identification as *Embrithosaurus schwarzi*.

32. SAM-PK-9128: *Embrithosaurus schwarzi*

Both distal femora, both ulnae, left tibia and fibula, right radius and a distal left radius.

Both ulnae are damaged and weathered. The weathered left ulna certainly has no olecranon process and the anterior articulation surface passes smoothly over onto the proximal side of the ulna, where the proximal ulna is very flat and slightly convex overall, with two very low olecranon crests present medially and laterally, and is most similar to the ulna of referred *Nochelesaurus alexanderi* specimen SAM-PK-6238. Both ulnae are significantly taller than the ulnae of the holotype of *Embrithosaurus*. The right ulna is much shorter and shows the weathered remains of an anterodorsal limiting ridge for the articulation surface, and a very low olecranon process. The posterodorsal corners of both ulnae have limiting ridges.

The shaft of the tibia is mediolaterally constricted and only 58 mm wide and the proximal articualtion surfaces are offset by about 50^0 from each other and the proximal and distal expansions are quite twisted at about $30\text{-}40^0$ off the same plane. There is no ridge on the lateral shaft above the depression and distally the

ventromedial expansion and ventrolateral upturning is not very pronounced. These features are all consistent with *Embrithosaurus*.

The radius is very symmetrical, as occurs in the holotype of *Embrithosaurus*, as the distal radius not very expanded ventrolaterally and the vertical ridge on the medial side of the distal portion of the radius, seen in *Bradysaurus* and *Nochelesaurus* only, is not present.

The distal femora are also consistent with *Embrithosaurus*, as the lateral condyle extends only 30 mm past the medial condyle. Identified as *Embrithosaurus schwarzi.*

33. SAM-PK-9148: *Embrithosaurus schwarzi*

Mounted right tibia, fibula, tarsal and pes on a wooden stand, and most of the right femur and left humerus.

Identified as *Embrithosaurus schwarzi* as the general morphology of the postcranial elements are gracile and an excellent match to the general morphology of the holotype elements of *Embrithosaurus schwarzi*. The fibula is very gracile, long and slender and lacks the raised, elongated ridge for muscle attachment on the anterior side of the shaft of the fibula, comprising four to five small, rugose, projecting knobs. The tibia has a very narrow shaft (50 mm mediolaterally wide) and angle between the medial and lateral facets of the proximal articulation surface of the tibia is large, at 60^0.

Embrithosaurus features: The humerus has a shallow intercondylar fossa and the two epicondyles do not project distally far beyond the radial and ulnar articulation surfaces, extending only 20 mm. However, the proximal and distal expansions are not very twisted and are only about $45\text{-}50^0$ apart and so appear flatter than in most specimens of *Embrithosaurus*. The anteroposterior width of the proximal expansion of the humerus is narrow and only 230 mm across.

The femur does not preserve the major trochanter and the internal trochanter is mostly sheared-off but does preserve a small anterior projection distally, consistent with the morphology of *Embrithosaurus* and *Bradysaurus*, to the exclusion of *Nochelesaurus*. The distal edge of the medial condyle does not extend far beyond the lateral condyle (35 mm) and the femur is wide (185 mm) anteroposteriorly across the distal condyles.

34. SAM-PK-9165: *Embrithosaurus schwarzi*

Left femur, left humerus, left acetabulum, right iliac blade with lateral sacral ribs, left distal ulna. The right iliac blade is diagnostic as *Embrithosaurus*. It is very thin, flat and straight, slightly laterally concave, vertically oriented and anteriorly does not show the lateral outwards curvature or upwards eversion seen in specimens of

Bradysaurus. The first lateral sacral rib is massive (as in *Embrithosaurus*), followed posteriorly by at least two much smaller lateral sacral ribs.

The proximal and distal expansions of the humerus are well twisted, to about 60^0 (most similar to *Embrithosaurus* and *Bradysaurus* and different from the flatter expansions of the humerus *Nochelesaurus*).

The femur has an extremely large major trochanter, thickly swollen compared to the much thinner postaxial flange of the femur. It projects posteriorly 20 mm and has a deep notch proximally and a shallower notch distally. Most obviously, the internal trochanter is extremely high, protruding 40-45 mm ventrally (so cannot belong to *Nochelesaurus,* which has a very low internal trochanter). Its proximal edge protrudes perpendicular to the shaft of the femur. Proximally, the internal trochanter is almost completely straight, and extremely gently curved. Distally, it is rugose and has a short anterior projection (as in *Embrithosaurus*).

35. SAM-PK-9355: *Embrithosaurus schwarzi* (tentative)

Left femur, maxilla and 10-20 cranial fragments, partial lower jaw, partial left scapulocoracoid, distal humerus, parts of clavicles/interclavicle, and +- 50 large postcranial unidentified broken fragments. This is a sub-adult individual. The material is in an extremely poor condition and most of it is not scientifically useful. The left femur is reasonably well preserved and has a large internal trochanter which is proximally gently curved, with a long (5-10 mm) anterior projection distal to the curved proximal region. The proximal edge emerges perpendicularly from the femoral shaft and reaches 30 mm high, which is very high considering the sub-adult size of the specimen. This is closest to *Embrithosaurus* in morphology.

A maxilla fragment is very thin and vertical, with vertically orientated teeth, as seen in *Embrithosaurus*. The angular boss is large considering the sub-adult size of the individual. It has a swollen rim proximally. Tentatively referred to *Embrithosaurus schwarzi.*

36. SAM-PK-11940: *Embrithosaurus schwarzi* (tentative)

Partial skull with a left lower jaw fragment and a partial humerus. This is a juvenile pareiasaur with a small humerus (240 mm long) and small skull (260 mm longitudinally at the midline, 280 mm longitudinally laterally). Most of this specimen is very fragmentary, damaged, weathered, unprepared and too poorly preserved to be useful. Cranial sutures are not visible. Cranially, there is a well-defined, low, maxillary-lacrimal ridge, the maxilla is very tall, straight, thin and vertical and the broken-off teeth are vertically aligned (so can only belong to a specimen of *Embrithosaurus* or *Nochelesaurus*). The posterior sides of the cheeks have very smooth bosses that are extremely low, very wide, bulbous, and as a result are very

indistinct (as in *Embrithosaurus* and *Bradysaurus*), with three or four bosses on the left quadratojugal. Tentatively assigned to *Embrithosaurus schwarzi*, by a process of elimination.

37. SAM-PK-12140: *Embrithosaurus schwarzi* (tentative)

Partial skull and cranial fragments. This small, juvenile skull (270 mm long at the midline) is mostly covered in matrix and is unprepared. Upper jaw teeth are vertical and have seven cusps with the three central cusps on an isolated trident and so this specimen cannot belong to *Bradysaurus*. There appears to be a small posterior knob-like process on the distal posterior pariccipital process, allowing for tentative identification as a juvenile specimen of *Embrithosaurus schwarzi.*

38. SAM-PK-12252: *Embrithosaurus schwarzi* (tentative)

Unprepared, dorsally deeply weathered, very large skull. This very large skull (420 mm long at the midline) is dorsoventrally severely crushed. It has large, bulbous posterior cheek bosses (so is either a specimen of *Embrithosaurus* or *Bradysaurus*). The angular bosses are relatively small, also not well preserved. The cheek is large on the right but small on the left, and so is also not well preserved. The maxillary region is not well preserved and the upper jaw teeth appear to be vertical, so this is tentatively identified as *Embrithosaurus schwarzi.*

39. SAM-PK-K00324: *Embrithosaurus schwarzi*

Right iliac blade and first three lateral sacral ribs. With the acetabulum facing perpendicularly laterally outwards the iliac blade is oriented about 30-40^0 off the midline, diverging anteriorly. The blade is relatively concave. The first lateral sacral rib is much larger than the second and third. Identified as *Embrithosaurus schwarzi*.

40. SAM-PK-K11637: *Embrithosaurus schwarzi* (tentative)

Very large skull with occluded lower jaw. This is a large skull (350 mm long at the midline). There is some grey plaster infill in reconstructed parts of this otherwise white skull. The maxillary-lacrimal ridge is very narrow, only 20-25 mm wide, with a lateral, distinct, small, stubby maxillary boss, above the maxillary foramen. Bosses on the posterior edge of the cheek are as follows: the corner boss is medium sized, followed dorsally by a small, round, distinct pointed boss and most dorsally on the quadratojugal by a medium to large, bulbous boss. This is most similar to the morphology of *Embrithosaurus*. The cheeks are wide as in *Bradysaurus*, 50-55 mm. Upper jaw teeth are very poorly preserved, but were certainly vertically aligned as in *Embrithosaurus* and *Nochelesaurus*. The posterior side of the distal parocipital process of the opisthotic has a low posterior swelling, similar to *Embrithosaurus*, and

lacks the large knob-like process of *Bradysaurus*. Tentatively assigned to *Embrithosaurus schwarzi.*

Nochelesaurus alexanderi (41-83)

41. AMNH FARB 5324: *Nochelesaurus alexanderi* (tentative)

Hundreds of fragments of a large pareiasaur, comprising parts of the pectoral girdle, limb and foot bones, extremely damaged and too fragmentary for most of the material to be useful. The corner boss on the posterior cheek is large, slender and elongated, pointed and horn-like, as seen in specimens of *Nochelesaurus*. Tentatively identified as *Nochelesaurus alexanderi* based on the morphology of the corner cheek boss.

42. CBT 114/CGP/1/812: *Nochelesaurus alexanderi* (tentative)

Partial right scapulocoracoid, interclavicle and scapula blade and a few small postcranial fragments. The scapula blade is anteroposteriorly narrow over its entire length. Tentatively identified as *Nochelesaurus alexanderi*.

43. CGP JA109: ***Nochelesaurus alexanderi***

Large, adult, partial and distorted skull with a “glassy” yellow appearance, with a partial occluded lower jaw and a partial proximal femur. No locality information available. This specimen has very distinctive cranial ornamentation. It exhibits large cheeks, discrete lateral bosses on the quadratojugal with no horizontal embayment and no thickening of the lower quadratojugal, very flat, distinct and pointed posterior cheek bosses, which includes a huge and extremely long “teat” shaped corner boss, the largest and longest corner boss observed on any pareiasaur specimen studied during this project, all consistent with identification as *Nochelesaurus*. The maxilla is narrow and vertical and the maxillary teeth are vertically directed. There is a low, maxillary lacrimal ridge with a sharp lateral edge, but no maxillary boss. The orbital marginal bosses on the prefrontal, postfrontal and postorbital are extremely distinct and high. The snout is square.The distal paroccipital processes of the opisthotics have a smooth and low, wide, posterior process that is dorsolaterally oriented (and not dorsomedially as in *Bradysaurus*). Consitent only with *Nochelesaurus* specimens, the femur has an extremely low internal trochanter, only 10 mm high, that is very straight, although proximally it is very rugose, irregular and slightly wider than most specimens of *Nochelesaurus* at 25 mm.

44. RMS 565/CGP/1/866: *Nochelesaurus alexanderi*

Well preserved and prepared dorsoventrally crushed, brown (medium shade) skull. Manus in white plaster jacket, partial femur, several hundred fragments of broken vertebrae, ribs and postcrania. The skull is only identifiable as *Nochelesaurus alexanderi*. The maxillary teeth are vertical, there is no maxillary boss, there is a well-defined but low and narrow maxillary lacrimal ridge, the bosses on the posterior margin of the cheek are small, distinct, pointed and elongated, especially the corner boss. Posteriorly there is a large gap between the posterior highest quadratojugal boss and the squamosal boss, the posterior side of the distal paroccipital process of the opisthotic lacks a distinct posterior knob-like process, but is low and swollen and oriented dorsolaterally. The angular boss is very large and reminiscent of a pareiasaurian claw, with a very thick swollen rim proximally.

45. RMS 1005/ CGP/1/821: *Nochelesaurus alexanderi* (tentative)

Unprepared large skull, partial lower jaw, and an almost scientifically unusable postcranium in a large, damaged white plaster jacket. This skull is damaged and unprepared. The snout is narrow (square, as high as wide) and there is a distinct, narrow (20 mm wide), low, maxillary-lacrimal ridge. The cheeks are large ($25\text{-}30^0$), most of the bosses of the posterior cheek are missing, but the corner boss is large, elongated, conical and horn-like. The maxilla is narrow and vertical and the sheared-off teeth appear to be vertical. The occiput is inaccessible and unpreprared. The cheeks are narrow (only 40 mm wide). Tentatively assigned to *Nochelesaurus alexanderi*.

46. BP/1/297: *Nochelesaurus alexanderi*

Juvenile skull (280 mm long) with occluded lower jaw and small, low angular boss (only 24 mm high). Almost metasedimentary in preservation, it is difficult to distinguish bone from matrix, very poorly prepared, variously damaged, sutures not identifiable. Identified as *Bradysaurus seeleyi* by Van den Brandt (2016), this skull is mediolaterally compressed and the anterior snout and lower jaw are pointed. Important features include vertically oriented upper jaw teeth; vertical, mediolaterally narrow premaxilla and maxilla; low maxillary-lacrimal ridge without a maxillary boss; prominent frontal posterolateral and central boss; cheeks flanges are not small as interpretted by Van den Brandt (2016) and extend $30\text{-}33^0$ below the tooth row. The posterior cheek bosses are not preserved and the occiput is not prepared. This skull is most consistent with *Nochelesaurus alexanderi*.

47. BP/1/4859: *Nochelesaurus alexanderi*

Most of a skull, late juvenile or sub adult sized, preserved as a dozen large fragments. Several dozen very small postcranial fragments exist. Identified as

Bradysaurus seeleyi by Van den Brandt (2016) the maxilla of this skull is vertical and very thin and lacks a maxillary boss, the upper jaw teeth are seven cusped and directed vertically. On the posterior edge of the two cheeks, the bosses are very distinct and pointed and there is a large gap between the dorsal most quadratojugal boss and the main squamosal boss, confirming identification as *Nochelesaurus alexanderi*.

48. BP/1/7165: *Nochelesaurus alexanderi* (tentative) "Juan's amazing pareiasaur" after Juan Carlos Cisneros.

Rib fragments, isolated and blocks of articulated vertebrae, distal right humerus, left humerus, intercavicle, tibia, partial right scapula blade, complete left scapulocoracoid, tarsus, proximal ulna, fibula, radius, a large dorsal cranial fragment and several small cranial fragments including the premaxilla and right and left maxilla.

This specimen is challenging to identify as it shares a mixture of *Bradysaurus/Embrithosaurus* (in the postcranium) and *Nochelesaurus* (in the cranium) features. The tibia is severely ventromedially elongated (as in *Bradysaurus* and *Nochelesaurus*) and the proximal articular surfaces are almost perpendicular to each other at about 80^0 off the same plane (as in *Embrithosaurus*). The left scapula blade is very short and distally very wide and flared, as in *Bradysaurus* and *Embrithosaurus*. The left humerus is very twisted with the proximal and distal expansions 60^0 apart, as in *Bradysaurus* and *Embrithosaurus*. The distal condyles of the humerus are "forked" in appearance due to a distally far extended (50 mm) lateral condyle, as in *Bradysaurus* and some specimens of *Nochelesaurus*. The olecranon process of the ulna is very high at 60 mm. The puboischiatic plate is wide, broad and flat, with a low midline pubic symphysis (only 60 mm thick) and certainly does not belong to a specimen of *Embrithosaurus*.

The cranium is referreable to *Nochelesaurus*: the right maxilla has three prepared teeth that have seven marginal cusps, including a long central trident with three very close cusps; the premaxilla has teeth which are vertically oriented (so not *Bradysaurus baini*) and, unique to this specimen, these teeth have a mixture of either five or seven cusped teeth, i.e. five cusps when the swollen base does not carry a marginal cusp mesially or distally, and seven when the base does carry a low cusp each side mesially and distally; there is a very distinct, 40 mm wide, maxillary-lacrimal ridge, and no maxillary boss present; and left paroccipital process of the opisthotic is preserved and lacks a posterior process, and is identifiable only as *Nochelesaurus alexanderi*. This is the ony case of fewer than seven cusped teeth occuring amongst this group of pareiasaurs, but this specimen has not been included in the diagnosis or phylogenetic characters scores of the species, as I interpret this specimen as an outlier.

This specimen exhibits a stange mix of features of different species and is therefore tentatively refered to *Nochelesaurus* on the basis of vertical maxillary teeth on a

narrow maxilla, the lack of the maxillary boss of *Bradysaurus* and *Embrithosaurus*, and the paroccipital process of the opisthotic lacking a posterior process, even though it has a very short and wide scapula blade and a very twisted humerus (both *Bradysaurus* and *Embrithosaurus* features).

49. BP/1/7252: *Nochelesaurus alexanderi*

Four small cranial fragments and a complete toe or finger made of three phalanges and a terminal claw. The teeth are shorn-off but the alveoli are vertically oriented. The lingual surface of a preserved and partially exposed lower jaw tooth has a very small, very pointed, very low cusp, low on the basal margin of the crown and the lingual surface has two to three vertical ridges, consistent with identification as *Nochelesaurus*.

50. BP/1/8006: *Nochelesaurus alexanderi* (tentative)

Partial right quadratojugal, ribs, five articulated unprepared anterior caudal vertebrae, a large vertebral fragment and a small unidentified postcranial fragment. The partial right quadratojugal is small and belongs to a juvenile pareiasaur. It has a prominent, elongated corner boss, which is as long as wide, with a short neck and a midway swollen rim, and relatively pointed distal end. Tentatively identified as *Nochelesaurus alexanderi*.

51. BP/1/8011: *Nochelesaurus alexanderi*

Distal humerus, acetabulum, partial distal femur, articulated partial distal femur and proximal tibia, partial acetabulum, distal fibula, vertebral fragments, a few small unidentified postcranial fragments, left jugal and partial left quadratojugal. The distal humerus has a very deep intercondylar fossa (as in *Nochelesaurus* and *Bradysaurus*) and the distal condyles extend far beyond the articular surface, creating a “forked” appearance (as in *Bradysaurus*) and as in some specimens of Nochelesaurus. The left quadratojugal preserves a very long and large corner boss, longer than wide, with two distinct lateral bosses on the lateral surface and on this basis this specimen is referred to *Nochelesaurus alexanderi*.

52. FMNH Field no 15: *Nochelesaurus alexanderi* (tentative)

Both first sacral ribs, a partial left foot, fibula, partial interclavicle and left clavicle, four articulated dorsal vertebrae and rib fragments, distal humerus, lateral clavicle, humerus, ulna, left femur with articulated tibia, four articulated vertebral blocks containing twenty one cervical, dorsal and caudal vertebrae, articulated humerus, radius and ulna, maxilla and lower jaw fragment, partial pelvis, and a femur.

The upper jaw teeth point downwards and the maxilla is only 5-10 mm wider than the tooth row, as in *Embrithosaurus* and *Nochelesaurus* specimens. The lower jaw

teeth have nine cusps, including a very small mesial basal marginal cusp. Diagnostic of *Nochelesaurus*, on the left femur the internal trochanter is very straight and only very slightly curved proximally, and the major trochanter is small and low, only 5 mm posteriorly projecting, the tibia has a very obliquely angled distal articular surface. On the humerus the intercondylar fossa is deep (30 mm). Features that are not typical of *Nochelesaurus* include: the proximal and distal expansions of the humerus are relatively twisted to about 45^0 apart; the humerus lacks the tubercle seen in certain specimens of *Nochelesaurus* and; the distal femoral flange extends distally only 30 mm beyond the shorter condyle.

53. FMNH UR 2436: *Nochelesaurus alexanderi*

Distal humerus, complete radius, and the proximal end of another radius. The radii are uninformative in terms of species diagnosis but the humerus has a deep intercondylar fossa (so not *Embrithosaurus*) and importantly has a roughly triangularly shaped tubercle on the side of the interdondylar fossa, as seen in certain specimens of *Nochelesaurus alexanderi*.

54. FMNH UR 2437: *Nochelesaurus alexanderi*

Humerus, radius, ulna, and a manus in five pieces. The humerus has proximal and distal expansions that are almost on the same plane, being only $20\text{-}30^0$ apart, and is therefore referable to *Nochelesaurus alexanderi*.

55. FMNH UR 2476: *Nochelesaurus alexanderi*

A pareiasaur comprising a left foot (five digits), a right foot (four digits), right tarsus, proximal left humerus, proximal radius, proximal left femur, and another pareiasaur comprising an articulated left femur, tibia, fibula and tarsus.

The isolated proximal left femur has a flat, straight internal trochanter, low (20 mm) as in *Nochelesaurus* and the external trochanter is very small and low, practically non existant, only 5 mm high, as in *Nochelesaurus* and it is only very, very slightly dorsoventrally thicker than the postaxial flange it is found on. Identified as *Nochelesaurus alexanderi.*

Note, the articulated left femur, tibia, fibula and tarsus belongs to a specimen of *Bradysaurus baini* (see 117. FMNH UR 2476 *Bradysaurus baini* below).

56. FMNH UR 2480: *Nochelesaurus alexanderi*

String of twenty-one weathered, articulated vertebrae, humerus, both tibia, a tarsus and some postcranial fragments. Consistent with specimens of *Nochelesaurus*, the proximal and distal expansions of the humerus are relatively flat and only about $30\text{-}40^0$ apart and there is a distinct, large tubercle on the border of the intercondylar

fossa, a deep intercondylar fossa (30-33 mm), and a wide humerus between the distal condyles (240 mm), wider than the narrower measurements of *Embrithosaurus* specimens. The distal tibia are both very extended or stretched ventromedially.

57. FMNH UR 2481: *Nochelesaurus alexanderi*

Elements of a juvenile pareiasaur: three vertebrae, partial pelvis with articulated femur and partial tibia, tarsus, fifteen phalanges, and a few unidentified postcranial fragments. The femur is only 270 mm long (juvenile) and is diagnostic as a result of the internal trochanter which is straight, very slightly curved, and very low (only 10 mm high) and partially broken off, most consistent with the morphology of *Nochelesaurus*, despite the major trochanter being relatively large and thick. Importantly, two partial osteoderms attached between neural spines of the three vertebrae, have rugose, tab-like ornamentation, most similar to *Nochelesaurus.*

58. SAM-PK-3717: *Nochelesaurus alexanderi*

Left humerus, partial interclavicle and a clavicular fragment. The interclavicle and clavicular fragment are not diagnostic, but the left humerus is well preserved and has the following morphological features: very little twisting or torsion between the proximal and distal expansions, only about 25^0 off the same plane (unique to *Nochelesaurus* amongst these pareiasaurs); the intercondylar fossa is deep (50 mm), a feature shared with *Bradysaurus*; a wide proximal humerus (anteroposteriorly measuring 280 mm (again shared with *Bradysaurus*)). Identified as *Nochelesaurus alexanderi***.**

59. SAM-PK-4324: *Nochelesaurus alexanderi*

Remains of a small, juvenile specimen comprising several dozen rib fragments, partial digit (terminal claw and phalanx), three articulated dorsal vertebrae, partial dorsal acetabulum, partial mid left humerus, most of the dorsal left cheek and the entire right cheek of the skull, and about a dozen other small, unidentified postcranial fragments. The left central supartemporal boss is very high and pointed, and in general the cranial ornamentation is very distinct. The bosses on the posterior edge of the right quadratojugal are distinct and pointed (so can only belong to *Nochelesaurus* or *Bradysaurus baini*) with two distinct lateral quadratojugal bosses. The distal end of the parocipital processes of the opisthotics are anteroposteriorly short (50-55 mm) and more importantly, the posterior edges of both are low and smooth, with no posterior process present. The cheeks are narrow (40 mm wide). The torsion between the proximal and distal humerus is relatively flat, only $30\text{-}40^0$. Identified as *Nochelesaurus alexanderi*.

60. SAM-PK-5012: *Brachypareia rogersi* (Broom 1912) (Holotype) = *Nochelesaurus alexanderi* (see chapter eight)

61. SAM-PK-5015: *Nochelesaurus alexanderi* (tentative)

Material comprising small proximal left ulna and distal radius of a small individual pareiasaur and several elements of a much larger pareiasaur: proximal left ulna, tarsal, both fibula, right distal clavicle/interclavicle and median clavicular fragment, right cheek (quadratojugal) and another cranial fragment, left tibia, left humerus, most of the left innominate, two large radii, manus and pes in a white plaster jacket, partial scapulocoracoid, and dozens of large, unprepared, fragmentary, unidentified postcranial elements.

The small ulna is very gracile, yet has a large olecranon process (25 mm high, 15 mm anteriorly projecting) creating a well-defined enclosed socket for articulation with the humerus. The larger left ulna also has a large but low olecranon process (only 15 mm high), extending far anteriorly (25 mm) to creating a socket. The small animal is unidentifiable.

The large elements show a mixture of *Nochelesaurus* and *Bradysaurus* features cranially. *Nochelesaurus* features: the right cheek has a large, distinct, elongated corner boss covered in rugose ornamentation on the posterior edge of the quadratojugal and a small, round, distinct, horizontally flattened boss above that, and a large bulbous dorsal-most quadratojugal boss with long anterior extensions. The lateral surfaces of the quadrtojugal have three distinct bosses. *Bradysaurus* features: The cheek is small, extending less than 20^0 below the tooth row) and is very wide, 60-65 mm.

Similarly, the large distal left tibia shows features of both *Bradysaurus* and *Nochelesaurus*: ventromedially expanded and projecting distal tibia, and mediolaterally very wide distal tibia (140 mm). The left humerus has a massive delto-pectoral crest, 80 mm wide (a *Bradysaurus* and *Nochelesaurus* feature) and the distal and proximal expansions are quite flat and only 40^0 apart (a *Nochelesaurus* feature only). The left acetabulum is very large, deep, and round. The large individual is tentatively assigned to *Nochelesaurus alexanderi* on the majority of the evidence.

62. SAM-PK-5019: *Nochelesaurus alexanderi*

Sub-adult skull with occluded lower jaw and four anterior cervical vertebrae with short rib fragments attached.

Referred to *Nochelesaurus strubeni* by Haughton and Boonstra (1929a) this skull is sub adult sized (330 mm anteroposteriorly long at the midline, 360 mm

anteroposteriorly long laterally). The external cranial surfaces are deeply weathered dorsally (allowing for suture identification) and over prepared and damaged on the lateral cheeks.

The angular boss is very large (so probably not *Bradysaurus*) considering the relatively small size of the skull and morphologically is thickest proximally and resembles a pareiasaurian terminal claw. The snout is square (almost as high as wide) the maxilla carries a narrow maxillary-lacrimal ridge and appears to lack a maxillary boss. The upper jaw teeth are vertically oriented and appear to have seven cusps on them. There are remnants of fairly large frontal central bosses (a *Nochelesaurus* feature) and the postfrontal shows the *Bradysaurus/Nochelesaurus* morphology of being roughly square, slightly longitudinally elongated and posteriorly curved medially.

The cheek are relatively large, reaching about 27^0 below the tooth row. The bosses on the posterior edge of the cheek are mostly sheared-off or worn-off, especially on the left, giving the false impression of a smooth surface, but on the right they are better preserved and show a fairly strong, long, pointed corner boss and a round pointed boss above that. The dorsal-most quadratojugal boss is however very low, bulbous and wide. Diagnostically important for identification as *Nochelesaurus*, the parocciptial process of the opisthotic is extremely small and gracile with no posterior process distally and the postparietal is wide, not narrow. Identified as *Nochelesaurus alexanderi*.

63. SAM-PK-6238: *Dolichopareia angusta* (Haughton and Boonstra 1929) (Holotype) = *Nochelesaurus alexanderi* (see chapter eight)

64. SAM-PK-6239: *Nochelesaurus alexanderi* (Haughton and Boonstra 1929) (Holotype) (Haughton and Boonstra 1929) (see chapter eight)

65. SAM-PK-6239A: ***Nochelesaurus alexanderi***

Partial skull (right cheek fragment only). This specimen is referable to *Nochelesaurus alexanderi* as a result of the distinctive morphology of the bosses on the posterior edge of the cheek and is included in the *Nochelesaurus alexanderi* cranial descriptive chapter of this project (chapter three).

66. SAM-PK-6240: *Brachypareia watsoni* (Haughton and Boonstra 1929) (Holotype) = = *Nochelesaurus alexanderi* (see Chapter 8: Taxonomic Review)

67. SAM-PK-8944: (SAM-PK-K07999, SAM-PK-K08000) *Nochelesaurus alexanderi*

Large skull with separate lower jaw, on a small pallet. Mounted articulated right forelimb (ulna, radius, carpus, manus) on wooden stand numbered as SAM-PK-

K07999. Articulated right hindlimb (distal femur, tibia, fibula, tarsus, digits) on another mounted wooden stand numbered as SAM-PK-K08000.

Important Note 1: The mounted right forelimb (SAM-PK-K07999) has been figured by Boonstra (1932c) Ann.S.Afr.Mus.28 pp.437-503 pl.42(2), right epipodial and manus of *Nochelesaurus alexanderi* as SAM-PK-8944 and was incorrectly re-accessioned by Iziko SAM staff as SAM-PK-K07999 some time after 1932. Therefore SAM-PK-K07999 is actually part of SAM-PK-8944.

Important Note 2: The right hind limb of SAM-PK-8944 has also been incorrectly re-accessioned as SAM-PK-K08000. For SAM-PK-K08000, the museum catalogue has the following note "figured as SAM-PK-8034 (the holotype of *Embrithosaurus schwarzi*) and is therefore part of the type". But this note cannot be correct as I have re-described the holotype postcranium of *Embrithosaurus schwarzi* (SAM-PK-8034) in this project (chapter four), which includes both femora, tibiae and fibulae. SAM-PK-K08000 cannot be part of SAM-PK-8034. Since SAM-PK-K08000 has the same mount type, preservation and preparation as the forelimb mount (SAM-PK-K07999) it is probably from the same individual (SAM-PK-8944). Therefore SAM-PK-K08000 is most probably part of SAM-PK-8944.

SAM-PK-8944 was referred to *Nochelesaurus alexanderi* by Boonstra (1934a). This large, adult skull is very narrow, somewhat naturally so and somewhat also the result of mediolateral compression, with narrow cheeks measuring only 40-45 mm at their widest (so not *Bradysaurus*). The maxillary teeth are directly vertically downwards and only slightly inwards, there is no maxillary boss present and a very low, narrow maxillary-lacrimal ridge that does not reach the discrete lacrimal boss complex. The posterior cheek bosses are large and distinct, although mostly worn-off. The distal paoroccipital process is very gracile, considering the large size of the skull and there is only a very tiny, dorsolaterally oriented, less than 5 mm posteriorly projecting process. The cranial ornamentation is very strong and distinct, the left cheeks is relatively small considering the large size of the skull, extending only about 25^0 below the tooth row (the right side is damaged). The postparietal appears to be wide (a feature unique to *Nochelesaurus* amongst this group of pareiasaurs). The central boss of the right frontal is large and distinct. The angular boss on the lower jaw is relatively short and is characterised by a very swollen rim proximally, and is bulged and tapering distally, resembling a pareiasaurian terminal claw as seen in many other specimens of *Nochelesaurus*.

The mounted distal right ulna is similar, but not identical to to the distal ulna of referred *Nochelesaurus alexanderi* specimen SAM-PK-6238: there is a right angled, square shaped, anterodorsal limiting ridge which abruptly ends and prevents the anterior articulation surface from extending over onto the flattened proximal surface, there is no olecranon process above the articulation surface, there is only a

very short (10-20 mm) concave curvature from the lateral side only (and none from the medial side) and there is a indistinct posterodorsal limiting ridge. Identified as *Nochelesaurus alexanderi.*

68. SAM-PK-9089: *Nochelesaurus alexanderi*

Partial pelvis (puboischiatic plate and both acetabulula), left femur, left humerus, right? fibula, large left lateral sacral rib with partial iliac blade, a few dozen other small fragments. (Note: A large right proximal ulna stored with the juvenile sized SAM-PK-9098 is labelled as "may be part of SAM-PK-9089" and has now been moved to SAM-PK-9089).

This is a hugely massive individual specimen. Femur: The posterior projection of the major trochanter of the femur is short, 10 mm, and the notch on the postaxial flange distal to the major trochanter is very shallow so this femur cannot belong to a specimen of *Embrithosaurus*, and as a result of the small major trochanter, both the proximal and distal notches on the postaxial border of the femur are very shallow. The internal trochanter is sheared-off but the adductor ridge is straight, extending parallel to the preaxial margin of the femur, and is positioned close to the preaxial border (as only seen in *Nochelesaurus*).

Humerus: The humerus shows the following features, consistent with both *Nochelesaurus* and *Bradysaurus*: a massive, robust "heart shaped" delto-pectoral crest, 80-90 mm anteroposteriorly; a short, curved, crescent-shaped, insertion point for muscle attachment is present on the humeral shaft of the dorsal proximal humerus; the intercondylar fossa is deep, 40 mm and; the proximal humerus is very wide, 275 mm which you would expect for such a large individual of any species. A unique feature to *Nochelesaurus* is that the proximal and distal expansions are very flat, not very twisted, and are only about 35-40^0 apart. The lateral condyle extends distally relatively far (45-50 mm) beyond the distal edge of the medial condyle, which is further than most *Embrithosaurus* and *Bradysaurus* specimens and supports identification as *Nochelesaurus*. The fibula is identical in morphology to the fibula of referred *Nochelesaurus* alexanderi specimen SAM-PK-6238.

Pelvis: The pelvis is not a good match to *Bradysaurus* or *Embrithosaurus* as it shows a mixture of proportions, but overall is more similar to *Bradysaurus* than *Embrithosaurus*. The pelvis is massive, anteroposteriorly short (260 mm) at the midline, longer than most specimens of *Embrithosaurus* and shorter than most of *Bradysaurus*. The pelvis is about 100 mm thick at the midline anteriorly, closer to the morphology of *Embrithosaurus* specimens. The midline median process is short (20 mm), but wide (100 mm) with a small notch laterally either side, as in *Bradysaurus*. The pelvis is very wide anteriorly, 380 mm, similar to *Bradysaurus*, and the ventral keel occupies a small portion of the ventral puboischiatic plate (as in *Bradysaurus*) but dorsally, the plate is concave and narrow (as in *Embrithosaurus*).

The right proximal ulna has a large olecranon process (25-30 mm high, 15-20 mm anteriorly projecting beyond the articulation surface). The articulation surface forms an enclosed socket with a well-defined anterodorsal border formed by concave lateral and medial sides of the olecranon process that meet, and the olecranon process is large and convex above that, with a well-defined posterodoral ridge. Identified as *Nochelesaurus alexanderi.* This specimen could be uilized to study the pelvis of *Nochelesaurus*.

69. SAM-PK-9114: *Nochelesaurus alexanderi* (tentative)

Partial lower jaw preserving a partial left ramus. The partial lower jaw comprises two large fragments and four small fragments. The lower jaw is unprepared and the dentary teeth are sheared-off. The first and sixth right dentary teeth are partly exposed and each have a very low basal cusp on the mesial margin and the sixth right tooth is partly exposed lingually showing two or three vertical ridges. Tentatively identified as *Nochelesaurus alexanderi*.

70. SAM-PK-9115: *Nochelesaurus alexanderi*

Sub-adult skull with partial occluded right lower jaw, isolated left lower jaw ramus, postcranium comprising proximal tibia, partial left and right scapulocoracoids, partial right radius and partial right foot in two white plaster jackets, distal ulna, distal fibula, a few postcranial fragments. The skull is distorted in several areas and directions, especially on the left snout and the posterior cheeks below the supratemporal corner boss are extremely laterally flared out.

This specimen was referred to *Bradysaurus seeleyi* by Boonstra (1934a) and to *Nochelesaurus alexanderi* by Van den Brandt (2016) as a result of the pointed, small and distinct bosses on the posterior edge of the cheeks and the lack of a large maxillary boss, both of which are correct observations. In addition, the general cranial ornamentation is very distinct, high and pointed, the orbital margins on the prefrontal, postfrontal and postorbital, are very distinct and the supratemporal corner boss is very small, narrow, elongated and pointed, and the most distinct I have seen in the project. Weathering on the left side of the skull allows for some sutures to be discernable. There is a low, swollen maxillary-lacrimal ridge. The cheeks are small to medium sized, extending about 24^0 below the tooth row and are mediolaterally narrow. The maxillary teeth are elongated and carry seven cusps each. The postparietal appears to be wide (as in *Nochelesaurus*) as the element is shifted or displaced somewhat at its lateral sutures with the supratemporal.

The skull and lower jaw are also dorsoventrally crushed as the normally upwards and slightly forwardly oriented lower jaw teeth, point sharply inwards and are almost horizontal, with the dorsal parts of the lower jaw also crushed and backwards curved. The maxilla is vertical on the right but dorsoventrally crushed on

the left to appear very wide and curved, with inwards pointing horizontal upper jaw teeth which I ascribe to distortion. A broken off angular boss is small, short, mediolaterally narrow and widest proximally. Althoug not a perfect match, this specimen is identified as *Nochelesaurus alexanderi* on the majority of the evidence.

71. SAM-PK-9137: *Nochelesaurus alexanderi*

Extremely large skull comprising numerous cranial fragments with the ventral snout, cheeks and occluded lower jaw as the largest fragment. Large wooden and plaster pallet preserving articulated left femur, tibia, fibula, tarsus and phalanges, three partial interclavicles (two large, one smaller), huge ulna on white plaster jacket, right tibia, right proximal tibia, proximal ulna and radius, partial right scapulocoracoid, four dorsal vertebrae with articulated osteoderms, a broken white plaster jacket containing a partial manus, 50-75 broken, damaged postcranial fragments in need of basic essential conservation and repair.

This specimen was referred to *Bradysaurus seeleyi* by Boonstra (1934a) and *Nochelesaurus alexanderi* by Van den Brandt (2016). This specimen is unquestionably referable to *Nochelesaurus alexanderi* due to the posterior bosses of the cheek matching the morphology of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239) more closely than any other specimen studied for this project. The posterior cheek bosses are horizontally flat, elongated and pointed, and the corner boss is long, with a narrow neck and a swollen distal rim. There are small distinct bosses on the lateral cheek. The cheek is large, extending approximately 35^0 below the tooth row. The skull is narrower than specimens of *Bradysaurus* and the maxilla carries vertical teeth with seven marginal cusps with three central cusps on an elongated trident. The maxilla has a low, swollen maxillary-lacrimal ridge and no maxillary boss (on a very large adult, fully developed skull).

Similarly, the left femur bears an internal trochanter that matches the morphology of the holotype of *Nochelesaurus alexanderi* (SAM-PK-6239) better than any other specimen studied. The internal trochanter is completely straight, and proximally low, only 25 mm high, it has an oblique proximal edge (not perpendicular), the adductor ridge is rugose and reaches distally all the way to the medial condyle. The right femur is similar, but the internal trochanter is not completey straight and has a very gently curved proximal end (curving 10 mm posteriorly). It is low (15-20 mm high), and has a short anterior projecting below the curve. The internal trochanter emerges obliquely from the femur, extending far distally. The major trochanter is small, projecting posteriorly < 5 mm and the postaxial border of the right femur is straight and not bulged. The right internal trochanter is dorsoventrally very thin, only 20 mm thick.

The ulna has a large and high olecranon process and an enclosed proximal articulation surface. The four partial osteoderms are poory preserved and prepared

but two of them are wide, very rugose and heavily ornamented, thick, and smoothly/evenly convex with a wide, shallow central pit. Identified as *Nochelesaurus alexanderi.*

72. SAM-PK-9169: *Nochelesaurus alexanderi*

Sub-adult sized puboischiatic plate with both acetabula, articulated interclavicle/clavicles with right scapulocoracoid and partial left scapulocoracoid, proximal left tibia, dorsal scapula blade, blocks of articulated vertebrae, radius, carpus and manus in white plaster jacket, tibia, fibula, tarsus and pes in a white plaster jacket, and a larger individual with interclavicle with articulated right scaulocoracoid, large humerus.

The large humerus is relatively flat as the distal and proximal ends are twisted apart by only about 30-40^0, as seen in specimens of *Nochelesaurus*. The sub-adult pelvis is wide, broad, flat and low, with a low or thin midline symphysis and does not look like the morphology of *Embrithosaurus*. Strangly, the sub-adult scapula blade is wide at its base and midway up, nevertheless I identify this specimen as *Nochelesaurus alexanderi*.

73. SAM-PK-11559: *Nochelesaurus alexanderi*

Left humerus. The delto-pectoral crest of this large left humerus is not preserved. The distal and proximal expansions are offset by 35^0 from each other and are therefore relatively flat and not very twisted (as in *Nochelesaurus*). The intercondylar fossa is 35 mm deep, the ectepicondyles extend distally 30 mm beyond the radial and ulnar articulation surfaces. Identified as *Nochelesaurus alexanderi*.

74. SAM-PK-11596: *Nochelesaurus alexanderi*

Nearly complete, articulated, semi prepared, in-situ, very large skull and relatively complete skeleton on display (2019) in the foyer of the Geology building, Stellenbosch University, Western Cape. Most of the snout and the entire left manus has been fabricated from plaster and the right forelimb, hindlimb and pes are not preserved. The skull is moderately dorsoventrally compressed and displaced to the left. The specimen is that of a large adult pareiasaur (skull length 370 mm longitudinally long at the midline, 420 mm longitudinally long laterally) exhibiting the following cranial features of *Nochelesaurus alexanderi*: distinct, 13 mm wide, 8 mm high frontal central boss; wide postparietal (sutures discernible on the right) encompassing paired occipital swellings or bosses (which are present on the supratemporals of *Bradysaurus* and *Embrithosaurus* specimens as a result of their narrow postparietals); very high and distinct orbital bosses on the prefrontals and postfrontals; distinct lacrimal bosses; no maxillary boss; vertical maxillary teeth;

bosses on posterior edge of quadratojugal distinct and horizontally plate-like; wide vertical gap between the posterior edge boss of the squamosal and dorsal-most quadratojugal boss; large angle or corner cheek boss, especially on the left; flat lateral quadratojugal; large cheek extending approximately 30^0 below the tooth row; all features of *Nochelesaurus alexanderi*. Interestingly, unique to this specimen, is a large and distinct boss on the nasal bone, above each external naris, clearly separate from the central nasal boss and not an anterolateral tab-like process of the central nasal boss.

Interestingly, as is the case with *Bradysaurus baini*, the second sacral rib is the largest and not the first, and has a longitudinal ridge on the dorsal medial surface, and is followed by two smaller, flat, sheet like sacral ribs. The exposed dorsal parts of the iliac blades are also very similar to those of *Bradysaurus baini*, being parallel posteriorly, but direct laterally outwards anteriorly at about 45^0 from the midline and everted upwards somewhat**.**

Postcranially, only dorsal surfaces are exposed. Four osteoderms support identification as *Nochelesaurus* (three articulated, one isolated) as they are are wide (+-50 mm), high (22 mm), and smoothly and evenly convex (so do not belong to *Embrithosaurus* which has flat or disc-like scutes with well defined, small central bosses). They are covered with very heavy and rugose ornamentation (so do not belong to *Bradysaurus baini* which has very light ornamentation) consisting of flattened tab-like processes that cover most of the scute and reach all the way to the edges of each scute. They have no distinct central boss. The scapula blades are mostly comprised of plaster, but the right distal dorsal scapula blade is better preserved and very narrow, only 14 cm wide, although partly damaged. Relatively flat humeral torsion between the proximal and distal expansions (only about 40^0 on the left) supports an identification of *Nochelesaurus*. The dorsal surfaces of the neural spines have a deep midline groove over approximately the 5^{th} to 12^{th} vertebrae, which do not reach or notch the anterior or posterior rims, but the 13^{th} to 22^{nd} neural spines are smoothly convex and covered in light, rugose ornamentation. At least 35 caudal vertebrae are preserved. This specimen could be uilized to study the pelvis of *Nochelesaurus*.

75. SAM-PK-11930: *Nochelesaurus alexanderi*

Both femora and the right tibia and fibula encased in white plaster. Both femora have low (30 mm high) internal trochanters which emerge obliquely from the proximally shaft of the femur. They are almost perfectly straight, with a very slight (5 mm) proximal curvature, and a very short anterior process immediately distal to the proximal curve. They are narrow and thin, only 15 mm wide. The adductor ridge is very long, extending far distally. The major trochanters are partially preserved. They are very gracile and do not extend posteriorly beyond the postaxial flange, but are

swollen to 30 mm in dorsoventral thickness. The proximal tibia is not well preserved. Identified as *Nochelesaurus alexanderi*.

76. SAM-PK-11948: *Nochelesaurus alexanderi*

Almost complete skull and skeleton on display in the Boonstra diorama, Iziko South African Museum, Cape Town, including the complete right forelimb (besides for the digits), complete right hind limb including pes, scapula girdle, pelvic girdle, complete vertebral column and most of the ribs. Separately, the museum curate and stores the left femur, left humerus, left fibula, left tibia, left tarsus, small broken fragments, and a few toe bones, in storage in the main collections facility.

The left femur is severely dorsoventrally crushed and very thin. The major trochanter is not preserved but the internal trochanter is, which is low (25-30 mm), very straight, with an oblique proximal edge, with a thickened proximal portion that has an irregular, uneven, proximal curvature or swelling, extending <10 mm. The lateral distal condyle extends far (60 mm) distally past the medial condyle. The proximal and distal expansions of the left humerus are almost on the same plane being only 20^0 offset from each other, and the angle is estimated to about 30^0 for the right humerus. The distal humerus is forked in appearance as the condyles extend distally far past (> 30 mm) the articulation surface. The delto-pectroal crest is large, robust and “heart shaped” 70 mm anteroposteriorly, with a damaged ventral surface.

The left tibia is anteroposteriorly crushed. The ventromedial expansion of the distal portion of the tibia is extremely long and there is a prominent vertical ridge on the lateral side of the shaft.

The scapula blade is anteroposteriorly very narrow and dorsally is only 140 mm long on the right and 130 mm on the left, with almost no distal flaring as the anterior and posterior sides are very straight, especially the anterior side. The dorsal scapula blades are mediolaterally very thick, 50 mm wide. The right scapula blade is of average length at 450 mm long, include the acromion process. The right ulna has a very large olecranon process, 60 mm high.

Anterior osteoderms comprising two parallel rows either side of the midline are preserved from the 5th to 13th vertebrae. They are medium to large in width, very rugose, covered in rugose tab-like processes, in an almost radial star-like pattern (comprising five or six tabs), creating a very irregular central boss that is low and covers most of each scute. These scutes are not evenly or smoothly convex.

The skull is dorsoventrally crushed, appearing very broad and low, such that the internarial bar is buckled and bent and the cheeks splay and flare outwards. The ribs and the, iliac blades are also dorsoventrally crushed and everted and flattened.

Cranial sutures are not discernible. The skull is large and adult sized and 350 mm long at the midline, 395 mm long laterally. The cheek is large, extending about 32^0 below the tooth row on the right. There is no maxillary boss present, but there is a very well defined, swollen, low and narrow (30-35 mm wide) maxillary-lacrimal ridge. The upper jaw teeth are oriented inwards by about 45^0 but were probably more vertical in life as the skull is quite dorsoventrally crushed. The posterior cheek bosses are as follows: the corner boss is elongated and conical, 30 mm long, round to pointed on the right cheek, the second and third boss are rounded, medium and much more pointed on the left cheek than on the right. These features are all consistent with the morphology of *Nochelesaurus alexanderi.*

77. SAM-PK-12047: *Nochelesaurus alexanderi*

Radius, carpus, large phalanx and terminal claw, distal interclavicle, tarsus, proximal ulna, partial snout and almost complete lower jaw, of a large adult pareiasaur.

The radius is large and is ventrolaterally expanded and projecting distally, creating a non-symmetrical radius, resulting in the distal expansion being wider than the proximal expansion of the radius (as in *Nochelesaurus*) and has the presence of a distinct, vertical, ridge on the medial side of the distal portion of the radius, extending from the swollen base of the radius, tapering dorsally and almost reaches midway up the shaft (as in *Nochelesaurus* and *Bradysaurus*). The proximal ulna is large and has a large and high (35 mm) olecranon process. The snout and lower jaw are very narrow and are mediolaterally compressed as can be determined from the unusual, very narrow, external naris. The angular boss is small, short (40 mm) and stubby, considering the large size of the lower jaw. The maxilla has a low, swollen maxillary-lacrimal ridge, but no maxillary boss. Since this is a large, adult pareiasaur, this must be a specimen of *Nochelesaurus*. The premaxilary teeth are vertically oriented, and on the right maxilla posteriorly they are backwards pointing. Identified as *Nochelesaurus alexanderi*.

78. SAM-PK-12057: *Nochelesaurus alexanderi* (tentative)

Dozens of caudal vertebrae, fragmentary vertebrae and ribs, small left and right femora, small right tibia, small partial pelvis and a larger right femur of a sub-adult, +- 150 rib and vertebral fragments. Most of this material belongs to a small, juvenile pareiasaur, and there is one large right femur that belongs to another individual.

The small femora are 250-260 mm long and mediolaterally compressed. The larger sub-adult femur is 355 mm long and has a very slight or gentle proximally curved internal trochanter which is not very high (35 mm) and is similar to the morphology of *Nochelesaurus*. The small pelvis is flat, wide, broad, and long, and is best described as a juvenile *Bradysaurus baini* and cannot belong to an *Embrithosaurus*. The internal trochanter of the left femora is broken off, but on the right it is

preserved and is high and very straight and very slightly curved proximally. Considering the anatomy of the pelvis, which is unlike *Embrithosaurus*, and that the femur is similar to both *Embrithosaurus* and *Nochelesaurus*, the specimen is probably *Nochelesaurus*. The internal trochanter is very narrow proximally and so cannot be *Bradysaurus*. Tentatively identified as *Nochelesaurus alexanderi.*

79. SAM-PK-12076: *Nochelesaurus alexanderi*

Partial dorsal skull roof and cheeks comprising eleven cranial fragments, basal tubera, partial lower jaw, left and right iliac blades with lateral sacral ribs, puboischiatic plate with left acetabulum, right acetabulum with articulated right dorsal femur and two maxilla fragments labelled SAM-PK-12076B.

Identified by Van den Brandt (2016) as *Nochelesaurus alexanderi*, the cranial ornamentation is very distinct and the corner boss on the left cheek forms an elongated, conical horn (40-50 mm long), which is rugose and ends in a sharp point. The dorsal bosses above the corner boss, are small and very pointed and sharp tipped.

The pelvis is very similar to *Bradysaurus baini*: the puboischiatic plate is wide, broad, flat and low and posteriorly extending at least 110 mm past the ischial buttress. The iliac blades are vertical, and very straight, posteriorly the dorsal portion is medially turned and anteriorly the ventral portion is slightly laterally turned and very slightly vertically everted. The ventral keel is thin and low (only 60 mm high) and covers a small portion of the ventral pelvis. There are at least four sacral ribs: the first two sacral ribs are the largest, with the second sacral rib slightly larger than the first (as in *Bradysaurus*), the next two are much smaller and plate-like. Identified as *Nochelesaurus alexanderi.* This specimen could be uilized to study the pelvis of *Nochelesaurus* (Specimen SAM-PK-12076B is a maxilla with inwards pointing teeth and a wide, curved maxilla and a large maxillary-lacrimal ridge/boss, identified as *Bradysaurus baini*).

80. SAM-PK-12129: *Nochelesaurus alexanderi* (tentative)

Small left femur and a cranial fragment. The cranial fragment is unprepared and not useful. The femur is small, 270 mm long, deeply weathered on all its edges, and possesses a virtually straight, low (15 mm high) internal trochanter, with an oblique proximal edge, most similar to *Nochelesaurus.* Tentatively assigned to *Nochelesaurus alexanderi.*

81. SAM-PK-K07999: (=SAM-PK-8944) *Nochelesaurus alexanderi*

82. SAM-PK-K08000: (=SAM-PK-8944) *Nochelesaurus alexanderi*

83. SAM-PK-K10898: *Nochelesaurus alexanderi*

Four small cranial and lower jaw fragments and a terminal claw. Most of the crowns of the teeth are not preserved but two dentary teeth each have a very low, very small basal cusp on the mesial margin and no corresponding cusp on the distal margin, creating a non-symmetrical cusps arrangement. Identified as *Nochelesaurus alexanderi.*

Bradysaurus baini (84-157)

84. AM 3748: *Pareiasaurus acutirostris* (*Koalemasuarus*) (Broom 1913) (Holotype) = *Bradysaurus baini* (see chapter eight)

85. AMNH FARB 2452: *Bradysaurus baini* (tentative)

Maxilla fragment with seven preserved teeth. The teeth are in good condition and reveal their shape and the marginal cusps. There are seven cusps on each tooth, with an elongated central trident with three cusps on it. A few lower jaw teeth are also preserved on the internal surface of the maxilla, which have a low triangular bulge on the lingual surface, probably *Bradysaurus baini* (Tentative).

86. AMNH FARB 5323: *Bradysaurus baini*

Large skull comprising three fragments, with much white plaster. The maxillary teeth point directed horizontally backwards and the cheek flanges are large. There are large maxillary bosses, on both sides of the skull, partially sheared-off. The bosses on the posterior edge of the cheek are large, bulbous and indistinct. The cheeks are mediolaterally thick, 55-60 mm at their widest. The lateral surface of the quadratojugal has indistinct bosses and rugose indistinct ridges instead as ornamentation. Positive identification as *Bradysaurus baini*.

87. 47/CGP/1/863: *Bradysaurus baini* (tentative)

Articulated right humerus and ulna and a left iliac blade. The iliac blade is extremely curved (deeply concave laterally) and therefore unlikely to belong to a specimen of *Embrithosaurus* which usually has straighter, flatter illiac blades. The humerus is very twisted as the proximal and distal expansions are about 50-60^0 apart (so not *Nochelesaurus*). The distal condyles extend far distally and are very “forked” in appearance. The ulna has a high and prominent olecranon process. Tentatively referred to *Bradysaurus baini*.

88. CDB 7: *Bradysaurus baini*

Very large pelvis and sternum with partial proximal femora and anterior caudal vertebrae, and two large blocks containing several articulated dorsal vertebrae and rib fragments each. Distal femur and two partial humeri.

The pelvic baldes are parallel to the midline posteriorly, and strongly laterally curved outwards anteriorly. The pelvis is very wide anteriorly, measuring 380 mm, and has distinct notches between the lateral pubic processes and the median pubic process, which is short anteriorly and thin dorsoventrally, and the midline pubic symphysis is only 70-80 mm in height. The orientation of the iliac blades is very flat and horizontal, so very everted. The puboischiatic plate is very flat, wide and long (at least 310 mm anteroposterioly long). The dorsal surface of the plate, between the iliac lades is very flat and wide and not concave. Ventrally, the midline pubic symphysis is mediolaterally narrow and forms a minority of the puboischiatic plate. The first sacral rib is massively large. Identified as *Bradysaurus baini*.

89. CGP/1/2268: *Bradysaurus baini*

Large skull with articulated anterior third of skeleton: complete large skull, occluded lower jaw, pectoral girdle and anterior vertebral column, extending from the atlas to the tenth vertebra, with articulated anterior osteoderms. This specimen is very large and very well prepared and stored on a temporary pallet on wheels.

Two parallel rows of osteoderms cover the dorsal neural spines of the third to seventh vertebrae. These anterior osteoderms are medium sized (40-50 mm wide), smoothly or evenly convex, with an incipient large central boss over most of the surface, covered in extremely light ornamentation, and without a thin disc-like periphery. Very similar to the osteoderms of the holotype of *Bradysaurus baini*.

Cranial ornamentation is relatively distinct. The lateral surface of the quadratojugal has two or three thickened rugose curve lines of bosses. The maxilla has a well-defined and swollen high maxillary-lacrimal ridge, which forms a distinct, large, wide, posterodorsally elongated and oval maxilla boss. The maxilla is wide and curved and the upper jaw teeth point backwards posteroventrally. The posterior side of the distal parocipital process has a large process that is elongated dorsomedially. The bosses on the posterior margin of the cheek are small, round, as wide as high, and relatively pointed.

90. CGP/1/2269: (juvenile) skull and anterior third of skeleton: *Bradysaurus baini*.

Curated at the Council for Geoscience, Pretoria, comprising a single block containing the articulated anterior third of a skeleton, including juvenile skull (260 mm long), with oversized large orbits, cranial sutures clearly visible, and occluded lower jaw with small angular bosses (20 mm high). The interclavicle, right clavicle and scapulocoracoid are beautifully preserved and articulated with midline dorsal osteoderms present above the first six cervical vertebrae. This specimen is unquestionably a young juvenile *Bradysaurus baini* due to the horizontally flattened and backwards pointing maxillary teeth; the wide and bulbous posterior cheek bosses; the narrow, square postparietal; the square postfrontal; the low and

indistinct cranial ornamentation; and the lightly rugose anterior dorsal osteoderms. The cranial ornamentation on this juvenile specimen is very low and indistinct and probably still developing or enlarging with ontogeny. Interestingly, as is the case in the slightly larger, sub-adult specimen NHMUK R49426 (holotype of *Bradysaurus seeleyi*), this juvenile specimen has a swollen, but low and wide, maxillary-lacrimal ridge with a maxillary boss that is underdeveloped or indistinct and still growing on this juvenile individual. Positively identified as juvenile *Bradysaurus baini.*

91. MP 47/CMARL: *Bradysaurus baini*

On exhibit at the Victoria West museum, Northern Cape, South Africa, this specimen is on loan from the Council for Geosciences and comprises an articulated pareiasaur with a skull with lower jaw and most of the postcranium, including a partial pelvis, pectoral girdle, forelimbs and hind limbs, and most of the vertebral column, apart from the caudal vertebrae and lacking the manus and pes. This is a juvenile or sub-adult pareiasaur with inwards pointing upper jaw teeth and a large and swollen maxilla-lacrimal ridge that includes a large maxillary boss.

92. RMS 1096/CGP/1/810: *Bradysaurus baini*

Small unprepared juvenile skull, only 300 mm long at the midline, made of much plaster. The upper jaw teeth are posteroventrally oriented, very flat and almost horizontal and the maxilla is wide and curved. The bosses on the posterior cheek appear to be low and bulbous and the cheek is relatively small. Identified as *Bradysaurus baini*.

93. RMS 1258: *Bradysaurus baini* (tentative)

Partial snout. The maxillary teeth are seven cusped with very thick and distinct vertical ridges, one per cusp, on the labial surfaces, which is dissimilar to *Embrithosaurus*. The crowns of the maxillary teeth are posteroventrally directed and the maxilla is wide. Tentatively identified as *Bradysaurus baini*.

94. RMS 1296: *Bradysaurus baini* (tentative)

Partial skull and anterior pelvic girdle elements. Unprepared and severely dorsoventrally crushed. The skull is small and belongs to a juvenile individual. The partially preserved angular bosses are very small. The only diagnostic feature is that the maxillary teeth are posteroventrally directed, and unless this is due to the dorsoventrally compression, the specimen is probably *Bradysaurus baini*.

95. BP/1/347: *Bradysaurus baini*

Hundereds of unprepared postcranial fragments of ribs, vertebrae and long bones. Weathered partial distal femur, tibia, radii, tarsus, distal fibula, partial interclavicle,

partial scapula and pelvis, humeral fragments, right cheek, partial lateral side of the face, snout. The maxillary teeth are oriented horizontally, and have seven cusps with a very long central trident containing the central three cusps. There is a prominent maxillary-lacrimal ridge that is low and wide, but without a distinct maxillary boss. The bosses on the posterior cheek are very low and bulbous and indistinct.

96. BP/1/1574: *Bradysaurus baini*

Partial clavicle/interclavicle, partial scapula blade, distal tibia, proximal right humerus, both astragalocalcania, finger or toe with terminal claw, both distal radii, distal ulna, proximal tibia, lateral sacral ribs, proximal ulna, dorsal scapula blade, distal fibula, left quadratojugal. Articulated left femur, with partial acetabulum and proximal tibia and fibula, glenoid fossa, both iliac blades and lateral sacral ribs, hundreds of fragments of the fingers, toes, ribs and unidentified postcranial elements. Right cheek flange. Several large unprepared blocks containing articulated vertebrae with ribs. Humeri of a smaller individual, possibly not pareiasaurian. The proximal right humerus and partial shaft is severely twisted to about 70 or 80^0 (so either *Embrithosaurus* or *Bradysaurus*) with a very similarly sized and shaped delto-pectoral crest to the holotype of *Embrithosaurus*. The distal radius is ventrolaterally very stretched and extended. The proximal ulna has a very large olecranon process (50-60 mm high). The posterior cheek bosses are medium sized, round to pointed, including the corner boss. The dorsal scapula blade is relatively narrow. The iliac blades are a match to the morphology of *Bradysaurus baini*, they are overall deeply concave laterally and very curved, posteriorly they are straight and parallel to the midline, anteriorly they are laterally outwardly curved and everted upwards. Identified as *Bradysaurus baini.*

97. BP/1/1577: *Bradysaurus baini*

Large pes comprising four digits, a relatively complete, but unprepared large lower jaw in three fragments, and two large fragments of the snout. Both angular bosses are large and long, with a distinct and thick raised distal rim about half way down their length, producing a rugose boss reminiscent of a flattened pareiasaurian terminal claw. All teeth are severely damaged and sheared-off, but it is possible to note on one lower jaw tooth, that at least seven cusps were present. The largest cranial fragment is part of the upper left premaxilla, maxilla, lacrimal and external nares. The maxilla is strongly curved, with very flat, elongated, horizontal teeth and there is a distinct round boss on the maxilla, as well as a lacrimal boss complex, all forming a swollen maxillary-lacrimal ridge. This combination of features is only found in specimens of *Bradysaurus baini.*

98. BP/1/2233: *Bradysaurus baini*

Large, unprepared, partial snout fragment comprising the ventral portion of a right maxilla and anterior ventral cheek (jugal and quadratojugal), with occluded partial right lower jaw. The maxilla is very curved and the seven cusped elongated teeth are horizontal and inwards pointing and the anterior cheek is relatively small, extending only about 25^0 below the tooth row.

99. BP/1/4848: *Bradysaurus baini*

A specimen comprising two large, deeply weathered and eroded cranial fragments, together preserving about 60% of a skull, without lower jaw. On the better preserved left side, the posterior cheek bosses are sheared-off, but appear to be large and bulbous, the postorbital marginal boss is distinct, and the ridge between the lateral cheek and the dorsal skull table is very thick and swollen. Diagnostic of *Bradysaurus baini*, the postparietal is square and narrow and the distal paroccipital processes are large and swollen.

100. BP/1/4857: *Bradysaurus baini* (tentative)

A very large right acetabulum (190 mm anteroposteriorly long), without iliac blades or puboischiatic plate, missing a large ventral section. The anteroposteriorly elongated (oval) and very large size of the acetabulum, suggests identification as *Bradysaurus baini*.

101. BP/1/5414: *Bradysaurus baini*

Most of a large lower jaw in two pieces, unprepared, with all teeth eroded and with much matrix medially and a relatively small left angular boss considering the large size of the jaw. The angular boss has a very low distal rim and no rugose ornamentation at all and tapers distally to a relatively sharp tip. This lower jaw is virtually identical in size and overall morphology to the lower jaw of the holotype of *Bradysaurus baini,* especially the size and shape of the angular boss.

102. BP/1/5430: *Bradysaurus baini* (tentative)

Distal femur with articulated tibia, unprepared caudal vertebra, partial clavicle/interclavicle, three osteoderms, distal radius and articulated carpus, partial distal humerus, a few isolated dorsal vertebrae and a large block containing nine articulated dorsal vertebrae, acetabulum and proximal femur, right scapulocoracoid. The articulated tibia is ventromedially very stretched or extended as in *Bradysaurus* and *Nochelesaurus*. The three scutes are flat, smoothly and evenly convex, with very , very light and fine radial rugose ornamentation comprising thin ridges and very small circular pits, most similar to the anterior cervical osteoderms of the holotype of *Bradysaurus baini*.

103. BP/1/7054: *Bradysaurus baini*

Juvenile specimen with a very small skull (270 mm long) mediolaterally compressed and as a result buckled dorsally, poorly prepared, almost metasedimentary preservation (difficult to distinguish bone from matrix) and damaged, with partial lower jaw. Postcranium comprising dozens of unprepared, damaged long rib fragments, 14-15 unprepared, damaged dorsal vertebrae with 10-15 osteoderms attached, small dorsal right femur, partial right acetabulum and scapula blade, and few more unprepared large postcranial pieces. Identified as *Bradysaurus seeleyi* by Van den Brandt (2016), based on a small cheek (which is actually a feature of *Bradysaurus baini*) and small posterior cheek edge bosses (a juvenile characteristic) the skull has a low, small maxillary boss (therefore cannot be a specimen of *Nochelesaurus*) which would be larger and more prominent if the individual were fully grown and a low swollen maxillary-lacrimal ridge. The cheeks are small ($20\text{-}25^0$) and the bosses on the posterior edge of the cheek are bulbous and rounded (so not *Nochelesaurus*). The upper jaw teeth are oriented posteroventrally. The posterior projection of the major trochanter is relatively long (so not *Nochelesaurus*) and the proximal region of the internal trochanter is curved (so not *Nochelesaurus*). The proximal edge of internal trochanter emerges perpendicularly (90^0) out of adductor ridge, as in *Bradysaurus* and *Embrithosaurus*. The osteoderms are thin and disk-like, evenly covered with lightly rugose ornamentation ridges and small pits, with no distinct central boss and therefore closest to *Bradysaurus* in morphology.

104. BP/1/7082: *Bradysaurus baini* (tentative)

Three large fragments comprising weathered unprepared small vertebral remains and one large upper jaw tooth. The tooth is mesiodistally very wide, and therefore not high or elongated, and has nine cusps made of three marginal cusps mesially and distally and three central cusps in a shortened, but present, central trident. Most similar to the morphology of the upper jaw teeth of SAM-PK-K11638, a well preserved *Bradysaurus baini* skull from the Iziko South African Museum Cape Town. Tentatively identified as *Bradysaurus baini.*

105. BP/1/7213: *Bradysaurus baini*

Partial premaxilla and maxilla, left cheek fragment, partial right lower jaw with angular boss and numerous postcranial elements comprising an ulna, both femora, radius, humerus, partial scapulocoracoid, seven articulated dorsal vertebrae, several isolated dorsal vertebrae, five articulated posterior caudal vertebrae, rib fragments, fibula, atlantal arch or axial intercentrum, partial proximal humerus, partial scapula blade with cleithrum, partial interclavicle, lateral first sacral rib, left iliac blade, tibia, terminal claws and phalanges, carpus, tarsus.

Collected in 2012 and identified as *Embrithosaurus schwarzi* by Day (2013) based on a femur with an s-shaped, curved internal trochanter (Lee (1994, 1997a, *Embrithosaurus schwarzi* diagnostic feature)).
The angular boss is long and very pointed. The base of the scapula blade is very narrow. The posterior bosses on the left cheek are massive, large, mediolaterally very wide (60-70 mm) indistinct and bulbous and most similar to *Bradysaurus baini*. The left cheek appears to be very small, extending only 15-20^0 below the level of the (estimated) tooth row. The maxilla is wide and curved with posteroventrally directed teeth and with a wide, although weathered, large and swollen maxillary-lacrimal ridge and maxillary boss.
Both femora have very large internal trochanters that are high (45 mm), very wide and very strongly curved proximally, with a perpendicular proximal edge, which is very similar to the internal trochanter of the holotype of *Bradysaurus baini*. The external trochanter is dorsoventrally thin and posteriorly does not project far. The humerus is very large and the proximal and distal expansions are twisted to 50-60^0 apart. The delto-pectoral crest is massive and 100 mm wide. The intercondylar fossa is deep and the distal condyles extend distally far beyond the articular surface, appearing "forked". The ulna is very long and has a 40 mm high olecranon process. Identified as *Bradysaurus baini*.

106. BP/1/7870: *Bradysaurus baini* (tentative)

Unprepared cranial and postcranial fragments containing ribs, distal radius and osteoderms of juvenile pareiasaur. The distal radius is small. The cranial ornamentation is rugose and the two partially exposed osteoderms are thin, disc-like scutes, that are evenly and gently convex, with very light ornamentation comprising slightly raised ridges and small pits, most similar to the scutes of *Bradysaurus baini*.

107. BP/1/7886: *Bradysaurus baini*

A juvenile specimen comprising hundreds of rib fragments, tarsus, three articulated digits, fibula, articulated radius and ulna, tibia, puboischiatic plate, distal interclavicle, dozens of unprepared postcranial fragments. Cranially, most of the left quadratojugal is preserved, with four small, rounded, bosses on the posterior margin and some lateral ornamentation. Tentatively referred to *B. seeleyi* by Van den Brandt (2016) on the basis of the small and rounded bosses on the posterior edge of the cheek, these bosses are consistent with the morphology present in other juvenile *Bradysaurus baini* specimens studied.
The almost complete puboischiatic plate is most diagnostic as it is dorsoventrally very flat and low and mediolaterally wide, producing a shallow u-shape in anterior or posterior view, it is anteroposteriorly slightly longer than mediolaterally wide. Since this is a juvenile specimen, precise measurements will not be very useful. The

midline pelvic symphysis (keel) is dorsoventrally relatively thin or low, as seen in *Bradysaurus baini*, and not as thick as the condition in *Embrithosaurus*.

108. BP/1/7953: *Bradysaurus baini*

Partial puboischiatic plate of the pelvis, distal humerus, proximal femur, partial left iliac blade, several large unidentified and unprepared postcranial fragments, partial left cheek flange and a few cranial fragments. The bosses on the posterior edge of the quadratojugal are large, wide and bulbous and the cheek is mediolateraly wide, most similar to *Bradysaurus* and *Embrithosaurus*. The lateral pubic process is massively developed, similar to *Bradysaurus* and the left iliac blade has three partial lateral sacral ribs attached with the second rib as the largest and the morphology of the blade matching that of *Bradysaurus* (anteriorly laterally curved outwards and vertically everted). Identified as *Bradysaurus baini*.

109. BP/1/8020: *Bradysaurus baini*

Six vertebral fragments preserving five to six partial, unprepared centra, two partial neural spies and two diagnostic osteoderms. One osteoderm is thick, almost as high (30 mm) as wide (40 x 30 mm wide), stubby, bulbous, very strongly convex, ovoid, with a hint of an incipient central boss, but eroded and damaged. The other is very flat (only 12-15 mm high) and disc like, smoothly or evenly gently convex, ovoid (50 x 35 mm wide) and covered in light ornamentation consisting of thin, rugose, radial ridges, very similar to the posterior dorsal osteoderms of the holotype of *Bradysaurus baini*

110. FMNH Field no 29: *Bradysaurus baini*

Partial skull (snout, left cheek, left supratemporal) and four articulated vertebrae. Very swollen maxillary-lacrimal ridge, including a distinct maxillary boss, on a maxilla that is very curved horizontally and wider than the tooth row by up to 20 mm anteriorly. The upper jaw teeth are horizontal and point backwards and are not visible in lateral view. There are large anterolateral nasal tabs, which are larger than the anteromedial and posterior nasal tabs. The frontal central boss is relatively small. The cheeks are small, extending only 20-25^0 below the tooth row. The distal paroccipital process of the opisthotic is very typical of *Bradysaurus baini*, 85 mm anteroposteriorly long, with a swollen posterior, dorsomedial, knob-like process, that extends posteriorly 25 mm. The left cheek has discrete, small, lateral bosses, made of thickened rugose ridges, two positioned posteriorly and two positioned anteriorly.

111. FMNH Field no 49: *Bradysaurus baini*

Large unprepared, weathered, partial skull made of five large fragments and a partial distal scapula blade. The upper jaw teeth point relatively inwards and are directed posteroventrally as in *Bradysaurus baini*. The maxillary boss is present but damaged and partially worn off. The maxilla is curved and wide and exceeds the tooth row by 10-20 mm in width.

112. FMNH UC 1525: *Bradysaurus baini*

In situ, semi-prepared skeleton on a large pallet with wheels, stored in the "oversize" collection room of the Field Museum of Natural History, Chicago, with separate partial skull and lower jaws stored in the main collection facility.

The pelvis is consistent with identification as *Bradysauru baini* on most features and measurements: The anterior process of the iliac blade is wide (30 mm); anterior iliac blades not vertical but upturned by 45^0; posterior blades are oriented parrellel to midline, anterior blades laterally bent outwards to 45^0; the neck of the ilium is oriented only about 30^0 above the horizontal; the puboischiatic plate is wide (300 mm anteriorly, 320 mm posteriorly) especially between the blades (190 anteriorly, 210 mm posteriorly) indicating a wide puboischiatic plate, with flat and wide (not narrow and concave) dorsal surface between the blades. The left scapula blade is short and distally very flared to 200 mm wide.

Osteoderms are typical of *Bradysaurus baini*: on the 5^{th} to 8^{th} vertebrae they are small (30-40 mm wide) smoothly and evenly convex, with an indistinct raised central portion of large boss, and with ornamentation comprising very narrow, scrappy, straight radial ridges, lacking in rugose, tab-like processes.

The major trochanters of the femora are very weak, only 5-10 mm posteriorly projecting. Importantly the left humerus shows the proximal and distal expansions are nearly perpendicular (80^0) to each other.

About 90% of the skull is fabricated from plaster and only small portions of the right maxilla and right cheek are actually preserved, which shows a maxillary boss but with vertically oriented upper jaw teeth on a vertical, thin maxilla, which is not usually seen in specimens of *Bradysaurus baini*. Identified as *Bradysaurus baini* on the majority of the features and measurements of the postcranium, despite the vertical upper jaw teeth.

113. FMNH UC 1526: ***Bradysaurus baini***

Sub-adult sized elements: vertebrae, both scapulae, humerus, ulna, both radii, both ilia, puboischiatic plate, both femora, a tibia, posterior end of mandible, fragments.

The pelvis shows features of *Bradysaurus baini*: anteroposteriorly long (290 mm), with a long, flat, posterior section; mediolaterally wide and flat puboischiatic plate (320 mm wideposteriorly); iliac blades are oriented parallel to the midline; median pubic process does not extend anteriorly far; and iliac blades with a very thick anterior process (over 20 mm wide). The internal trochanter on the femur, projects ventrally very far, 50 mm from the femur and is very curved and the external trochanter extends about 10 mm posteriorly. The proximal and distal planes of the humerus are nearly perpendicular, at 70^0 apart. Sub-adult individual status is confirmed as the olecranon process is not well developed, and the proximal articular surface is not well delimited proximally on this small specimen.

114. FMNH UC 1533: *Bradysaurus baini* (tentative)

Complete mounted skull and skeleton on exhibit at the Field Mueum of Natural History, Chicago.

The anterior iliac blades are not vertically oriented and are instead everted or turned upwards about 30^0 on the left and 50 degress on the right, and the posterior blades are parellel to the midline. The anterior processes are also curved laterally outwards by 30-45^0 off the midline, all features of *Bradysaurus baini*. The puboischiatic plate is very wide (400 mm anteriorly, 350 mm posteriorly) and dorsally between the blades (180 mm anteriorly, 200 mm posteriorly), all features of *Bradysaurus baini.* The median pubic process is large and distinct with deep notches laterally.

The proximal and distal expansions of the humeri are 80-90^0 apart and the intercondylar fossa is deep, 30-45 mm, most similar to *Bradysaurus baini.*

The internal trochanter of the femur is almost perfectly straight (as in *Nochelesaurus*) and only very slightly curved proximally on both femora. This is most similar to the morphology seen in *Nochelesaurus* and to a lesser extent in *Embrithosaurus*. However, the internal trochanter is very high, extending 55 mm out of the femoral shaft (different from the low condition in *Nochelesaurus*). The major trochanter is thick and large and projects 20 mm posteriorly, similar to *Embrithosaurus*.

Cranially there is a large and swollen maxillary-lacrimal ridge with a large distinct maxillary boss on the right side. The cheeks are very large, extending about 30^0 on the left and 40^0 on the right, below the tooth row, similar to *Embrithosaurus*. The angular bosses are very large and very long as in *Embrithosaurus*. The cheeks are mediolaterally narrow as in *Embrithosaurus*. The upper jaw teeth are vertically oriented and only very sligthy posteroventrally directed as in *Embrithosaurus* and *Nochelesaurus*. Bosses on the posterior edge of the cheek are large and bulbous as in *Embrithosaurus* and *Bradysaurus*. The skull is therefore most similar to

Embrithosaurus. However, I tentatively assign this specimen to *Bradysaurus baini*, based on the morphology of the pelvis.

115. FMNH UR 2439: *Bradysaurus baini*

Proximal femur, distal portion of another femur, distal humerus in articulation with proximal ulna, radius in articulation with several carpals, manus. The proximal femur has a large, round, curved, flattened proximal internal trochanter, referable to *Bradysaurus baini*.

116. FMNH UR 2461: *Bradysaurus baini* (tentative)

Skull fragment with cranial ornamentation, and a large right glenoid cavity. The large right glenoid cavity has a massively large supraglenoid buttress (110 mm long, 60 mm wide) above the articular surface of glenoid and the subscapular groove on the medial surface is positioned 60 mm behind the anterior edge of the scapula (which is quiet far as in *B.baini*) and is 85 mm long, 30 mm wide, filled in with matrix, but about 20 mm deep. The anterior border of the scapula is deeply concave on the lateral surface, as in *B.baini.*

117. FMNH UR 2476: *Bradysaurus baini*

A pareiasaur comprising a left foot (five digits), a right foot (four digits), right tarsus, proximal left humerus, proximal radius, proximal left femur, and another pareiasaur comprising an articulated left femur, tibia, fibula and tarsus.

The articulated left femur, tibia, fibula and tarsus, show the femur's distal flange reaching 50 mm beyond the articular surface (as in *Nochelesaurus*), but the internal trochanter is flattened, very curved, "coin-like", highly raised (50 mm high) as in the holotype of *Bradysaurus baini*. The distal articular surface of the tibia is extremely obliquely angled at the smaller articular surface. Identified as *Bradysaurus baini*.

Note, the isolated proximal left femur, belongs to a specimen of *Nochelesaurus* (see 55. FMNH UR 2476 *Nochelesaurus alexanderi* above).

118. FMNH UR 2484: *Bradysaurus baini*

String of six large dorsal vertebrae with attached osteoderms. The dorsal surface of the neural spines are diamond shaped, large, rugose, and with random pitting. The osteoderms are relatively flat and slightly convex dorsally, with the central 50% slightly raised to form an incipient central boss. The periphery of the osteoderms, beyond the raised central portion, has sharp, short, very thin, raised radial ridges. Some osteoderms have a raised central region with a large (5-8 mm wide) hollow in the middle. Identified as *Bradysaurus baini*.

119. NHMUK R1970: ***Bradysaurus baini***

Historically important specimen with cranial material comprising most of the palate and braincase as a single fragment and a large partial snout with occluded lower jaw as another fragment. Postcranial material comprises most of the dorsal vertebrae. The top half of the skull is completely weathered away with only the palate, lower jaw and maxilla with some upper and lower jaw teeth remaining. NHMUK R1970 was identified by Lee (1994, 1997a) as *Bradysaurus baini,* noting that the specimen does not differ from the holotype of *Bradysaurus baini* (NHMUK R1971) in any significant way. In his assignment of NHMUK R1970 to *Bradysaurus baini,* Lee is correct, particularly as the maxillary teeth of the specimen are horizontally oriented and backwards pointing, a unique trait of *B. baini*. The palate is very similar to the holotype of *Bradysaurus baini* in all dimensions and features.

120. NHMUK R1971: *Bradysaurus baini* (Seeley 1892) (Holotype) (see chapter eight)

121. NHMUK R4066: *Bradysaurus baini*

Very complete postcranium including most of a skeleton, hindlimbs, forelimbs, skull fragments and some pedal elements. The right femur is most identifiable as *Bradysaurus baini* as the internal trochanter is proximally very wide, tall and high, and very curved and rounded. The external trochanter is large and prominent and the shaft of the femur is convexly outwardly bulged preaxially and postaxially. Identified as *Bradysaurus baini*.

122. NHMUK R49426: *Bradysaurus seeleyi* (Haughton and Boonstra 1929) (Holotype) (see chapter eight)

123. SAM-PK-745: *Bradysaurus baini*

Three large articulated vertebrae, with two intercentra. These very large vertebrae are posterior dorsal pareiasaurian veretbrae, immediatelly anterior to the sacrum, probably the 17^{th} to 19^{th} vertebra. The neural spines are weathered off and the postzygapophyses are large and pareiasaurian in morphology. The intercentra are similar to those of the holotype of *Bradysaurus baini*: flattened disks, mediolaterally wide, and upward curving laterally, with fine ventral rugose ornamentation or uneven cortical surfaces. With little information available regarding the morphology of the intercentra of *Embrithosaurus* and *Nochelesaurus*, I tentatively refer this specimen to *Bradysaurus baini*.

124. SAM-PK-3533: *Bradysaurus baini*

Very large pareiasaur specimen comprising dozens of isolated, damaged and unprepared vertebrae, dozens of rib fragments, partial left acetabulum with iliac

blade, partial right acetabulum, caudal vertebrae, proximal left femur, right tibia, and an additional +- 150 broken postcranial fragments that according to the museum catalogue contains parts of the right and left humerus, ulna radii and a partial pes. This specimen is in absolutely desperate need of repair.

The left major trochanter is moderately sized, measuring 10 mm posteriorly, with a deep notch proximally on the postaxial side on the femur, and a slight notch distally on the postaxial flange, consistent with the morphology of *Bradysaurus baini.* The left internal trochanter is sheared-off, but it proximally very wide, 35-40 mm and appears to represent the remains of a strongly curved, wide internal trochanter (as in *Bradysaurus*).

The partial pelvis is anteroposteriorly very long, measuring 400 mm from the anterolateral edge of the lateral pubic process of the puboischiatic plate to the posterolateral corner of the ischial buttress. The dorsal surface of the puboischiatic plate is very wide and flat as in *Bradysaurus* (not narrow and concave as in *Embrithosaurus*). The left iliac blade is thick and relatively straight and vertical (slightly concave) and anteriorly the blade curves laterally outwards by 30-40^0 off the midline and everts upwards, only slightly.

The tibia is wide (75 mm) at the narrowest section of the shaft and the proximal articulation surfaces are off the same plane by only 30-40^0. Distally, the tibia is ventromedially expanded and projecting, ventrolaterally upturned and mediolaterally wider (at 135 mm) than *Embrithosaurus*. Identified as *Bradysaurus baini.*

125. SAM-PK-3718: *Bradysaurus vanderbyli* (Haughton and Boonstra 1929) (Holotype) (see chapter eight)

126. SAM-PK-4346: *Bradysaurus baini*

Atlas, axis, and the third anterior cervical vertebrae articulated, several anterior and posterior caudal vertebrae, dozens of isolated centra, neural spines and vertebral fragments, six articulated dorsal vertebra with two osteoderms attached, three articulated dorsal vertebra, partial clavicular arm, both acetabula, dozens of rib fragments, partial tibia, a crushed distal femur, distal fibula, several large unidentified, postcranial fragments and a sub-adult sized partial skull comprising partial left and right cheeks, dorsal skull table, partial snout and lower jaw fragments.

Two small osteoderms are stud-like (as high as wide), 20-25mm wide, convex, with very little ornamentation and are not diagnostic as they are found in at least *Embrithosaurus* and *Bradysaurus*. The maxilla has elongated, seven cusped teeth that are horizontally backwards pointing, emanating from a wide and curved maxilla

(as in *Bradysaurus*) and the bosses on the posterior edge of the cheeks are medium sized, round and pointed, with a very distinct, elongated, corner boss. Although it is challenging to be certain of the morphology of this fragmentary specimen, the cheeks do appear to be relatively small and the partial angular bosses appear to be medium to small (as in *Bradysaurus*). Identified as *Bradysaurus baini.*

127. SAM-PK-4347: *Bradysaurus baini* (tentative)

Material comprising dorsal left ulna, distal left femur, left tarsal element. Partial large adult skull (+-50% preserved) and lower jaw, lacking occiput and palate, made of about dozen large fragments with much white plaster.

Identified as *Bradysaurus baini* by Haughton and Boonstra (1929a) this specimen has a small maxillary boss (so cannot be *Nochelesaurus*) and an obvious, swollen, low maxillary ridge; the maxilla is very wide and curved and carries horizontally oriented, backwards pointing teeth, as in *Bradysaurus*.

Both angular bosses are very large, elongated, and bulged, characterised by a swollen rim proximally (not midway), tapering off distally to a very blunt, flattened tip (reminiscent of a pareiasaurian terminal claw) and they are much larger than those of the holotype of *Bradysaurus baini*. The posterior cheek is very wide (60 mm) and carries low, bulbous, indistinct bosses on the right, as in *Bradysaurus baini*, and laterally has four, small, circular, distinct bosses (as seen in *Nochelesaurus* and *Embrithosaurus*). The cheek appears to be very small (a *Bradysaurus* feature) extending less than 20^0 below the tooth row, but it is difficult to accurately measure. Interestingly, the corner boss of the left cheek is much longer, more distinct and pointier (similar to *Nochelesaurus*) than on the right. Overall, the cranial ornamentation is very distinct, more similar to *Nochelesaurus* than *Bradysaurus*. Above the articulation surface, the dorsal left ulna has a large olecranon process (25 mm high, 20 mm anteriorly projecting) formed by concave curvatures laterally and medially that create a well-defined, enclosed or hooked socket. The lateral condyle of the femur extends very far (65 mm) past the distal edge of the medial condyle, similar to *Nochelesaurus*. Although this specimen shows features of both *Bradysaurus* and *Nochelesaurus*, I agree with the previous authors and tentatively assign the identification to *Bradysaurus baini* based on the majority of the features.

128. SAM-PK-4350: *Bradysaurus baini*

Several articulated vertebral blocks, partial right iliac blade with lateral sacral ribs, three digits in a plaster jacket, two distal scapula blades, small right humerus, clavicular and interclavicular parts, some unidentified postcranial fragments and a very small skull with occluded partial right lower jaw and, separately, two left lower jaw fragments.

Referred to *Brachypareia rogersi* by Boonstra (1934a), the skull is of a very small juvenile individual (250 mm long at the midline, 265 mm long laterally) with a disproportionally large orbit (confirming its juvenile nature) and with many cranial sutures unfused and visible. It is very low, wide, broad and flat in appearance with an obviously bulged maxilla as a result of a thick maxillary-lacrimal ridge and a low, still developing, maxillary boss. Notibly, the posterior dorsal surface of the skull is deeply weathered such that the two large equally sized cavities are present and the rest of the skull is also weathered. The maxilla is strongly curved and the upper jaw teeth severely backwards pointing and almost horizontally aligned. The angular boss on the lower jaw is very small (juvenile feature) and broken and would have been about 25-30 mm long if in tact. The bosses on the posterior edge of the cheek are, wide, low and bulbous. Although damaged, there appears to be large posterior processes on the posterior edge of the distal paroccipital processes of the opisthotic. The postfrontal is roughly square, slightly longitudinally elongated, and posteriorly curved medially (as in *Bradysaurus* and *Nochelesaurus*).

The right humerus has proximal and distal expansions greatly twisted to approximately 70^0 from the same plane (as in *Embrithosaurus* and *Bradysaurus*), the proximal expansion is very wide and the distal condyles project far below the radial and ulnar articulation surfaces (appearing "forked"), all features of *Bradysaurus*. Identified as a very young juvenile *Bradysaurus baini*, in morphology, size, appearance and anatomical features, this skull is remarkably similar and almost identical to CGP/1/2269, a juvenile *Bradysaurus baini* from the Council for Geosciences, Pretoria.

129. SAM-PK-4351: *Bradysaurus baini* (tentative)

Several blocks of articulated dorsal vertebrae, left clavicle/interclavicle, partial right scapulocoracoid, partial radius, 50-75 small to large broken postcranial fragments in need of re-assembly and repair, three large cranial fragments preserving parts of the left and right cheek and the dorsal skull table.

The sub-adult sized postcranium is too poorly preserved, unprepared, damaged and broken to be anatomically useful, and has much historic glue and broken plaster joins. The cranial fragments reveal posterior cheek bosses that are bulbous and large on the squamosal, but there are four small to medium sized, rounder, more distinct and more pointed bosses on the quadratojugal with no bosses on the lateral quadratojugal but only rugose ridges, and with a cheek that is relatively thick (most consistent with a sub adult *Bradysaurus*). Tentatively assigned to *Bradysaurus baini*, as per Boonstra's (1934a) assignment and the current museum catalogued species assignment.

130. SAM-PK-4999: *Bradysaurus baini*

Sub-adult pareiasaur comprising partial midline interclavicle, parts of two different puboischiatic plates (one large plate including the right acetabulum, and one small plate from another individual), large left lateral sacral rib, left fibula with distal tibia attached, right tibia, four articulated anterior caudal vertebrae, small partial proximal left humerus, lower jaw, maxilla, and about two dozen small to large, unidentified postcranial fragments.

The large puboischiatic plate preserves the right side and only a portion of the left and definitely belongs to a specimen of *Bradysaurus baini* as the acetabulum is dorsoventrally flattened and anteroposteriorly elongated, the plate is anteroposteriorly long at the midline (295 mm), anteriorly wide (360 mm), posteriorly wide (320 mm), wide, and it is low and flat dorsally and ventrally. The midline ventral keel that is dorsoventrally not very thick or high (only 75 mm high), and is mediolaterally narrower than the condition in specimens of *Embrithosaurus*, covering a minority of the wide, flat, plate ventrally. The keel extends dorsolaterally upwards at a shallower angle than the condition in specimens of *Embrithosaurus*. The median pubic process is damaged, but is certainly very short, barely projecting beyond the anterior rim of the lateral processes of the pelvis.

The small partial proximal left humerus is also consistent with *Bradysaursus baini* (this is a sub-adult individual) with a relatively wide delto-pectoral crest. The tibia is consistent with *Bradysaursus baini* as the angle between the lateral and medial facets of the proximal articulation surface of the tibia is small (40^0). The angular bosses are small (sub-adult), consistent with *Bradysaurus baini*, and the lingual surface of the dentary teeth have a low, swollen bulge. The maxilla shows on the left a well-defined swollen, low maxillary-lacrimal ridge continuous with a indistinct lacrimal boss complex, without a distinct maxillary boss present (sub-adult) and the maxillary teeth are only moderately backwards pointing, at about 45^0 off the vertical or horizontal plane.

131. SAM-PK-5002: ***Platyoropha broomi* (Haughton and Boonstra 1929) (Holotype) = *Bradysaurus baini* (see chapter eight)**

132. SAM-PK-5011: *Bradysaurus baini*

Fibula, median stem of interclavicle, proximal right tibia, partial right scapulocoracoid, tarsal, right femur, and a few large unidentified fragments.

There are no diagnostic features on the interclavicle, fibula or scapulocoracoid, but the femur (which is severely dorsoventrally crushed and shortened) is identifiable to *Bradysaurus baini* as a result of the proximal region of the internal trochanter which is very strongly curved and rounded, with a concave preaxial (anterior) side and a

convex postaxial (posterior) side. The proximal edge of internal trochanter emerges perpendicularly (90^0) out of the femur and extends far ventrally (50 mm) beyond the femur; there is a very short anterior process/projection on the distal portion of internal trochanter.

Shared femoral features of *Bradysaurus* and *Embrithosaurus* include a moderately distally extended lateral condyle, beyond the distal edge of the medial condyle (30 mm) compared to the much longer condition present in most specimens of *Nochelesaurus* (70 mm); and an anteroposteriorly wider femur across the distal condyles of 200 mm; compared to the narrow condition of *Nochelesaurus* specimens. The postaxial shaft of the femur is damaged and does not reveal much anatomical information. Identified as a specimen of *Bradysaurus baini.*

133. SAM-PK-5013: *Bradysaurus baini*

Partial pelvis comprising two large lateral sacral ribs, two acetabula, partial posterior puboischiatic plate with midline ventral keel, weathered right iliac blade, distal left femur, proximal left tibia, two other postcranial fragments. The partial posterior puboischiatic plate presents a wide, flat dorsal surface anteriorly and posteriorly at least 150 mm wide (wider than most specimens of *Embrithosaurus*); the ventral keel is narrow, forming a minority of the ventral surface of the plate, and it is dorsoventrally not very thick, measuring only 70-80 mm high. The lateral condyle of the femur extends distally only 30 mm past the distal edge of the medial condyle. Identified as *Bradysaurus baini.*

134. SAM-PK-5597: *Bradysaurus baini*

Extremely broken and fragmentary pareiasaur comprising **+-**100 large, unprepared, damaged, physically extremely dirty and dusty fragments comprising the proximal and distal femur, acetabulum, cranial fragments, another proximal femur, partial left iliac blade, a block containing seven articulated vertebrae, distal fibula, distal tibia, partial left scapulocoracoid, and several vertebral fragments and unidentified postcranial fragments. This material is an extremely poor state of preservation and it is completely unprepared, extremely fragmentary and physically extremely dirty. Most of the copious material is unusable in the current state, which has clearly not been altered since field collection.

However, an internal trochanter with a strongly curved proximal end appears to be present on the proximal femur preserved, and a maxilla fragment shows a wide, curved maxilla with teeth directed obliquely about 45^0 inwards with a very well developed posterodorsal maxillary boss (50 mm long, 20 mm wide, 20 mm high) on the left maxilla, just above the large maxillary foramen, on the lateral side of the external naris. Identified as *Bradysaurus baini.*

135. SAM-PK-5624: *Bradysaurus baini*

SAM-PK-5624 is a very complete, articulated, mounted *Bradysaurus* skeleton on permanent display at Iziko South African Museum, Cape Town (2019) comprising a skull (lacking snout) and lower jaw, presacral and sacral vertebrae, six anterior caudal vertebra, nine posterior caudal vertebra, shoulder girdle, both humeri, radii and ulnae, pelvic girdle, both femora and tibia, left fibula, both astragalocalcania, left carpal.

Currently assigned to *Bradysaurus seeleyi* by Boonstra (1934a), this is very complete specimen of a *Bradysaurus baini*, identified by the: wide, horizontally curved maxilla that facilitates inwards pointing upper jaw teeth; a very large, knob-like posteriorly projcting process on the parocipittal process of the opisthoic, the posterior cheek bosses are not large or bulbous, they are small, rounded, as wide as high, and more pointed and distinct and the corner boss is small but elongated, conical and almost horn-like and with a discrete lateral cheek boss. The maxillary-lacrimal ridge is wide and prominent and distinct, with possibly a maxillary boss sheared-off. The angular boss is large. The cheek flanges are small (20-25^0). The skull is certainly mediolaterally compressed and as result the dorsal cranial bones are noticabley buckled, bent, rippled and deformed. The ulna has a large olecranon process (33-36 mm high both sides) above an anterodorsal limiting ridge or hook, lacking olecranon crests; the humerus lacks the tubercle present in some specimens *Nochelesaurus*, the scapula blade is short and wide. Pelvic features include: the anterior process of the preserved right iliac blade is everted to about 45^0 upwards and is curved strongly laterally outwardly to orient 30-40^0 from the midline; the puboischiatic plate is very wide anteriorly and is long anteroposteriorly and the pubic symphysis is thin or low. The caudal vertebrae have “L shaped” backwards pointing lateral projections, as in the holotype of *Bradysaurus baini*. Referred to *Bradysaurus baini.*

136. SAM-PK-8941: *Bradysaurus baini* (tentative)

Sub-adult skull with occluded lower jaw, distal radius, carpus and manus in plaster jacket, both humeri, tarsal and pes in a plaster jacket, left acromion process and scapula blade, both proximal ulnae, one distal ulna, several dorsal and caudal vertebrae, interclavicle, left clavicle with articulated proximal scapula blade, distal radius, partial scapulocoracoid, distal femur, rib fragments, and 25-30 unidentified fragmentary postcranial fragments.

Identified by Haughton and Boonstra (1929a) as *Bradysaurus vanderbyli*, based on smooth posterior cheeks, this specimen is severely distorted, crushed, damaged and unprepared and the true anatomy of most elements is difficult to determine.

The skull is obliquely dorsoventrally crushed and measures 330 mm longitudinally at the midline and about 360 laterally and is therefore a sub-adult. The angular boss is

remarkable small and short only 30 mm long, and blunted distally as a result of dorsoventral crushing. The maxillary teeth are distorted and flattened on the right, and on the left appear to be inwardly oriented at about 45^0.

The posterior edge of the cheeks appear very smooth as a result of weathering and were most probably large, bulbous and indistinct based on the worn-off surfaces (so this not a specimen of *Nochelesaurus*). Even taking into account the dorsoventral crushing, the distal portions of the paroccipital processes of the opisthotics are remarkably small, possibly the result of the juvenile nature of the skull, but they do show a notacable, knob-like posterior process. The maxilla is swollen and has a low, wide, maxillary-lacrimal ridge and perhaps a low maxillary boss. The cheeks are relatively large, $25\text{-}30^0$ approximately.

The expansions of the humerus are twisted to about 50^0 apart. The scapula blade base, just above the acromion process, and at the mid-level, is relatively wide. The scapula blade is short (sub-adult specimen) and is wide and flared dorsally. The olecranon process of the ulna is very large, considering this individual is not yet fully developed. It is high (40 mm) above the enclosed articulation surface. Tentatively identified as *Bradysaurus baini*.

137. SAM-PK-9095: *Bradysaurus baini*

Nearly complete skull of a juvenile pareiasaur with occluded lower jaw, in two large fragments, with a partial interclavicle median stem.

This specimen was referred to *Brachypareia rogersi* by Boonstra (1934a) using general features common to most *Tapincoephalus* Assemblage Zone pareiasaurs, and to *B. baini* by Lee (1994, 1997a) and Van den Brandt (2016). This skull is dorsoventrally and obliquely crushed and appears low and wide and is extremely crudely prepared and therefore challenging to accurately study. Not surprisingly for a small, juvenile skull, the angular boss is very small (20 mm long, 15mm mediolaterally wide at the thickest). The cheeks appear to be very small on the left (20^0) and very large on the right (40^0), the exaggerated size on the right the result of dorsoventral oblique crushing and displacing the right cheek lower (and thereby enlarging it) than it should be. For such a small, presumably juvenile skull, the maxillary-lacrimal ride is very well developed and is large, high, wide and swollen. The poor preservation and preparation excludes positive identification of a distinct maxillary boss. The bosses on the posterior edge of the cheek are large, bulbous and indistinct. The upper jaw teeth are directed horizontally backward and there is a posteriorly projecting knob on the parocipital process. Positively identified as a juvenile *Bradysaurus baini*.

138. SAM-PK-9104: *Bradysaurus baini*

Left side of a very large skull, distal left and right femur, distal right tibia, proximal left tibia, large tarsus, pes in white plaster jacket, distal ulna, partial right scapulocoracoid, partial left scapulocoracoid and clavicle, fibula, seven articulated vertebrae. Also preserved is a separate smaller individual, comprising a left maxilla, cheek and occluded lower jaw, several cranial fragments, small tarsus and a small proximal left femur.

The large skull is very poorly preserved, damaged and unprepared. It is extremely large, one of the largest if not the largest specimens I have studied in this project, measuring 410 mm long at the midline and 430 mm long laterally. Sutures of the postfrontal are identifiable on both sides, and it is roughly square, slightly longitudinally elongated, and curves and extends posteromedially (as in *Bradysaurus* and *Nochelesaurus* only). This specimen was referred to *Bradysaurus baini* by Boonstra (1934a), but to *Nochelesaurus alexanderi* by Van den Brandt (2016) on the basis of pointed, flattened posterior cheek bosses. However, the bosses on the posterior edge of the cheek are not well preserved and it is very difficult to identify their morphology. They can be interpreted as relatively distinct, horizontally flat and pointed, or as rounder and larger and less pointed. They are not certainly not bulbous or indistinct. The cheek is unusually very large for a specimen of *Bradysaurus baini*, extending about 35-40^0 below the tooth row. The very large maxillary-lacrimal ridge is only partially preserved and damaged is a very swollen. The upper jaw teeth point directly horizontally backwards and even a little upwards a little as a result of distortion. The paroccipital process of the opisthotic is not well exposed, but shows at least a medium sized posterior, dorsomedially elongated, knob-like process. The postparietal is narrow, as in *Bradysaurus baini* and *Embrithosaurus*.

The large distal femur is extremely large and robust, and the lateral condyle extends distally not very far at only 40 mm past the medial condyle. Identified as a very large adult *Bradysaurus baini*.

The small proximal left femur has a large internal trochanter, which is proximally very strongly curved. The distal portion is not preserved. The major trochanter is also prominent and large, extending posteriorly almost 10 mm, even though it is partly worn and eroded, and is anteroposteriorly quite thick. It has a large notch proximal to it and a shallow notch distally. The small partial skull has maxillary teeth that are posteoventrally directed and also are unusually very large cheek, extending about 35-40^0 below the tooth row. The bosses on the posterior edge of the cheek are small, low and bulbous, with two distinct, small lateral bosses. The cheek is very thick. Identified as a juvenile *Bradysaurus baini*.

139. SAM-PK-9121: *Bradysaurus baini*

Sub-adult sized skull with articulated atlas and axis and separate partial lower jaw, tarsus, distal tibia, distal fibula and a 10-15 small unidentified poscranial fragments.

This specimen was referred to *B. seeleyi* by Boonstra (1934a). The skull is very wide, certainly dorsoventrally crushed as the jugals are severely and unnaturally buckled and bulged laterally outwards. The dorsal snout is made of plaster, but ventrally and on the left, the snout is preserved. The left maxilla shows a low, wide, maxillary-lacrimal swelling or ridge with no distinct maxillary boss. A more distinct maxillary boss would probably develop with ontogeny. The corner boss of the cheek is large and followed dorsally by medium sized (not very large) bulbous, indistinct bosses, which will probably become larger and more bulbous and indistinct with ontogeny. The lateral quadratojugal is very thick with small bosses and rugose ornamentation.

Diagnostically, the maxillary teeth are directed horizontally backwards or are medially inflicted (and a few teeth are even slightly upwardly oriented as a result of the dorsoventrally crushing). The eighth left upper jaw tooth reveals three central cusps on an elongated trident and two lateral cusps, indicating seven cusped teeth. The angular boss on the lower jaw is large considering the relatively small size of the angular jaw. It is swollen proximally and resembles a pareiasaurian terminal claw in shape and is slightly concave just distal to the swollen rim. Identified as *Bradysaurus baini.*

140. SAM-PK-9136: *Bradysaurus baini*

Distal left humerus, white plaster jacket containing partial articulated left hindlimb (distal fibula, tarsus and pes), a second white plaster jacket containing a partial right forelimb (distal radius, carpus, manus). The hindlimb and forelimb are not very diagnostic but the distal humerus is consistent with the anatomy of *Bradysaurus baini* in the following ways: the intercondylar fossa is very deep (45 mm), and both distal condyles extend moderately far beyond the radial and ulnar surfaces (45 mm). As seen in all co-occurring South African middle Permian pareiasaurian taxa, there is a distinct swollen ridge (intercondylar ridge border) on the dorsal distal margin of the humerus. I retain Haughton and Boonstra's (1930b) identification of *Bradysaurus baini* for this specimen.

141. SAM-PK-9142: *Bradysaurus baini* (tentative)

Extremely poorly preserved late sub-adult aged, unprepared and damaged pareisaur comprising a partial pelvis, partial scapulocoracoids, clavicle/interclavicle, left cheek

fragment, nasal cranial fragment, left femur, partial scapula blade, and 50-100 postcranial fragments.

In the current extremely poor state of preservation, preparation and storage, most of the material cannot be used for anatomical studies. The left femur is better preserved and has an internal trochanter with a gently curved proximal end that emerges at 90^0 from the shaft of the femur. The major tochanter is poorly developed and dorsoventrally thin. The distal scapula blade is 175 mm wide.The posterior cheek bosses are very smooth, low and bulbous. Tentatively identified as *Bradysaurus baini.*

142. SAM-PK-9143: *Bradysaurus baini*

Articulated hindlimb (pes, tarsus, tibia, fibula, femur) in a white plaster jacket in desperate need of repair and conservation, a second white plaster jacket containing an articulated partial forelimb (partial distal radius, ulna and manus), and a cranial fragment containing the basal tubera and occipital condyle. The individual elements that comprise the hindlimb and forelimb are mostly damaged, broken and disarticulated such that in the current state this material is not usable. I retain Boonstra's original (1932b, 1932c) identification of *Bradysaurus baini*, made when the material was likely in a much better state.

143. SAM-PK-9170: *Bradysaurus baini*

Partial large skull, partial left scapula blade, basal tubera and a few small cranial fragments. This is a very large individual. The partial skull is very poorly preserved, prepared and is severely distorted and damaged. It shows the remnants of a large maxillary boss or swollen maxillary-lacrimal ridge (30 mm wide, 50 mm posterodorsally elongated, 10-15 mm high) on the left side and the upper jaw teeth are inwards pointing. The scapula blade is extremely large, very wide at the base (135 mm) near the middle of the cleithrum, and at the distal end of the blade which is very curved anteriorly and posteriorly and flared to at least 230 mm in anteroposterior width. Identified as *Bradysaurus baini*.

144. SAM-PK-11487: *Bradysaurus baini*

Large left femur. This very large femur (425 mm long) has a postaxial shaft that is slightly convexly bulged, as in *Bradysaurus* and *Embrithosaurus.* The major trochanter is small, projecting posteriorly only a short distance (<5 mm) and thin in dorsoventral thickness (only 26 mm wide), a good match to the morphology of *Bradysaurus*. There is no notch separating the major trochanter from the postaxial flange distally (as seen in *Nochelesaurus* and *Bradysaurus)*. The lateral condyle extends distally relatively far (50 mm) beyond the medial condyle. The internal trochanter is positioned far away from the preaxial border, and proximally is

strongly curved, and so can only belong to *Bradysaurus*, with a short anterior projection distal to the proximal curve. The proximal edge of the internal trochanter emerges perpendicularly (90^0) out of the femur (as in *Bradysaurus* or *Embrithosaurus*) and is relatively high (50-55 mm). The adductor ridge is low due to erosion, and is wide and rugose and extends far distally, almost reaching the facet of the medial condyle. Identified as *Bradysaurus baini*.

145. SAM-PK-12014: *Bradysaurus baini*

Large skull with a partial lower jaw, and a right cheek flange and maxilla fragment from another individual. The large, wide, broad, low skull has a very wide (50 mm), swollen, posterodorsal (70-80 mm long) maxillary-lacrimal ridge that has a huge and distinct maxillary boss, positioned ventrolaterally each side, being 10-20 mm higher than the maxillary-larimal ridge. This specimen has the largest maxillary bosses observed of all specimens studied. On the right, the maxillary boss is very rugose and thickly ridged, a condition I have not seen before in any other specimen studied for this project. The postparietal appears to be narrow, but sutures are difficult to identify. The cheek is small, extending only about 20^0 below the tooth row. The maxilla is very wide and horizontally curved ventrally and the upper jaw teeth are mostly not preserved but appear to be horizontally oriented on the right. Bosses on the posterior cheek are not wide, low, bulbous or indistinct, instead thye are smaller, rounder, pointier and more distinct. The corner boss is round and forms a short conical structure, followed dorsally by two small, round, pointed bosses, about as wide as high as posteriorly extending, and finally a wider, rounder boss highest on the quadratojugal is present The cheeks are wide (50 mm). Identified as *Bradysaurus baini.*

146. SAM-PK-12048: *Bradysaurus baini*

Fragmentary snout (right premaxilla, maxilla and occluded lower jaw), six articulated caudal vertebrae with chevrons and a tarsus. This specimen was identified as *Bradysaurus baini* by Van den Brandt (2016). The upper jaw teeth are medially inflicted and nearly horizontally directed, and bear seven marginal cusps composed of a central elongated trident with three cusps and two lateral cusps either side with large spaces between the lateral cusps. The maxilla is ventrally very wide and horizontally curved, and laterally it is weathered and has the reminants of a wide, maxillary-lacrimal ridge and possibly a distinct maxillary boss. Identified as *Bradysaurus baini*.

147. SAM-PK-12090: *Bradysaurus baini*

Partial skull and lower jaw made of eleven large fragments. Completely unprepared, the snout, parts of both cheeks, part of the dorsal skull roof, both angular bosses of the lower jaw, and the occipital condyle are preserved.

Diagnostically, the upper jaw teeth are virtually horizontally oriented, with seven marginal cusps carried via three central cusps on a long trident and two lateral cusps further apart either side of the crown. Both maxilla are preserved and each have large, distinct round to pointed maxillary bosses (40 mediolaterally wide, 40-50 mm posterodorsally elongated, and 20-25 mm high). The corner boss of the posterior cheek is large, wide, low and bulbous, followed dorsally by a small distinct, rounded to pointed boss. The basal tubera of the basisphenoid are massive and robust (90 mm wide) and anteriorly constricted and with their posterior edges positioned far away (30-35 mm) from the posterior edge of the occipital condyle. Although damaged, the parocipital processes of both opisthotics have large swollen posterior knob-like processes (left side: 30 mm wide, 30 mm high, 30 mm posteriorly projecting). The angular boss is relatively small considering the large size of the adult skull, which is also the case in the holotype of *Bradysaurus baini*. It is long (50 mm) narrow (35-40 mm at the widest) and conical or horn-shaped as it tapers very gently distally after it's barely perceptible, mid-way, swollen rim and very pointed distally. Identified as a specimen of *Bradysaurus baini.*

148. SAM-PK-12115: *Bradysaurus baini*

Large skull and occluded lower jaw. Damaged, weathered, unprepared. Salient features of *Bradysaurus baini* include: a large maxillary boss or swollen posterodorsal maxillary-lacrimal ridge (35 mm wide, 20 mm high) continuous with the lacrimal boss complex; narrow postparietal bone (left side sutures identified); wide, low, bulbous posterior cheek bosses; distinct posterior knob-like process on the posterior edge of the distal opisthotics; lateral quadratojugal with straight rugose ridges, but without distinct bosses; relatively small cheeks only extends 25^0 below the tooth row; maxillary teeth oriented posteroventrally (45^0); angular boss small, elongated, swollen proximally, very pointed distal tip.

149. SAM-PK-12128: *Bradysaurus baini* (tentative)

Two cranial fragments preserving the posterior right cheek and dorsal skull roof. The posterior cheek bosses are all large, wide, low, bulbous and indistinct and the lateral quadrtojugal only has rugose ridges and no distinct bosses. Only *Bradysaurus* and *Embrithosaurus* have these kinds of posterior cheek bosses, but *Embrithosaurus* is usually accompanied by distinct lateral cheek bosses. Tentatively identified as *Bradysaurus baini*.

150. SAM-PK-12133: *Bradysaurus baini*

Cranial fragment and left iliac blade with two lateral sacral ribs. The iliac blade is unquestionable *Bradysaurus baini* as its morphology precisely matches the morphology of the holotype: the posterior blade is very straight, upright and directed parellel to the midline; anteriorly the blade is severely laterally outwardly

bent by about 50^0 off the midline, and everted upwards by about 45^0. The cranial fragment has maxillary teeth that have seven cusps, are elongated and are directed at about 45^0 inwards. Identified as *Bradysaurus baini*.

151. SAM-PK-12216: *Bradysaurus baini* (tentative)

Very large skull with occluded lower jaw and a few cranial fragments. This skull is unprepared and covered in obscuring matrix. It is also weathered and eroded, meaning that only the most basic and general anatomy can be identified with certainty. The posterodorsal maxillary-lacrimal ridge is low and about 35 mm wide, with rugose ridges but no distinct maxillary boss. The bosses of the posterior edge appear to be very smooth, very low, bulbous and indistinct. The cheeks are small, extending only about 20-25^0 below the tooth row. The upper jaw teeth appear to be quite vertically orented. Sutures are identifiable and reveal a narrow postparietal and a wedged, triangular supernumerary bone laterally, left and right, each of which suture with the supratemporal bones on the lateral corners of the occiput. This is the only case of a confirmed supernumerary bone on the posterior dorsal skull roof of a pareiasaur from the *Tapinocephalus* AZ and has not been included in the diagnosis or phylogenetic characters of the species, as I interpret this specimen as an outlier. Tentatively referred to *Bradysaurus baini.*

152. SAM-PK-12222: *Bradysaurus baini*

Partial skull in white plaster jacket on tray, both femora, separate right cheek flange. The right cheek flange has very large bulbous posterior edge bosses on it and on the partial skull the maxillary teeth are inwardly pointing at about 45^0 off the horizontal or vertical plane. The external trochanter is large and distinct and posteriorly projects 20 mm beyond the femoral shaft. The internal trochanter is very strongly curved and round and folded over proximally and has a perpendicular proximal edge. Identified as *Bradysaurus baini.*

153. SAM-PK-12251: *Bradysaurus baini*

Partial juvenile skull, right iliac blade and a distal femur. Small angular boss, posterior cheek bosses large and bulbous, maxillary-lacrimal ridge present, but no distinct maxillary boss yet developed as a result of the juvenile age of this specimen. The maxillary teeth point inwards and the cheeks are large at 30^0 reach below the tooth row.

154. SAM-PK-K00196: *Bradysaurus baini* (tentative)

Two cranial fragments: maxilla and lower jaw. The anterior left maxilla preserves eight teeth that are seven cusped with three central cuss on a trident and two lateral cusps either side. The teeth appear to be relatively flat and horizontally

directed and the maxilla is very wide and curved. Tentatively assigned to *Bradysaurus baini.*

155. SAM-PK-K00325: *Bradysaurus baini*

Right humerus, one small cranial fragment and a few small unidentified postcranial fragments. The large humerus (430 mm long) has proximal and distal expansions that are relatively twisted to about 55-60^0 apart (as seen in *Bradysaurus* and *Embrithosaurus*) and distally the humerus extends far (30 mm) beyond the articular surfaces, appearing "forked". The intercondylar fossa is shallow and the delto-pectoral crest is very small and gracile, only 55 mm wide. Tentatively referred to *Bradysaurus baini*.

156. SAM-PK-K11638: *Bradysaurus baini*

Well preserved, slightly dorsoventrally crushed and very well prepared large orange-brown coloured skull with separate lower jaw.

This is a very well preserved and very well prepared large *Tapinocephalus* AZ pareiasaur skull. Van den Brandt (2016) identified this skull and lower jaw as a specimen of *Bradysaurus baini*. I consider this large individual as a specimen of *Bradysaurus baini* as a result of the maxillary teeth which are horizontally medially directed and the shape of the maxilla which is mediolaterally extremely wide and strongly curved to facilitate the horizontal teeth. The well prepared paroccipital process of the opisthotic is distally anteroposteriorly not very long (only 50 mm), but does have a posterior process (25 mm wide, 50 mm long) that is dorsomedially oriented, which is however low and only extends posteriorly 15-20 mm. The cranial ornamentation is generally very low. The cheeks are medilaterally very wide (60 mm) at the level of the dorsal-most, quadratojugal posterior edge boss. The bosses on the posterior edge of the cheek are medium sized, rounded, as wide as high (25-30 mm) and relatively pointed.

Cranial sutures are not discernible. The frontal has a distinct, small, central boss. The cheeks are relatively small, only extending about 20^0 below the tooth row. The maxilla carries a wide, low, maxillary boss formed by a well-defined, wide, low, swollen, rugose, posterodorsal maxillary-lacrimal ridge, which merges imperceptibly with the lacrimal boss complex. The angular bosses are broken off but are mediolaterally narrow at their bases and appear to have been relatively small when intact.

It is important to note that the upper and lower jaw teeth of this specimen are quite different from the holotype and most specimens of *Bradysaurus baini*, in that the upper jaw teeth have more than the typical 7 cusps, at 8-9 marginal cusps as a result of an additional low, basal cusp, on the mesial and distal margins of the crowns and

with a short, central trident carrying three very close cusps. The lower jaw teeth have nine cusps, as a result of three symmetrically arranged marginal mesial and three marginal distal cusps, below the central three cusps, which include a low, basal cusp. Identified as *Bradysaurus baini*.

157. GPIT-RE-1602: *Bradysaurus baini*

Skull curated at Tubingen, Germany. This is probably the specimen of *Bradysaurus baini* from the Geological Palaeontological Institute, Tubingen, listed without a specimen number, by Boonstra (1934a). I did not study this specimen by direct access, but was kindly furnished good quality photographs by Christian Kammerer, from which is can be seen that the skull has inwards pointing upper jaw teeth, generally low ornamentation, low, wide, indistinct bosses on the posterior cheek and a dorsomedially oriented process on the posterior side of the distal paroccipital process.

Dual species identification (158 - 180)

Bradysaurus/Embrithosaurus (158 - 163)

158. 113/CGP/1/811: *Bradysaurus/Embrithosaurus*

Articulated lower jaw and partial left cheek in much white plaster with smaller cranial fragments. The angular boss is small, and long and pointed. The bosses on the posterior edge of the cheek are medium sized, round, to bulbous and do not match the morphology of *Nochelesaurus*. Identified as either *Bradysaurus* or *Embrithosaurus*.

159. BP/1/7266: *Bradysaurus/Embrithosaurus*

Dorsal skull roof and a few vertebral fragments. The postparietal is narrow indicating identification as either *Embrithosaurus* or *Bradysaurus*.

160. BP/1/8050: *Bradysaurus/Embrithosaurus*

Left cheek flange and partial dorsal skull roof, a few small cranial fragments, right femur, three articulated and weathered vertebrae, articulated partial proximal ulna, radius, and distal humerus. The cheek flange has large, wide, bulbous bosses on the posterior edge and so belongs to either *Bradysaurus* or *Embrithosaurus* and the cheek is mediolaterally very thin. The ulna has a very large olecranon process, 50 mm high. The femur is not well preserved but is unprepared and so does not allow access to the preserved internal trochanter.

161. SAM-PK-9144: *Bradysaurus*/*Embrithosaurus*

Postcranium comprising approximately 50 small to large broken fragments preserving a partial left femur, partial left scapulocoracoid, partial pelvis, iliac blades, acetabula, and midline puboischiatic plate, a tarsus, left humerus, proximal left tibia, proximal ulna, and a white plaster jacket containing a partial left radius, carpus and manus.

The femur does not preserve the diagnostic internal trochanter, which is sheared-off, but it appears to be proximally curved (so cannot belong to a specimen of *Nochelesaurus*) and it has a short anterior projection or process distally and the proximal region appears to be positioned away from the preaxial border of the femur (so could belong to either *Bradysaurus* or *Embrithosaurus*), distally the lateral condyle does not extend far (only about 30 mm) beyond the distal edge of the medial condyle, similar to the conditions observed in both *Bradysaurus* and *Embrithosaurus.*

The puboischiatic plate shares many features with *Embrithosaurus*: it is very thick anteriorly (105 mm) and presents a midline median pubic process that is "tongue shaped" as a result of curved rounded edges (as in *Embrithosaurus*). It extends anteroventrally far, 40-50 mm, and is 75 mm wide. However, the plate is dorsally very wide, broad and flat and at least 360 mm anteroposteriorly long, and therefore overall looks more like *Bradysaurus baini*. The distal humerus is most similar to *Bradysaurus baini* as the condyles extend very far distally (45 mm) beyond the articular surfaces, presenting a "forked" appearance and the intercondyar fossa is deep (40 mm). The proximal ulna is extremely massive and presents an enclosed, hooked articulation surface, with a huge olecranon process above it, 40-45 mm high, and anteriorly projecting 25-30 mm beyond the articular surface. The proximal articulation surfaces of the tibia are relatively flat and only about 40^0 apart (within the range of *Bradysaurus* and *Nochelesaurus*). The partial iliac blades are fragmentary but show a very flat and straight blade, only slightly concave, most similar to *Embrithosaurus*.

Identified as either *Embrithosaurus* or *Bradysaurus*. Restoration of this very fragmentary specimen would facilitate a more detailed and accurate analysis.

162. SAM-PK-12043: *Bradysaurus/Embrithosaurus*

Left scapulocoracoid with partial clavicle and interclavicle, missing scapula blade. The acromion process is typically shaped and large as seen in all members of this group of middle Permian South African pareiasaurs and the posterior border of the coracoid forms an angle of about 135^0 with the posterior border of the scapula blade, also very typical for this group. The base of the scapula blade, just above the acromion process is anteroposteriroly wide (110 mm) and the glenoid fossa

isanteroposteriorly long (190 mm) excluding this specimen from *Nochelesaurus*. Identified as either *Bradysaurus* or *Embrithosaurus.*

163. SAM-PK-12068: *Bradysaurus/Embrithosaurus*

Partial juvenile skull comprising 10 cranial fragments. The palatal fragment has parallel rows of palatal denticles, including a few denticles on the posterior edge of the transverse pterygoid process. The occipital condyle and basal tubera are typical for the group, large and constricted anteriorly towards the basipterygoid processes. Parts of the left and right cheeks and the right occiput are preserved, showing long, thin rugose ridges and a posterior cheek squamosal boss that is large, wide, low and bulbous and probably belonged to specimen of *Bradysaurus* or *Embrithosaurus*. The cheek is narrow (juvenile). Identified as either *Bradysaurus* or *Embrithosaurus.*

Bradysaurus/Nochelesaurus (164 - 170)

164. BP/1/1040: *Bradysaurus/Nochelesaurus*

Large proximal left humerus, deeply weathered, damaged and poorly preserved. Very wide measuring at least 285 mm in width proximally (consistent with *Nochelesaurus* and *Bradysaurus*), with a prominent triangular diagonal ridge dorsally, with the smaller anterior ridge worn, but present.

165. BP/1/1783: *Bradysaurus/Nochelesaurus*

Sub-adult median Interclavicle, with articulated partial left and right clavicles, two atlantal arches, one cervical rib, and partial damaged atlas and axis. The database catalogue of the ESI notes “skull donated to Smithsonian, Washington, DC (N Hotton)”. The median right clavicular arm has no notch medial to the ventral process and so this specimen is probably not *Embrithosaurus schwarzi.*

166. BP/1/7247: *Bradysaurus/Nochelesaurus*

Juvenile right quadratojugal (cheek flange) and a large proximal rib head. The cheek flange is mediolaterally narrow (40 mm) and the lateral surface has only one small boss or prominent short rugose ridge. The bosses on the posterior edge of the quadratojugal are small, round and pointed and belong to a juvenile speciman of either *Bradysaurus* or *Nochelesaurus*.

167. FMNH Field no 44: *Bradysaurus/Nochelesaurus*

Small (juvenile) proximal ulna, proximal radius, distal radius, and digits. The ulna has a large olecranon process, 25 mm high above the proximal articular surface. It is tall and narrow and not as low and wide as the olecranon processes, when present, of *Embrithosaurus*.

168. SAM-PK-1204: *Bradysaurus*/*Nochelesaurus*

Large sub-adult sized elements comprising several articulated dorsal vertebra, partial skull and lower jaw, partial interclavicle, proximal fibula, proximal left tibia, left femur, partial right femur, both distal radii, distal tibia, most of the cervical and dorsal vertebrae as isolated elements, tarsus, unprepared fragments or articulated sections, both partial scapulocoracoids and scapula blades, and +- 50 unidentified postcranial fragments. This specimen is in desperate need of repair and reconstruction.

The femora resemble the anatomy of the femora of *Nochelesaurus*. The right femur is sub-adult sized. Both femora have protruding internal trochanters, high (30 mm), 25 mm wide proximally, which are straight (as in *Nochelesaurus*). The right major trochanter is partly preserved and appears to be very short posteriorly (as in *Nochelesaurus*).

The preserved left cheek has a prominent, elongated corner boss, followed by two or three small, rounded, pointed bosses dorsally. Laterally are two small bosses on the quadratojugal. Cranial sutures are very challenging to detect, but the skull appears to have a narrow postparietal (as in *Bradysaurus* and *Embrithosaurus*). The cheek is narrow, for a relatively large skull. The angular boss is large, even for this large skull, and has a unique shape. Proximally it is mediolaterally very wide with a massive thick swollen rugose rim. It then is deeply and strongly concave and constricted distally, before thickening again to a distal, round, knob-like tip. Some unprepared osteoderms are large, wide, flat and disc-like, smoothly and evenly convex, with light ornamentation and no central boss (similar to *Bradysaurus baini*). Identified as either *Bradysaurus* or *Nochelesaurus*.

169. SAM-PK-5008: *Bradysaurus/Nochelesaurus*

Partial, sub-adult sized skull comprising four large cranial fragments preserving most of the right cheek, the premaxilla and right maxilla, a small unidentified cranial fragment and a partial left maxilla. Based on the bosses on the posterior edge of the cheek, I would identify this specimen as *Nochelesaurus alexanderi* since the bosses are pointed and very distinct, especially the corner boss. However, based on the maxilla and upper jaw teeth, I would identify this specimen as *Bradysaurus baini* since the teeth are oriented horizontally backwards, with seven cusps with three central cusps on an isolated trident, and importantly with a curved (not vertical) maxilla. The presence or absence of a maxillary boss, which would settle the matter, cannot be determined as the maxilla region is not preserved well on either side of the skull.

170. SAM-PK-9001: *Bradysaurus/Nochelesaurus*

Extremely huge specimen comprising almost complete left and right scapulocoracoids, a distal humerus, six articulated posterior dorsal vertebrae with several weathered osteoderms, a single vertebra, two lateral sacral ribs, one other small postcranial fragment , and a partial skull with partial occluded left lower jaw

This is probably the largest middle Permian South African pareiasaur specimen studied during this project, the dorsal and ventral buttresses of the glenoids are extremely robust. The dimensions of the scapula blades are most similar to *Embrithosaurus* and *Bradysaurus:* scapula blade length of 450 mm, including the acromion processes, distally flared to 200 mm wide, an anteroposteriorly wide scapula base (100-110 mm) and at the mid-level (150 mm). The scapula blade is notably thicker than any other specimen I have studied, at 55 mm mediolaterally wide at the distal end.

The right partial skull is severely damaged, over prepared and anteroposteriorly crushed producing a distorted, vertically elongated, narrow orbit. The angular boss is very small considering the large size of the skull, being dorsoventrally relatively long (50 mm), anteroposteriorly and mediolaterally equally narrow (35 mm), excluding identification as *Embrithosaurus*, and suggesting *Bradysaurus*, with a midway along, low swollen rim, and a blunt tip. The bosses on the posterior edge of the better preserved left cheek are sheared-off, but can be interpreted as medium sized, rounded, relatively distinct boss that could be associated with any of the three species of pareiasaurs in this group. The right cheek has a weathered and smoothed over posterior edge. The right cheek is relatively large, extending 30^0 below the tooth row and the cranial ornamentation is very distinct and high. Importantly, the sutures between the postparietal and both supratemporals are discernible (as shifted cranial plates) and unquestionably show a wide postparietal that includes the two lateral occipital bosses or swelling either side of the midline. This strongly suggests identification as *Nochelesaurus*, but the wide and short scapula blade is much more like *Bradysaurus* in morphology. The five partial, weathered osteoderms appear evenly convex and similar to *Bradysaurus* with little ornamentation, but they are very weathered. Identified as either *Bradysaurus* or *Nochelesaurus*.

Embrithosaurus/Nochelesaurus (171 - 180)

171. AMNH FARB 5568: *Embrithosurus/Nochelesaurus*

Imperfect juvenile skull, severely mediolaterally compressed. The upper and lower jaw teeth have seven marginal cusps and point straight downwards. There is no maxillary boss. Identified as either *Embrithosurus* or *Nochelesaurus*.

172. RMS 1030/CGP/1/855: *Embrithosaurus*/*Nochelesaurus*

Partial weathered snout with vertically oriented maxillary teeth. Identified as either *Embrithosaurus* or *Nochelesaurus*

173. RMS 1304/CGP/1/820: *Embrithosaurus*/*Nochelesaurus*

Partial anterior right lower jaw and maxilla. The maxillary teeth are vertical and appear to have seven cusps and so belong to a specimen of either *Embrithosaurus* or *Nochelesaurus*.

174. BP/1/1772: *Embrithosaurus/Nochelesaurus*

Small juvenile cranial fragment containing a partial thin maxilla with nine sheared-off teeth and an occluded lower jaw fragment. The thin maxilla and vertical teeth preclude identification as *Bradysaurus* and it must be identified as either *Embrithosaurus or Nochelesaurus.*

175. BP/1/5418: *Embrithosaurus/Nochelesaurus*

Deeply weathered snout with vertical upper jaw teeth.

176. BP/1/5435: *Embrithosaurus/Nochelesaurus*

Partial skull comprised of several dozen large and small fragments, weathered and unprepared, with vertical upper jaw teeth and very rugose cranial ornamentation.

177. BP/1/7037: *Embrithosaurus/Nochelesaurus*

Partial snout comprised of two large fragments and one small fragment containing a scute. Very weathered, the maxillary teeth are vertical and have at least seven cusps including a central long trident with three close cusps together. One large partially preserved tooth on the smaller snout fragment, appears to be very wide and to possess many cusps, perhaps a nine cusp configuration (as in *Embrithosaurus* and certain specimens of *Bradysaurus*). The scute is small (30-40 mm wide) with its ventral surface alone exposed. Identified as either *Embrithosaurus* or *Nochelesaurus* on the basis of vertically oriented maxillary teeth.

178. SAM-PK-1208: *Embrithosaurus*/*Nochelesaurus*

Very poorly prepared, damaged and weathered, large partial skull with partial occluded lower jaw, and atlas and partial axis. The skull appears mediolaterally narrow, but this is probably the result of distortion. This is a very damaged specimen. All that can be said for certain is that the damaged upper jaw teeth are vertically oriented, so belonging to either *Embrithosaurus* or *Nochelesaurus*.

179. SAM-PK-8933: *Embrithosaurus/Nochelesaurus*

Partial skull consisting of two large cranial pieces, together making up the snout with occluded lower jaw. Approximately 30 more small to medium sized cranial fragments. This specimen was assigned to *Bradysaurus seeleyi* by Haughton and Boonstra (1929a) and *Bradysaurus baini* by Van den Brandt (2016) based on the presence of a maxillay boss on the right maxilla. However, this low and wide cranial specimen is a juvenile skull or at most a sub-adult, with no maxillary boss and only has a narrow, swollen maxillary-lacrimal ridge. The upper jaw teeth are vertically oriented and so cannot belong to a specimen of *Bradysaurus baini*. There are seven marginal cusps on each maxillary tooth. The left cheek extends approximately 30^0 below the tooth row. Cranial reconstruction of the 30 fragments should make this specimen more identifiable. Identified as either *Embrithosaurus* or *Nochelesaurus.*

180. SAM-PK-12231: *Embrithosaurus/Nochelesaurus*

Extremely weathered and eroded large snout. This large adult snout has a typical, low, swollen posterodorsal maxillary-lacrimal ridge, and no maxillary boss and the sheered-off upper jaw teeth appear to be vertically orientated, so this specimen cannot be *Bradysaurus* and is identified as either *Embrithosaurus* or *Nochelesaurus*.

Unidentifiable (181 -240)

181. AM Unnumbered Skull: Unidentifiable

Large, partial, weathered, unprepared pareiasaur skull: Unidentifiable.

182. AM 4068: Unidentifiable

Large pareiasaur snout, with lower jaw and angular boss, unidentifiable. Two medium sized paraeiasaurian cranial snouts, from two different individuals, probably *Anthodon*. Medium sized Dicynodont snout, medium sized humerus, occipital plate of a medium to large sized Dicynodont skull, Dinocephalian lower jaw.

183. AMNH FARB unknown specimen number (*P. strubeni* holotype)

Specimen not found. Unidentifiable.

184. AMNH FARB 2231: Unidentifiable

Partial lower jaw. Unidentifiable as the teeth not preserved.

185. AMNH FARB 2232: Unidentifiable

Partial lower jaw approximately 75% complete, missing a large section of the right anterior corner of the jaw. The mandibular teeth are sheared-off and both angular

bosses are not preserved. Sixteen alveoli are present on the left side, where the entire sequence is preserved. Unidentifiable.

186. AMNH FARB 2233: Unidentifiable

Partial lower jaw fragments comprising seven fragments. No teeth preserved. Unidentifiable.

187. AMNH FARB 2234: Unidentifiable

Partial lower jaw of a juvenile pareiasaur comprising two large fragments, teeth not preserved. The angular boss is low and small (juvenile). Unidentifiable.

188. AMNH FARB 2235: Unidentifiable

Unprepared partial juvenile skull comprising two unprepared blocks and a few other large unprepared fragments. Unidentifiable.

189. AMNH FARB 3897: Unidentifiable

Partial skull and fragmentary lower jaw, several articulated dorsal vertebrae, distal humerus, iliac blade, proximal ulna, partial femur and several dozen small to large unidentified postcranial fragments. Unidentifiable.

190. AMNH FARB 5604: Unidentifiable

Limb bone fragments. Unidentifiable.

191. AMNH FARB 23878: Unidentifiable

Two articulated large vertebrae, mid dorsal, damaged and missing large sections. Unidentifiable.

192. AMNH FARB 23879: Unidentifiable

Pareiasaurian lower jaw fragment with natural molds (hollow impressions) of seven dentary teeth. Eleven marginal cusps on each tooth. Unlikely to originate from the *Tapinocephalus* AZ. Unidentifiable.

193. AMNH FARB 24169: Unidentifiable

Unidentifiable postcranial fragment.

194. AMNH FARB 24170: Unidentifiable

Unidentifiable dermal armour fragments.

195. A 109/CGP/1/858: Unidentifiable

Large left acetabulum. Unidentifiable.

196. CBT 9: Unidentifiable

Proximal humerus, tibia, tarsus, and a few rib fragments. The tibia is crushed and has a large 50^0 angle between the lateral and medial dorsal articular surfaces (as in *Embrithosaurus)* and distally the tibia is stretched and extended far ventromedially (as in *Bradysaurus* and *Nochelesaurus*). Unidentifiable.

197. GM 64: Unidentifiable

Partial interclavicle including median stem. Unidentifiable.

198. JP 56/ CGP/1/847: Unidentifiable.

Partial and unprepared cranial fragment containing a partial cheek. Unidentifiable.

199. RMS 1095: Unidentifiable

Unprepared postcrania, very poorly preserved. Unidentifiable.

200. RMS 1257: Unidentifiable

Partial fragmentary lower jaw. Unidentifiable.

201. S 260: Unidentifiable

Speciman not found. Unidentifiable.

202. BP/1/298: Unidentifiable

This “skull” consists of four unprepared fragments of bone with matrix, less than 100 mm in width each, with one possible boss preserved, and is unidentifiable.

203. BP/1/1578: Unidentifiable

30-40 % of a large, partial, anterior lower jaw, comprising one large and two small fragments. The teeth are sheared-off at the base. Unidentifiable.

204. BP/1/1781: Unidentifiable

A lower jaw according to the ESI catalogue, sent to France on loan to Prof Anthony, Paris, France (DEACC) *Pareiasaurus sp*.

205. BP/1/1782: Unidentifiable

Large partial left lower jaw fragment including a medium sized, long, slightly distally tapering to the distal rim, relatively pointed, posteroventrally directed angular boss and 11 dentary teeth broken off at their bases. Unidentifiable.

206. BP/1/4855: Unidentifiable

Large partial left lower jaw fragment including a large, sheared-off angular boss and five dentary teeth broken off at the crowns. Unidentifiable.

207. BP/1/5620: Unidentifiable

Four thin cranial fragments with ornamentation comprising small circular pits, long and irregularly shaped rugose ridges. Unidentifiable.

208. BP/1/5644: Unidentifiable

Proximal radius of a large pareiasaur. Unidentifiable.

209. BP/1/5858: Unidentifiable

Unidentifiable very small, long and thin bones, probably not pareiasaurian.

210. BP/1/6870: Unidentifiable

Nine small fragments, mostly cranial, unprepared and badly weathered, preserving two worn off teeth with pareiasaurian marginal cusps and a proximal rib head. Unidentifiable.

211. BP/1/6871: Unidentifiable

Three large partial unprepared articulated pareiasaurian vertebrae with partial thin, disc-like osteoderms and without neural spines, and two small unidentified postcranial fragments. Unidentifiable.

212. BP/1/6976: Unidentifiable

Partial anterior dentary with shorn-off teeth, partial large vertebra and a few large unidentified postcranial fragments, all unprepared. Unidentifiable.

213. BP/1/7014: Unidentifiable

Two large ostedoerms, wide (50-60 mm) flat (15-20 mm high) with very rugose surfaces with a low central boss (10-15 mm wide) surrounded by regular, star-like, radial, low, rugose ridges with long, wide grooves and large, shallow, pits between the ridges. The ornamentation is much more rugose, pronounced and thicker than

the ornamentation of scutes of *Bradysaurus*. The central boss is not high, round, distinct or knob-like, as in *Nochelesaurus* and the scutes do not have a flat, thin disc-like periphery as seen in *Embrithosaurus*. Unidentifiable.

214. BP/1/7019: Unidentifiable

Weathered partial vertebra. Unidentifiable.

215. BP/1/7035: Unidentifiable

Seven weathered partial vertebrae, one possible cranial fragment and one unidentified postcranial fragment. Unidentifiable.

216. BP/1/7036: Unidentifiable

Severely weathered postcranial pareiasaurian remains comprising right ulna and tibia, femoral fragments, a caudal vertebral fragment and a few unidentified small postcranial fragments. A partial weathered right lower jaw is preserved with a very small angular boss. The olecranon process is extremely massive at about 65 mm high above the proximal articular surface. Unidentifiable.

217. BP/1/7167: Unidentifiable

One large plaster jacket containing an unprepared postcranium, and two large boxes containing dozens of postcranial fragments including ribs, vertebral fragments, articulated caudal vertebrae, a tarsus, a partial femur, a partial radius and tibia. Unidentifiable.

218. BP/1/8024: Unidentifiable

Partial acetabulum, several fragmentary weathered vertebrae, centra, neural spines, ribs, a terminal claw, one small rugose cranial fragment. The dorsal surfaces of the neural spines show a convex, lightly rugose ornamentation morphology on some spines and an anteroposterioly oriented, shallow groove morphology on other spines. Unidentifiable.

219. BP/1/8025: Unidentifiable

Nine small, weathered fragments comprising two postzypopothesis, unidentified postcrania and crania and one small cranial fragment with a worn off tooth. Unidentifiable.

220. FMNH UR 2465: Unidentifiable

Dentary fragment with teeth broken off. Unidentifiable.

221. NHMUK R1714 (43525): *Pareiasaurus bombidens* (Owen 1876) (Holotype) (see chapter eight)

222. SAM-PK-3434: Unidentifiable

Partial snout, right cheek and lower jaw preserved as five large cranial fragments that fit together, and separately an atlantal intercentrum preserved in two pieces. This partial cranial specimen is poorly preserved, weathered, fragmentary and damaged. All that can be gleamed is that this individual was sub-adult sized, with a narrow snout, well-defined swollen, maxillary-lacrimal ridge, without a maxillary boss, and with vertically oriented upper jaw teeth anteriorly (so probably either *Embrithosaurus* or *Nochelesaurus*) and more horizontally oriented (45^0 inwards) teeth posteriorly. The partial right cheek appears to be small, extending only about 20^0 below the tooth row (a condition consistent with *Bradysaurus*).The upper jaw teeth appear to have seven cusps and a central, elongated trident with three central cusps. Unidentiiable.

223. SAM-PK-8934: Unidentifiable

Partial interclavicle, partial right and left scapulocoracoids with partial scapula blades, partial puboischiatic plate, both distal femora, and approximately 50 -75 postcranial fragments comprising partial iliac blades, humeri and vertebrae. These elements are not very large and belong to a sub-adult sized pareiasaur. The femora are too poorly preserved and as a result are not diagnostic. This specimen is too poorly preserved and too fragmentary to be identifiable.

224. SAM-PK-9118: Unidentifiable

Partial left lower jaw in two fragments. This left lower jaw ramus is sub-adult sized. The teeth are worn-off and the angular boss is relatively small with a swollen rim midway along its length, and a stubby, rounded appearance (40 mm long, 50 mm anteroposteriorly at the base, 35 mm mediolaterally at the swollen rim midway down its length). Unidentifiable.

225. SAM-PK-9156: Unidentifiable

Partial interclavicle and clavicle fragments and four humeral fragments. These postcranial fragments from a juvenile specimen are unidentifiable.

226. SAM-PK-9168: Unidentifiable

Late **s**ub-adult sized skull with occluded lower jaw, hundreds of rib fragments, vertebrae labelled 10-13, 16-19, 21-22, 23-25, 32-63, a few articulated osteoderms, partial pelvis and acetabulum with occluded left proximal femur, right femur, left iliac blade and articulated sacral ribs, white plaster jacket housing a fibula, tarsus

and pes, another white plaster jacket housing the other foot, partial left and right humeri, proximal ulna and radius, numerous broken, unidentified postcranial fragments.

Sub-adult (skull 310 mm longitudinally at the midine, 340 mm long laterally either side) individual with the dorsal snout reconstructed. This specimen was assigned to *B. seeleyi* by Haughton and Boonstra (1929a) and to *Bradysaurus baini* by Van den Brandt (2016) on the basis of very large cheeks, strong rugose posterodorsally oriented lines creating a swollen structure on the lower lateral quadratojugal, a medium sized posterior knob on the paroccipital processes and large, low, round and bulbous posterior cheek bosses.

However, the upper jaw teeth are vertically oriented (as in *Emrithosaurus* and *Nochelesaurus*) and the bosses on the posterior cheek are only bulbous on the squamosal and dorsal-most quadratojugal. The corner boss is elongated, conical and horn-like and very pointed, and the boss above that is small, round and pointed. The basal tubera are ridiculously large, the largest, widest, most robust seen in this study at 105 mm wide. The paroccipital processes of the opisthotics are damaged but do not appear to be very large. The cheeks are very narrow, only 45 mm wide at their widest. Cranially, this specimen is not *Bradysaurus baini*.

Both femora have internal trochanters that are proximally very strongly curved, by the same amount and degree, and rounded, as in specimens of *Bradysaurus baini*. The pelvis is broad, wide and at least 300 mm long at the midline. The pubic symphysis is low (70 mm) and the median pubic process “tongue” shaped, with rounded edges, very similar to *Embrithosaurus*, but it is much shorter and does not reach the anterior level of the lateral pubic processes (so not *Embrithosaurus* or *Bradysaurus*).

The distal humerus is extremely forked (as in *Bradysaurus* and possibly *Nochelesaurus*) as the condyles extend distally 55 mm beyond the articular surfaces (as in *Bradysaurus*) The ends of the humerus appear to be well twisted, to about 60^0 apart, but they are severely damaged and it is not possible to be certain. Identification uncertain as this specimen shows several features of *Bradysaurus*, *Embrithosaurus* and *Nochelesaurus*.

227. SAM-PK-12015: Unidentifiable

Occipital condyle and basal tubera of the parabasisphenoid. This cranial braincase fragment is juvenile sized and weathered. The posterior edge of the occipital condyle is positioned only 15 mm from the posterior edge of the basal tubera. The parabasisphenoid/basisphenoid body is wide posteriorly at the posterior thickened ends of the basal tubera, and anteriorly it is strongly constricted, mediolaterally narrowing, giving it an hourglass shape in ventral view. This is the condition in all

South African middle Permian pareiasaurs and so this fragment is not identifiable to species level. Unidentifiable.

228. SAM-PK-12054: Unidentifiable

Partial pes comprising two partial digits, one terminal claw and a few carpal bones. Unidentifiable.

229. SAM-PK-12071: Unidentifiable

Partial occipital condyle and basal tubera of the parabasisphenoid. This cranial braincase fragment is large adult sized. The posterior edge of the occipital condyle is positioned 20 mm from the posterior edge of the basal tubera. The parabasisphenoid/basisphenoid body is wide posteriorly at the posterior thickened ends of the basal tubera, and anteriorly it is strongly constricted, mediolaterally narrowing, giving it an hourglass shape in ventral view. This is the condition in all South African middle Permian pareiasaurs and so this fragment is not identifiable to species level. Unidentifiable.

230. SAM-PK-12072: Unidentifiable

Cranial fragment. Poorly preserved, unprepared cranial fragment of a pareiasaur cheek, with ornamentation consisting of long rugose ridges. This cranial fragment could belong to any of the valid pareiasaurian taxa of the *Tapinocephalus* AZ. Unidentifiable.

231. SAM-PK-12077: Unidentifiable

Small vertebra. I am not convinced this vertebra is pareiasaurian. Unidentifiable.

232. SAM-PK-12080: Unidentifiable

Small right humerus. Juvenile right humerus comprising separate proximal and distal ends, which do not fit well together as a small section of the shaft between them is not preserved. It is not possible to determine the degree of offset between the proximal and distal expansions. The delto-pectoral crest is sheared-off. It is also damaged and worn and not well preserved. Identification to species level is not possible. Unidentifiable.

233. SAM-PK-12116: Unidentifiable

Partial skull. Small juvenile, partial skull preserving the right side of the skull. Unprepared and distorted so that the right cheek is severely laterally concave. Cheek size appears to be very large, but the obvious distortion interferes with the accuaracy of this interpretation. The maxilla has a strong maxillary-lacrimal ridge and no obvious maxillary boss. Upper jaw teeth orientation is inconclusive. The

posterior cheek bosses are large at the corner, followed dorsally by two small, rounded to pointed bosses. Unidentifiable.

234. SAM-PK-12127: Unidentifiable

Three articulated vertebrae, damaged osteoderms and a pes. Completely unprepared, this material is currently unusable. There are a few osteoderms, damaged and cut through, that could be prepared and maybe useful in the future. Unidentifiable.

235. SAM-PK-12137: Unidentifiable

Small acetabulum and large tarsus and basal tubera. The acetabulum is small (90-100 mm anteroposterioly wide) and belongs to a juvenile animal. The tarsus is large (120 mm at its widets) and the basal tubera is large (95 mm wide), indicating they belonged to another larger individual. Unidentifiable.

236. SAM-PK-K00197: Unidentifiable

Occipital condyle and basal tubera. The basal tubera are large and wide (90 mm posteriorly) and constricted anteriorly at the basipterygoid process (45 mm wide) and the posterior edge is 25 mm from the posterior edge of the occipital condyle. Unidentifiable.

237. SAM-PK-K04506: Unidentifiable

Eight small, weathered postcranial fragments. I am not convinced this is a pareiasaur. Only one fragment has light, rugose ornamentation on it, but this does not appear to be a cranial fragment as it is very thick (100 mm).

238. SAM-PK-K07665: Unidentifiable

Maxilla and lower jaw fragment. The maxilla and lower jaw fragment is very worn, weathered and damaged and preserves the sheered-off crowns of about 15 teeth. Unidentifiable.

239. SAM-PK-K07916: Unidentifiable

No specimen, only a tag which notes the specimen is “on loan to B Rubidge, 1992”. Museum database electronic catalogue notes “this fragment of a supposed vertebra has been thrown away. Letter written from Dr Rubidge to Dr Smith”. Unidentifiable.

240. SAM-PK-K10547: Unidentifiable

Phalanx, small maxilla fragment and a small cranial fragment. Unidentifiable.

APPENDIX B: CHARACTER LIST

Edited from:

Van den Brandt *et al.* (2019)

who adapted it from Liu and Bever (2018)

This list of characters is identical to the character list (characters 1-139) provided in the online supplementary data of Turner *et al.* (2015), except that I have retained the modifications made to characters 13 and 37 by Liu and Bever (2018); and the modifications made to characters 44, 48, 50, 51 and 68 by Van den Brandt *et al.* (2019).

Van den Brandt *et al.* (2019):

Van den Brandt *et al.* (2019) revised five character statements through rewording (44, 48, 50, 51, and 68).

- **Character 44**. Expanded quadratojugal (cheek) flange: absent, no cheek flange, quadratojugal (cheek) does not extend below level of tooth row to create a check flange, the ventral surface of the quadratojugal is continuous with and forms a straight edge with that of the maxilla (0); small cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row 0^0 - 40^0 (1);large cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row 41^0 or more (2).
- **Character 48**. Quadratojugal, ventral margin, ornamentation (bosses): absent, no ornamentation (bosses) on the ventral margin of the quadratojugal (0); present, ornamentation (bosses) on the ventral margin of the quadratojugal (1).
- **Character 50**. Cheek ornamentation style (quadratojugal and squamosal): no ornamentation on the posterior or ventral margins of the cheek (0); ornamentation present on the posterior or ventral margins of the cheek in the form of low rounded bosses (1); ornamentation present on the posterior or ventral margins of the cheek in the forms of well-developed, more distinct, taller, more pointed bosses (2); ornamentation present on the posterior or ventral margins of the cheek in the form of prominent, conical horns with sharp, pointed tips (3).
- **Character 51**. Temporal emargination (otic notch): absent, or very small (0), emargination present on the posterior border of the cheek, in the dorsal portion of the squamosal, just below the occipital shelf of the supratemporal, being horizontal and extending medially along the internal surface of the squamosal.
- **Character 68**. Upper jaw teeth (premaxilla and maxilla), number on each side: 20 or more (0), 18 or less (1).

Based on personal observations, Van den Brandt *et al.* (2019) made the following changes to the scores contained in the matrix of Liu and Bever (2018):

- **Character 4:** exoccipital, lateral flange: changed from (?) to present (1); *Embrithosaurus schwarzi.*
- **Character 5:** exoccipital, lateral flange, size: changed from (?) to lateral flange of the exoccipital well-developed and extends well along the paroccipital process of the opisthotic (1); *Embrithosaurus schwarzi.*
- **Character 23:** medial prepalatal foramen bordered by the premaxilla and the vomer: changed from (?) to present (1); *Embrithosaurus schwarzi.*
- **Character 31:** maxilla, boss: changed from feebly developed or absent (0)

to prominent boss or horn present (1); *Embrithosaurus schwarzi* and *Bradysaurus baini.*

- **Character 39:** tabular, (supernumerary element): changed from (?) to absent (1); *Nochelesaurus alexanderi.*
- **Character 41:** tabular (supernumerary element), contact: changed from do not contact each other posteriorly (0), to (?)*; Embrithosaurus schwarzi, Bradysaurus seeleyi.*
- **Character 66:** teeth, cusp arrangement: changed from (?) to cusps regularly spaced along the tooth crown (1). Based on Tsuji *et al.* (2013); *Bunostegos*.
- **Character 68:** upper jaw teeth (premaxilla and maxilla), number on each side: changed from 20 or more (0) to 18 or less (1); *Embrithosaurus schwarzi.*

This study:

I have revised character statements 14 and 102 through rewording to improve clarity. For character 69, state (1), 2-7 cusps applied to only *Bradysaurus baini*, *Bradysaurus seeleyi* and *Nochelesaurus.* This project changed the state to 7-9 cusps for all these taxa, which means that state (1), 2-7 cusps is no longer applicable to any taxa, and was therefore removed as an option. The new conditional states are: concical, single cusp (0); 7-9 cusps on ach maxillary tooth (1); 9-11 cusps (2); more than 11 cusps (3). The states of all taxa were updated accordingly. For character 74, I swapped the definitions of state (0) and (1), as the existing definitions did not match the data, and it now does (all known pareiasaurs have teeth on the transverse flange of the pterygoid).

- **Character 14:** Basisphenoid, ventral surface of each basipterygoid process, turbercles: featureless, lacking tubercles (0); tubercles present on the ventral surface of each basipterygoid process (basisphenoid), immediately behind the interpterygoid vacuity and the transverse suture with the pterygoid (1).
- **Character 69:** Maxillary teeth, cusps number: concical, single cusp (0); 7-9 cusps on ach maxillary tooth (1); 9-11 cusps (2); more than 11 cusps (3).
- **Character 74:** Pterygoid, transverse flange, dentition: no dentition on the transverse flange of the pterygoid (0); teeth present on the transverse flange of the pterygoid (1).
- **Character 102:** Humerus, intercondylar depression, transverse ridge (intercondylar ridge border): on the distal dorsal end of the humerus, a transverse ridge separating the ulnar fossa (intercondylar depression) from the articulation (olecranon fossa) surface is absent (0); present (1).

Based on personal observations, I have made the following changes to the scores contained in the matrix of Van den Brandt *et al.* (2019):

- **Character 3:** prootic, medial wall, ossification: I changed from (?) to present (1); *Nochelesaurus.*
- **Character 4:** exoccipital, lateral flange: I changed from (?) to present (1); *Nochelesaurus.*
- **Character 5**: exoccipital, lateral flange, size: I changed from (?) to lateral flange of the exoccipital well-developed and extends well along the paroccipital process of the opisthotic (1); *Nochelesaurus.*
- **Character 14:** basisphenoid, ventral surface of each basipterygoid process: I changed from featureless, lacking tubercles (0) to tubercles present on the ventral surface of each basipterygoid process (basisphenoid) , immediately behind the interpterygoid vacuity and the transverse suture with the pterygoid (1); *Nochelesaurus.*
- **Character 19**: vomer, alar flange (lateral flange): I changed from (?) to present (1); *Nochelesaurus*.
- **Character 23:** medial prepalatal foramen bordered by the premaxilla and the vomer: I changed from (?) to present (1); *Nochelesaurus*.
- **Character 33:** snout dimensions (anteriorly): I changed from broader than high (0) to as high as wide (1); *Nochelesaurus.*
- **Character 38:** pineal foramen, position: I changed from (?) to placed more anteriorly, close to the frontal-parietal suture (1); *Bradysaurus.*
- **Character 39:** tabular (supernumerary element): I changed from (?) to absent (1); *Bradysaurus.*
- **Character 42:** postparietal, form: I changed from (?) to integrated into skull table (1); *Nochelesaurus.*
- **Character 43:** postparietal, fusion: I changed from (?) to fused into a single element and exposed well dorsally (1); *Nochelesaurus.*
- **Character 44:** expanded quadratojugal (cheek) flange: I changed from large cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row 41^0 or more (2) to small cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row 0^0 - 40^0 (1); *Bradysaurus* and *Nochelesaurus.*
- **Character 64:** articular (region), lateral shelf: I changed from (?) to present, there is a lateral extension of the surangular or articular, the lateral surface of the effected element extends dorsolaterally (1); *Nochelesaurus.*
- **Character 68:** upper jaw teeth (premaxilla and maxilla), number on each side: I changed from 20 or more (0), to 18 or less (1); *Nochelesaurus.*
- **Character 69:** maxillary teeth, cusp number: I changed from 2–7 cusps on each maxillary tooth (1=0) to 7–9 cusps (2=1); *Bradysaurus* and *Nochelesaurus.*
- **Character 70:** mandibular teeth, cusp number: I changed from 2–7 cusps on each mandibular tooth (1) to 7–9 cusps (2); *Bradysaurus* and

Nochelesaurus.

- **Character 71:** mandibular teeth, lingual surface, shape: I changed from (?) to has a distinct, triangular lingual ridge, narrowing towards the crown of the tooth (1); *Nochelesaurus*. I changed from smooth (0) to has a distinct, triangular lingual ridge, narrowing towards the crown of the tooth (1); *Bradysaurus.*
- **Character 72:** marginal teeth, lingual surface, horizontal cingulum: I changed from (?) to present (1); *Nochelesaurus.*
- **Character 76:** pterygoid, quadrate ramus: I changed from (?) to deep excavation on posterolateral surface (1); *Nochelesaurus* and *Embrithosaurus.*
- **Character 79:** atlas-axis fusion: I changed from (?) to to altas pleurocentrum separate from the axial intercentrum (1); *Bradysaurus* and *Nochelesaurus.* I changed from pleurocentrum of the atlas and axial intercentrum fused (0) to altas pleurocentrum separate from the axial intercentrum (1); *Embrithosaurus.*
- **Character 80:** presacral vertebrae, number: I changed from 20 presacral vertebrae (1) to 19 or fewer presacral vertebrae (2); *Embrithosaurus* and *Bradysaurus.*
- **Character 81:** lumbar vertebrae: I changed from (?) to absent (0); *Nochelesaurus.*
- **Character 82:** sacral vertebrae, number: I changed from (?) to four (2); *Nochelesaurus.*
- **Character 83:** caudal vertebrae, number (tail length): I changed from (?) to long, with more than 25 caudal vertebrae (0); *Nochelesaurus.*
- **Character 88:** scapula, blade, shape: I changed from (?) to straight preaxial and postaxial margins expanding gradually (0); *Nochelesaurus.*
- **Character 92:** humerus, torsion: I changed from less than or equal to 45^0 (1) to the planes of proximal and distal expansion makes an angle of greater than or equal to 60^0 (0); *Embrithosaurus*. I changed from (?) to the planes of proximal and distal expansion makes an angle of greater than or equal to 60^0 (0); *Bradysaurus.*
- **Character 98:** epicondylar distal projection: I changed from epicondyles do not project (far) past the radial and ulnar articulation surfaces (0) to project past the radial and ulnar articulation surfaces, appearing 'forked' (1); *Bradysaurus.*
- **Character 99:** entepicondyle and ectepicondyle relative size: I changed from (?) to equal (0); *Nochelesaurus*. I changed from ectepicondyle reduced (1) to equal (0); *Embrithosaurus*.
- **Character 102:** humerus, intercondylar depression, transverse ridge: I changed from on the distal dorsal end of the humerus, a transverse ridge separating the ulnar fossa (intercondylar depression) from the articulation (olecranon fossa) surface is absent (0) to present (1); *Bradysaurus* and *Nochelesaurus.*
- **Character 103:** humerus, ulnar fossa (intercondylar depression), depth:

I changed from shallow depression (0) to deep fossa (1); *Nochelesaurus*.

- **Character 107:** manus, phalangeal formula: I changed from (?) to 23332 reduced (1); *Nochelesaurus* and *Bradysaurus.*
- **Character 108:** Sacral ribs, second and third: I changed from (?) to dorsoventral compression is slight (0), *Nochelesaurus*.
- **Character 110:** Ilium, blade, expansion: I changed from (?) to well anteriorly (1); *Nochelesaurus.*
- **Character 111:** ilium, anterior margin, lateral eversion: I changed from flat or slightly everted (0) to surface strongly everted, oriented almost horizontal (1); *Bradysaurus.*
- **Character 112:** Ilium, posterior process: I changed from (?) to strongly reduced (1); *Nochelesaurus.*
- **Character 113:** ilium, shaft, orientation: I changed from vertical or posterodorsally inclined (0) to anterodorsally inclined, forming an angle with the vertical of more than 20^0 (1); *Embrithosaurus*. I changed from vertical or posterodorsally inclined (0) to inclined even further anteriorly, forming an angle of more than 45^0 with the vertical (2); *Bradysaurus.*
- **Character 114:** acetabulum, dorsal buttress: I changed from (?) to strongly developed (1), *Nochelesaurus*.
- **Character 115:** acetabulum, anterior shape: I changed from round (0) to notched (1); *Embrithosaurus* and *Bradysaurus*.
- **Character 116:** pubis, process on the anterior border: I changed from (?) to present (1). ('lateral pubic process' of Walker, 1973, Gaffney, 1990); *Nochelesaurus.*
- **Character 117:** pubis, median process: I changed from (?) to present (1); *Nochelesaurus.*
- **Character 122:** femur, trochanter major, form: I changed from large, more distinct (1) to small, slightly thickened (0); *Nochelesaurus.*
- **Character 124:** femur, postaxial flange, width: I changed from narrows in the middle of the length of the femur (0) to consistently wide, appearing straight (1); *Embrithosaurus.*
- **Character 125:** femur, internal trochanter, shape: I changed from (?) to proximally curved preaxially (1); *Bradysaurus.*
- Character 127: astragalus and calcanium: I changed from (?) to fused, with the presence of the obturator foramen (1)*, Nochelesaurus.*
- **Character 135:** osteoderm, appearance: I changed dorsal surface of the osteoderms smooth, convex, without a central boss (0); to possess a distinct rounded central boss (1); *Nochelesaurus*.
- **Character 136:** osteoderm, ornamentation: I changed external surface of the osteoderms smooth and without ornamentation (0) to ridges fewer, larger, lumpier, and less regularly spaced (2); *Embrithosaurus*. I changed from (0) external surface of the osteoderms smooth and without ornamentation to (?); *Nochelesaurus*.

- **Character 139:** gastralia: I changed (?) to absent(1); *Embrithosaurus.*

Character List:

Character scores that have changed as a result of this project are in bold text. Character scores that were changed by Van den Brandt *et al.* (2019) are also noted in bold text, with the author noted.

Braincase (characters 1-28, except 21, 22)

1. Basicranial articulation: Pterygoid and/or epipterygoid articulation with the basipterygoid process is mobile (0); articulation is immobile (1).

Embrithosaurus:

- SAM-PK-8034: immobile (1)

Nochelesaurus:

- SAM-PK-6239: immobile (1)
- SAM-PK-6239A: not preserved
- SAM-PK-6238: immobile (1)
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: immobile (1)
- NHMUK R49426: immobile (1)

Note: Lee (1997b): Basicranial articulation is immobile in all adequately known pareiasaurs.

2. Sphenethmoid, ossification: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- SAM-PK-6239: present (1)
- SAM-PK-6238: not preserved
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: present (1)
- NHMUK R49426: present (1)

Note: Lee (1997b): Sphenethmoid, ossification present in all adequately known pareiasaurs.

3. Prootic, medial wall, ossification: absent (0): present (1).

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- **SAM-PK-6239: present (1), changed from (?)**
- **SAM-PK-6238: present (1), changed from (?)**
- SAM-PK-6240: not accessible

Bradysaurus:

- NHMUK R1971: present (1)
- NHMUK R49426:not preserved

4. Exoccipital, lateral flange: absent (0); present (1).

Embrithosaurus:

- **SAM-PK-8034: present (1), Van den Brandt *et al*. (2019) changed from (?) to present (1)**

Nochelesaurus:

- **SAM-PK-6239: present (1), changed from (?)**
- **SAM-PK-6238: present (1), changed from (?)**
- SAM-PK-6240: not preserved.

Bradysaurus:

- NHMUK R1971: present (1)
- NHMUK R49426: not preserved

5. Exoccipital, lateral flange, size: small flange (0); lateral flange of the exoccipital well-developed and extends well along the paroccipital process of the opisthotic (1).

Embrithosaurus:

- **SAM-PK-8034: lateral flange of the exoccipital well-developed and extends well along the paroccipital process of the opisthotic (1), Van den Brandt *et al*. (2019) changed from (?).**

Nochelesaurus:

- **SAM-PK-6239: well developed (1), changed from (?)**
- SAM-PK-6238: not well preserved
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971, SAM-PK-5624: well developed (1)
- NHMUK R49426: not preserved

6. Paroccipital process, suture: not sutured to the squamosal and supratemporal (0); paroccipital process of the opisthotic is antero-posteriorly expanded and sutured to ventrally-directed flange from the squamosal and supratemporal (1).

Embrithosaurus:

- SAM-PK-8034: paroccipital process of the opisthotic is antero-posteriorly expanded and sutured to ventrally-directed flange from the squamosal and supratemporal (1)

Nochelesaurus:

- SAM-PK-6239: paroccipital process of the opisthotic is antero-posteriorly expanded and sutured to ventrally-directed flange from the squamosal and supratemporal (1)
- SAM-PK-6238: paroccipital process of the opisthotic is antero-posteriorly expanded and sutured to ventrally-directed flange from the squamosal and supratemporal (1)
- SAM-PK-6240: paroccipital process of the opisthotic is antero-posteriorly expanded and sutured to ventrally-directed flange from the squamosal and supratemporal (1)

Bradysaurus:

- NHMUK R1971: paroccipital process of the opisthotic is antero-posteriorly expanded and sutured to ventrally-directed flange from the squamosal and supratemporal (1)
- NHMUK R49426: paroccipital process of the opisthotic is antero-posteriorly expanded and sutured to ventrally-directed flange from the squamosal and supratemporal (1)

Note: Lee (1997b): paroccipital process of the opisthotic is strongly sutured to squamosal and supratemporal in all adequately known pareiasaurs.

7. Paroccipital process, orientation: projects laterally from the neurocranium (0); is U-shaped in occipital view (1).

Embrithosaurus:

- SAM-PK-8034: U-shaped in occipital view (1)

Nochelesaurus:

- SAM-PK-6239: U-shaped in occipital view (1)
- SAM-PK-6238: U-shaped in occipital view (1)
- SAM-PK-6240: U-shaped in occipital view (1)

Bradysaurus:

- NHMUK R1971: U-shaped in occipital view (1)
- NHMUK R49426: U-shaped in occipital view (1)

8. Ventral otic fissure: present (0); absent (1).

Embrithosaurus:

- SAM-PK-8034: absent (1)

Nochelesaurus:

- SAM-PK-6239: absent (1)
- SAM-PK-6238: absent (1)
- SAM-PK-6240: absent (1)

Bradysaurus:

- NHMUK: R1971: absent (1)
- NHMUK R49426: absent (1)

Note: Lee (1997b): ventral cranial fissure absent in all adequately known

pareiasaurs.

9. Parabasisphenoid and basioccipital, braincase floor: not thickened (0); thickened (1).

Embrithosaurus:

- SAM-PK-8034: thickened (1)

Nochelesaurus:

- SAM-PK-6239: thickened (1)
- SAM-PK-6238: thickened (1)
- SAM-PK-6240: thickened (1)

Bradysaurus:

- NHMUK R1971: thickened (1)
- NHMUK R49426: thickened (1)

Note: Lee (1997b): thickened in all adequately known pareiasaurs.

10. Cultriform process: present (0); absent (1).

Embrithosaurus:

- SAM-PK-8034: present (0)

Nochelesaurus:

- SAM-PK-6239: not preserved, left as present (0) as in all pareiasaurs
- SAM-PK-6238: not preserved, left as present (0) as in all pareiasaurs
- SAM-PK-6240: not preserved, left as present (0) as in all pareiasaurs

Bradysaurus:

- NHMUK R1971: not preserved, left as present (0) as in all pareiasaurs
- NHMUK: R49426: not assessable, left as present (0) as in all pareiasaurs

Note: Lee (1997b): cultriform process is present in all adequately known pareiasaurs.

11. Cultriform process, length: relatively long, more than the half of the distance between the anterior extent of the rostrum (tip of snout) to the basal tubera (0); short, less than a third of this distance (1).

Embrithosaurus:

- SAM-PK-8034: short (1)

Nochelesaurus:

- SAM-PK-6239: not preserved, left as short (1) as in all pareiasaurs
- SAM-PK-6238: not preserved, left as short (1) as in all pareiasaurs
- SAM-PK-6240: not preserved, left as short (1) as in all pareiasaurs

Bradysaurus:

- NHMUK R1971: not preserved, left as short (1) as in all pareiasaurs
- NHMUK R49426: not assessable, left as short (1) as in all pareiasaurs

Note: Lee (1997b): cultriform process is short all adequately known pareiasaurs.

12. Cultriform process, shape of anterior tip: pointed (0); blunt (1).

Embrithosaurus:

- SAM-PK-8034: blunt (1)

Nochelesaurus:

- SAM-PK-6239: not preserved, left as blunt (1) as in all pareiasaurs
- SAM-PK-6238: not preserved, left as blunt (1) as in all pareiasaurs
- SAM-PK-6240: not preserved, left as blunt (1) as in all pareiasaurs

Bradysaurus:

- NHMUK R1971: not preserved, left as blunt (1) as in all pareiasaurs
- NHMUK R49426: not assessable, left as blunt (1) as in all pareiasaurs

Note: Lee (1997b): anterior tip of cultriform process is very blunt in all adequately known pareiasaurs.

13. Basisphenoid, body: wide, strongly constricted, giving it an hourglass shape in ventral view (0); wide, not strongly laterally constricted (1); narrow with relatively straight margin (2).

Embrithosaurus:

- SAM-PK-8034: constricted (0)

Nochelesaurus:

- SAM-PK-6239: constricted (0)
- SAM-PK-6238: constricted (0)
- SAM-PK-6240: constricted (0)

Bradysaurus:

- NHMUK R1971: constricted (0)
- NHMUK R49426: constricted (0)

14. Basisphenoid, ventral surface, turbercles: featureless, lacking tubercles (0); tubercles present on the ventral surface of the neurocranium just behind the basipterygoid processes (1).

Embrithosaurus:

- SAM-PK-8034: lacking tubercles (0)

Nochelesaurus:

- SAM-PK-6239: not preserved
- **SAM-PK-6238: tubercles present (1), changed from (0) lacking tubercles.**
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: lacking tubercles (0)

- NHMUK R49426: lacking tubercles (0)
  Note: Lee (1997b) Scutosaurus and Pareiasaurus have a distinct tubercle on each basipterygoid process, i.e. either side of the midline. I confirmed this in Scutosaurus specimens with photographs and by direct study.

15. Basioccipital, ventral surface, central boss: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: absent (0)

Nochelesaurus:

- SAM-PK-6239: absent (0)
- SAM-PK-6238: absent (0)
- SAM-PK-6240: absent (0)

Bradysaurus:

- NHMUK R1971: absent (0)
- NHMUK R49426: absent (0)
  Jail & anvier (2005) J: New character, applicable to Arganaceras and Scutosaurus only (and Elginia wuyongae). Note: Scutosaurus has this median tubercle.

16. Basal tubera: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- SAM-PK-6239: present (1)
- SAM-PK-6238: present (1)
- SAM-PK-6240: present (1)

Bradysaurus:

- NHMUK R1971: present (1)
- NHMUK R49426: present (1)

Lee (1997b): basal tubera present in all adequately known pareiasaurs.

17. Basal tubera, position: situated posteriorly, closer to the occipital condyle than the basipterygoid process (0); basal tubercles situated approximately midway between the occipital condyle and the basipterygoid processes, or even further anteriorly (1).

Embrithosaurus:

- SAM-PK-8034: closer to condyle (0)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: closer to condyle (0)
- SAM-PK-6240: closer to condyle (0)

Bradysaurus:

- NHMUK R1971: closer to condyle (0)
- NHMUK R49426: closer to condyle (0)

Note: Most derived pareiasaurs, such as Scutosaurus, P. nasicornis, are midway.

18. Choana, shape: situated in a lateral position, bounded laterally by the maxilla, diverge posteriorly, parallel to tooth row throughout (0); parallel, positioned more medially, delimited posterolaterally by the palatine (1); choanae even more medially positioned, with the palatine constituting more than 50% of the lateral border, medial border formed entirely by the vomer (2).

Embrithosaurus:

- SAM-PK-8034: very medially positioned (2)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: very medially positioned (2)
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK: R1971: very medially positioned (2)
- NHMUK R49426: very medially positioned (2)

Note: Lee (1997b): very medially positioned in all adequately known pareiasaurs.

19. Vomer, alar flange (lateral flange): absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: not preserved

Nochelesaurus:

- SAM-PK-6239: not preserved
- **SAM-PK-6238: present (1), changed from (?)**
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: present (1)
- NHMUK R49426: present (1)

Note: New character from Damiani & Modesto (2001) and Jalil and Janvier (2005). Seems to be present in all pareiasaurs where it is preserved according to the Turner et al. (2015) data matrix, so probably not important within pareaiasaurs.

20. Foramen palatinum posterius, size: small or absent and delineated by the bones of the skull roof (0); large, medially positioned and defined by the palatine and the ectopterygoid without participation of the bones of the skull roof (1).

Embrithosaurus:

- SAM-PK-8034: large, medially positioned and defined by the

palatine and the ectopterygoid without participation of the bones of the skull roof (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: large, medially positioned and defined by the palatine and the ectopterygoid without participation of the bones of the skull roof (1)
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: large, medially positioned and defined by the palatine and the ectopterygoid without participation of the bones of the skull roof (1)
- NHMUK R49426: large, medially positioned and defined by the palatine and the ectopterygoid without participation of the bones of the skull roof (1)

Note: Lee (1997b): fpp is large and defined by the palatine and the ectopterygoid in all adequately known pareiasaurs.

21. Skull roof, radiating ridges: dermal sculpturing in the form of relatively straight ridges radiating from the center of dermal skull roof bones absent (0); regular ridges present (1).

Embrithosaurus:

- SAM-PK-8034: regular ridges present (1)

Nochelesaurus:

- SAM-PK-6239: regular ridges present (1)
- SAM-PK-6238: regular ridges present (1)
- SAM-PK-6240: regular ridges present (1)

Bradysaurus:

- NHMUK R1971: regular ridges present (1)
- NHMUK R49426: regular ridges present (1)

Note: New character by Tsuji (2010, 2013).

22. Circular pits: cranial sculpture in the form of circular pits absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: circular pits present (1)

Nochelesaurus:

- SAM-PK-6239: circular pits present (1)
- SAM-PK-6238: circular pits present (1)
- SAM-PK-6240: circular pits present (1)

Bradysaurus:

- NHMUK R1971: circular pits present (1)
- NHMUK R49426: circular pits present (1)

Note: New character by Tsuji (2010, 2013).

23. Medial prepalatal foramen bordered by the premaxilla and the vomer: absent (0); present (1).

Embrithosaurus:

- **SAM-PK-8034: medial prepalatal foramen present (1), changed from (?) by Van den Brandt *et al*. (2019).**

Nochelesaurus:

- **SAM-PK-6239: medial prepalatal foramen present (1) , changed from (?)**
- SAM-PK-6238: prepalatal foramen not found, unprepared skull
- SAM-PK-6240: inaccessible

Bradysaurus:

- NHMUK R1971: medial prepalatal foramen present (1)
- NHMUK R49426: medial prepalatal foramen present (1)

Note: Jalil and Janvier (2005) new character.

24. Interpterygoid vacuity, length: long, at least 15% of skull length (0) short, less than 15% of skull length (1).

Embrithosaurus:

- SAM-PK-8034: short (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: short (1) < 20 mm in anteroposterior length
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: short (1)
- NHMUK R49426: short (1)

Note: Short in all pareiasaurs according to Turner et al. (2015) matrix scores, and long in some outgroups.

25. Interpterygoid vacuity, anterior shape: V-shaped (0); U-shaped (1); transversely-oriented (2).

Embrithosaurus:

- SAM-PK-8034: transversely-oriented (2)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: transversely-oriented (2)
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: transversely-oriented (2)
- NHMUK R49426: transversely-oriented (2)

Note: Transversely-oriented in all middle Permian South African basal taxa and Bunostegos according to Turner et al. (2015) data matrix scores. Scutosaurus is anteriorly very, very long, u-shaped normally and v-shaped when over prepare. In all middle Permian South African basal taxa it is transverse overall, with a shallowly u-shaped anterior border.

26. Pterygoid, transverse flange, shape: large and directed laterally (0); reduced, directed more anteriorly than laterally, without contact with the cheek (1).

Embrithosaurus:

- SAM-PK-8034: reduced, directed more anteriorly than laterally, without contact with the cheek (1)

Nochelesaurus:

- SAM-PK-6239: reduced, directed more anteriorly than laterally, without contact with the cheek (1)
- SAM-PK-6238: reduced, directed more anteriorly than laterally, without contact with the cheek (1)
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: reduced, directed more anteriorly than laterally, without contact with the cheek (1)
- NHMUK R49426: reduced, directed more anteriorly than laterally, without contact with the cheek (1)

Note: Lee (1997b): reduced and does not reach the cheeks in all adequately known pareiasaurs.

27. Pterygoid, transverse flange, orientation: extends ventrally below the level of the alveolar ridge (0); oriented primarily horizontally, so the level of the palate is higher, not reaching the level of the alveolar ridge (1).

Embrithosaurus:

- SAM-PK-8034: oriented primarily horizontally, so the level of the palate is higher, not reaching the level of the alveolar ridge (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: oriented primarily horizontally, so the level of the palate is higher, not reaching the level of the alveolar ridge (1)
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: oriented primarily horizontally, so the level of the palate is higher, not reaching the level of the alveolar ridge (1)
- NHMUK R49426: oriented primarily horizontally, so the level of the palate is higher, not reaching the level of the alveolar ridge (1)

Note: Is (1) in all pareiasaurs scored on Turner et al (2015) data matrix, but

as (o) in some outgroups.

28. Supraoccipital, form: large, with longitudinal contact with the postparietal (0); high and narrow, forming along all of its length a solid sagittal suture with a ventral projection of the postparietal (1).

Embrithosaurus:

- SAM-PK-8034: high and narrow, forming along all of its length a solid sagittal suture with a ventral projection of the postparietal (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: high and narrow, forming along all of its length a solid sagittal suture with a ventral projection of the postparietal (1)
- SAM-PK-6240: high and narrow, forming along all of its length a solid sagittal suture with a ventral projection of the postparietal (1)

Bradysaurus:

- NHMUK R1971: high and narrow, forming along all of its length a solid sagittal suture with a ventral projection of the postparietal (1)
- NHMUK R49426: high and narrow, forming along all of its length a solid sagittal suture with a ventral projection of the postparietal (1)

Skull Roof: (characters 29-58, and 21, 22)

29. External naris, form: round and small (0); very anteroposteriorly elongate (1).

Embrithosaurus:

- SAM-PK-8034: round and small (0)

Nochelesaurus:

- SAM-PK-6239: round and small (0)
- SAM-PK-6238: round and small (0) (mediolaterally crushed)
- SAM-PK-6240: round and small (0)

Bradysaurus:

- NHMUK R1971: round and small (0)
- NHMUK R49426: round and small (0)

Note: Is round and small in all pareiasaurs scored on Turner et al. (2015) data matrix, except for Sanchuansaurus in Lui and Bever (2018) data matrix, but is anteroposteriorly long in some outgroups.

30. External naris, maxilla contribution: maxilla either excluded from naris or forms only its ventral/posterior edge (0); maxilla extends also to the posterodorsal margin of naris (1).

Embrithosaurus:

- SAM-PK-8034: maxilla forms only the ventral/posterior edge (0)

Nochelesaurus:

- SAM-PK-6239: maxilla forms only the ventral/posterior edge (0)
- SAM-PK-6238: maxilla forms only the ventral/posterior edge (0)
- SAM-PK-6240: maxilla forms only the ventral/posterior edge (0)

Bradysaurus:

- NHMUK R1971: maxilla forms only the ventral/posterior edge (0)
- NHMUK R49426: maxilla forms only the ventral/posterior edge (0)

31. Maxilla, boss: a boss or horn on the maxilla immediately behind the external naris feebly developed or absent (0); prominent boss or horn present (1).

Embrithosaurus:

- **SAM-PK-8034: prominent boss or horn present (1), change from (0) by Van den Brandt *et al*. (2019)**

Nochelesaurus:

- SAM-PK-6239: boss absent (0)
- SAM-PK-6238: boss absent (0)
- SAM-PK-6240: boss absent (0)

Bradysaurus:

- NHMUK R1971: prominent boss or horn present (1)
- NHMUK R49426: boss absent (0) , due to juvenile/sub-adult size specimen

32. Maxilla, dorsal process: reduced, not reaching the nasal, so that the lacrimal contributes to the ventral border of the naris (0); large anterodorsal extension of the maxilla, excluding the lacrimal from the external naris (1).

Embrithosaurus:

- SAM-PK-8034: reduced, not reaching the nasal (0)

Nochelesaurus:

- SAM-PK-6239: reduced, not reaching the nasal (0)
- SAM-PK-6238: reduced, not reaching the nasal (0)
- SAM-PK-6240: reduced, not reaching the nasal (0)

Bradysaurus:

- NHMUK R1971: reduced, not reaching the nasal (0)
- NHMUK R49426: reduced, not reaching the nasal (0)

33. Snout dimensions (anteriorly): broader than high (0); as high as wide (1).

Embrithosaurus:

- SAM-PK-8034: broader than high (0)

Nochelesaurus:

- **SAM-PK-6239: as high as wide (1), changed from (0)**
- SAM-PK-6238: as high as wide (1)
- SAM-PK-6240: as high as wide (1)

Bradysaurus:

- NHMUK R1971: broader than high (0)
- NHMUK R49426: broader than high (0)

34. Postfrontal, shape: mediolaterally narrow, more than 2 times as long as wide, contributes to the orbital margin (0); widened mediolaterally, around 2 times as wide as long, no or only feeble contribution to the orbital rim (1).

Embrithosaurus:

- SAM-PK-8034: widened mediolaterally, around 2 times as wide as long, no or only feeble contribution to the orbital rim (1)

Nochelesaurus:

- SAM-PK-6239: widened mediolaterally (1), but is narrower than *Embrithosaurus*.
- SAM-PK-6238: widened mediolaterally (1), but is narrower than *Embrithosaurus*.
- SAM-PK-6240: badly preserved/unprepared

Bradysaurus:

- NHMUK R1971: widened mediolaterally (1), but is narrower than *Embrithosaurus*.
- NHMUK R49426: widened mediolaterally (1), but is narrower than *Embrithosaurus*.

Note: Mediolaterally wide (1) in all pareiasaurs scored on Turner et al (2015) data matrix, and is (0) in some outgroups. Lee (1995) postfrontal is mediolaterally wide (and anteroposteriorly short) with small orbital contribution in all pareiasaurs.

35. Postfrontal, 'horn': absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: postfrontal horn absent (0)

Nochelesaurus:

- SAM-PK-6239: postfrontal horn absent (0)
- SAM-PK-6238: postfrontal horn absent (0)
- SAM-PK-6240: postfrontal horn absent (0)

Bradysaurus:

- NHMUK R1971: postfrontal horn absent (0)
- NHMUK R49426: postfrontal horn absent (0)

Note: New character by Tsuji et al (2013) for Bunostegos, Arganaceras and Elginia.

36. Orbit, shape: circular, no posterior emargination (0); posterior emargination of orbits (1).

Embrithosaurus:

- SAM-PK-8034: circular, no posterior emargination (0)

Nochelesaurus:

- SAM-PK-6239: circular, no posterior emargination (0)
- SAM-PK-6238: circular, no posterior emargination (0)
- SAM-PK-6240: circular, no posterior emargination (0) dorsoventrally crushed to appear flatter than in life

Bradysaurus:

- NHMUK R1971: circular, no posterior emargination (0)
- NHMUK R49426: circular, no posterior emargination (0)

Note: Lee (1997b): circular orbits in all known pareiasaurs.

37. Circumorbital tuberocities: circumorbital skull elements lacking tubercles or bosses (0); circumorbital tubercles small (1); circumorbital tubercles large (2).

Embrithosaurus:

- SAM-PK-8034: circumorbital tubercles small (1)

Nochelesaurus:

- SAM-PK-6239: circumorbital tubercles small (1)
- SAM-PK-6238: circumorbital tubercles small (1)
- SAM-PK-6240: circumorbital tubercles small (1)

Bradysaurus:

- NHMUK R1971: circumorbital tubercles small (1)
- NHMUK R49426: circumorbital tubercles small (1)

38. Pineal foramen, position: pineal foramen situated about halfway along the interparietal suture (0); placed more anteriorly, close to the frontal-parietal suture (1).

Embrithosaurus:

- SAM-PK-8034: anteriorly positioned (1)

Nochelesaurus:

- SAM-PK-6239: anteriorly positioned (1)
- SAM-PK-6238: anteriorly positioned (1)
- SAM-PK-6240: badly preserved/unprepared

Bradysaurus:

- **NHMUK R1971, CGP/1/2269: anteriorly positioned (1), changed from (?)**
- NHMUK R49426: anteriorly positioned (1)

39. Tabular (supernumerary element): present (0); absent (1).

Embrithosaurus:

- SAM-PK-8034: absent (1)

Nochelesaurus:

- **SAM-PK-6239: absent (1), Van den Brandt *et al*. (2019) changed from (?)**
- SAM-PK-6238: absent (1)
- SAM-PK-6240: absent (1)

Bradysaurus:

- **NHMUK R1971: absent (1), changed from (?)**
- NHMUK R49426: absent (1)

40. Tabular (supernumerary element), form: small, largely an occipital element (0); integrated into skull table (1).

Embrithosaurus:

- SAM-PK-8034: n/a (?)

Nochelesaurus:

- SAM-PK-6239: n/a (?)
- SAM-PK-6238: n/a (?)
- SAM-PK-6240: n/a (?)

Bradysaurus:

- NHMUK: R1971: n/a (?)
- NHMUK R49426: n/a (?)

41. Tabular (supernumerary element), contact: do not contact each other posteriorly (0); very well-developed, make contact posteriorly, excluding the postparietals from the posterior edge of the skull table (1).

Embrithosaurus:

- **SAM-PK-8034: n/a (?), Van den Brandt *et al*. (2019) changed from (0)**

Nochelesaurus:

- SAM-PK-6239: n/a (?)
- SAM-PK-6238: n/a (?)
- SAM-PK-6240: n/a (?)

Bradysaurus:

- NHMUK R1971: n/a (?)
- **NHMUK R49426: n/a (?), Van den Brandt *et al*. (2019) changed from (0)**

42. Postparietal, form: small, largely an occipital element (0); integrated into skull table (1).

Embrithosaurus:

- SAM-PK-8034: integrated into skull table (1)

Nochelesaurus:

- **SAM-PK-6239: integrated into skull table (1), changed from (?)**
- **SAM-PK-6238: integrated into skull table (1), changed from (?)**
- **SAM-PK-6240: integrated into skull table (1), changed from (?)**

Bradysaurus:

- NHMUK R1971: integrated into skull table (1)
- NHMUK R49426: integrated into skull table (1)

43. Postparietal, fusion: paired (0); fused into a single element and exposed well dorsally (1).

Embrithosaurus:

- SAM-PK-8034: single element (1)

Nochelesaurus:

- **SAM-PK-6239: single element (1), changed from (?)**
- **SAM-PK-6238: single element (1) changed from (?)**
- **SAM-PK-6240: single element (1) changed from (?)**

Bradysaurus:

- NHMUK R1971: single element (1)
- NHMUK R49426: single element (1)

44. Expanded quadratojugal (cheek) flange: absent, no cheek flange, quadratojugal (cheek) does not extend below level of tooth row to create a check flange, the ventral surface of the quadratojugal is continuous with and forms a straight edge with that of the maxilla (0); small cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row $0^0 – 40^0$ (1); large cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row 41^0 or more (2).

Embrithosaurus:

- SAM-PK-8034: large cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row 41^0 or more (2).

Nochelesaurus:

- **SAM-PK-6239: small cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row $0^0 – 40^0$ (1), changed from (2)**
- **SAM-PK-6238: small cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row $0^0 – 40^0$ (1), changed from (2)**
- **SAM-PK-6240: small cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row $0^0 – 40^0$ (1), changed from (2)**

Bradysaurus:

- **NHMUK R1971: small cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row 0^0 – 40^0 (1), changed from (2)**
- NHMUK R49426: small cheek flange present, quadratojugal (cheek) flange extends below the level of the maxillary tooth row 0^0 – 40^0 (1)

45. Jugal, anterior process: does not extend to anterior orbital rim (0); extends at least to level of orbital rim (1).

Embrithosaurus:

- SAM-PK-8034: extends to at least level of orbital rim (1)

Nochelesaurus:

- SAM-PK-6239: extends to at least level of orbital rim (1)
- SAM-PK-6238: extends to at least level of orbital rim (1)
- SAM-PK-6240: extends to at least level of orbital rim (1)

Bradysaurus:

- NHMUK R1971: extends to at least level of orbital rim (1)
- NHMUK R49426: extends to at least level of orbital rim (1)

Note: Does not reach orbital rim in some or all outgroup taxa.

46. Jugal, suture with maxilla: straight, jugal thins out smoothly towards anterior, or upright, but no dramatic vertical 'step' (0); “stepped”, anteriormost tip of jugal very narrow but expands broadly posteriorly along with a dramatic thinning of the posterior process of the maxilla (1).

Embrithosaurus:

- SAM-PK-8034: jugal has straight suture with maxilla (0)

Nochelesaurus:

- SAM-PK-6239: jugal has straight suture with maxilla (0)
- SAM-PK-6238: jugal has straight suture with maxilla (0)
- SAM-PK-6240: jugal has straight suture with maxilla (0)

Bradysaurus:

- NHMUK R1971: jugal has straight suture with maxilla (0)
- NHMUK R49426: jugal has straight suture with maxilla (0)

Note: Zero in all pareaisaurs according to Turner et al (2015) data matrix scores.

47. Quadratojugal, anterior extent: does not reach level of posterior border of orbit (0); reaches posterior border of orbit (1).

Embrithosaurus:

- SAM-PK-8034: quadratojugal reaches posterior border of orbit (1)

Nochelesaurus:

- SAM-PK-6239: quadratojugal reaches posterior border of orbit (1)
- SAM-PK-6238: quadratojugal reaches posterior border of orbit (1)

- SAM-PK-6240: quadratojugal reaches posterior border of orbit (1)

Bradysaurus:

- NHMUK R1971: quadratojugal reaches posterior border of orbit (1)
- NHMUK R49426: quadratojugal reaches posterior border of orbit (1)

Note: Seems to be the same in all pareiasaurs.

48. Quadratojugal, ventral margin, ornamentation (bosses): absent, no ornamentation (bosses) on the ventral margin of the quadratojugal (0); present, ornamentation (bosses) on the ventral margin of the quadratojugal (1).

Embrithosaurus:

- SAM-PK-8034: absent, no ornamentation (bosses) on the ventral margin of the quadratojugal (0)

Nochelesaurus:

- SAM-PK-6239: absent, no ornamentation (bosses) on the ventral margin of the quadratojugal (0)
- SAM-PK-6238: absent, no ornamentation (bosses) on the ventral margin of the quadratojugal (0)
- SAM-PK-6240: absent, no ornamentation (bosses) on the ventral margin of the quadratojugal (0)

Bradysaurus:

- NHMUK R1971: absent, no ornamentation (bosses) on the ventral margin of the quadratojugal (0)
- NHMUK R49426: absent, no ornamentation (bosses) on the ventral margin of the quadratojugal (0)

Note: Lee (1997b: 47) meant the ventral surface of cheek with or without bosses as the posterior surface always has bosses. Liu and Bever (2018) data matrix scores still has all basal South African pareiasaurian taxa and all outgroup taxa as no bosses on ventral margin of cheek (0) and all other pareisaurs with ventral bosses (1), so this is the real intention of the character.

49. Junction of skull table and cheek: both flat surfaces, form a distinct angle where they meet, particularly behind the orbits (0); postorbital portion of this junction is rounded, no clear edge between these two surfaces behind the orbit (1).

Embrithosaurus:

- SAM-PK-8034: both flat surfaces, skull table and cheek form a distinct angle (0)

Nochelesaurus:

- SAM-PK-6239: both flat surfaces, skull table and cheek form a distinct angle (0)
- SAM-PK-6238: both flat surfaces, skull table and cheek form a distinct angle (0)

- SAM-PK-6240: both flat surfaces, skull table and cheek form a distinct angle (0)

Bradysaurus:

- NHMUK R1971: both flat surfaces, skull table and cheek form a distinct angle (0)
- NHMUK R49426: both flat surfaces, skull table and cheek form a distinct angle (0)

50. Cheek ornamentation style (quadratojugal and squamosal): no ornamentation on the posterior or ventral margins of the cheek (0); ornamentation present on the posterior or ventral margins of the cheek in the form of low rounded bosses (1); ornamentation present on the posterior or ventral margins of the cheek in the form of well-developed, more distinct, taller, more pointed bosses (2); ornamentation present on the posterior or ventral margins of the cheek in the form of prominent, conical horns with sharp, pointed tips (3).

Embrithosaurus:

- SAM-PK-8034: ornamentation present on the posterior or ventral margins of the cheek in the form of low rounded bosses (1)

Nochelesaurus:

- SAM-PK-6239: well-developed, more distinct, taller, more pointed (2)
- SAM-PK-6238: well-developed, more distinct, taller, more pointed (2)
- SAM-PK-6240: well-developed, more distinct, taller, more pointed (2)

Bradysaurus:

- NHMUK R1971: ornamentation present on the posterior or ventral margins of the cheek in the form of low rounded bosses (1)
- NHMUK R49426: ornamentation present on the posterior or ventral margins of the cheek in the form of low rounded bosses (1)

51. Temporal emargination (otic notch): absent, or very small (0), emargination present on the posterior border of the cheek, in the dorsal portion of the squamosal, just below the occipital shelf of the supratemporal, being horizontal and extending medially along the internal surface of the squamosal.

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- SAM-PK-6239: damaged/missing
- SAM-PK-6238: present (1)

- SAM-PK-6240: badly preserved, unprepared

Bradysaurus:

- NHMUK R1971: present (1)
- NHMUK R49426: present (1)

52. Temporal, otic notch, position: restricted to posterior half of cheek (0); closely approaches the orbital margin (1).

Embrithosaurus:

- SAM-PK-8034: posterior half of cheek (0)

Nochelesaurus:

- SAM-PK-6239: ?
- SAM-PK-6238: posterior half of cheek (0)
- SAM-PK-6240: ?

Bradysaurus:

- NHMUK R1971: posterior half of cheek (0)
- NHMUK R49426: posterior half of cheek (0)

53. Temporal, ventral emargination: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: absent (0)

Nochelesaurus:

- SAM-PK-6239: absent (0)
- SAM-PK-6238: absent (0)
- SAM-PK-6240: absent (0)

Bradysaurus:

- NHMUK R1971: absent (0)
- NHMUK R49426: absent (0)

Note: Only present in outgroups according to Turner et al (2015) data matrix scores.

54. Postorbital region of skull, length: length at least equals anteroposterior extension of orbit or is longer (0); postorbital region shorter than anteroposterior extension of orbit (1).

Embrithosaurus:

- SAM-PK-8034: (1) postorbital region short

Nochelesaurus:

- SAM-PK-6239: (1) postorbital region short
- SAM-PK-6238: (1) postorbital region short
- SAM-PK-6240: (1) postorbital region short

Bradysaurus:

- NHMUK R1971: (1) postorbital region short
- NHMUK R49426: (1) postorbital region short

Note: Strange. All pareiasaurs are scored as (1) short postorbital region, and two outgroups are scored as (0), when in fact all pareiasaurs have a postobital region longer than the length of the orbit! Data left as is.

55. Frontal, contribution to the orbit: present (0); frontals excluded from the orbit by contact between the prefrontal and postfrontal (1).

Embrithosaurus:

- SAM-PK-8034: frontals excluded from orbit (1)

Nochelesaurus:

- SAM-PK-6239: frontals excluded from orbit (1)
- SAM-PK-6238: frontals excluded from orbit (1)
- SAM-PK-6240: frontals excluded from orbit (1)

Bradysaurus:

- NHMUK R1971: frontals excluded from orbit (1)
- NHMUK R49426: frontals excluded from orbit (1)

Note: Lee (1995): Frontals excluded from the orbit in all adequately known pareiasaurs.

56. Frontal, shape: slim and long, four times as long as wide (0); frontals short, with a length not more than two times the width (1).

Embrithosaurus:

- SAM-PK-8034: frontals short (1)

Nochelesaurus:

- SAM-PK-6239: frontals short (1)
- SAM-PK-6238: frontals short (1) length just over 2 times its width
- SAM-PK-6240: badly preserved, unprepared

Bradysaurus:

- NHMUK R1971: frontals short (1)
- NHMUK R49426: frontals short (1)

Note: Lee (1995) Frontals short with a length not more than two times the width in all adequately known pareiasaurs.

57. Frontal, central boss: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: frontal central boss present (1)

Nochelesaurus:

- SAM-PK-6239: frontal central boss present (1)
- SAM-PK-6238: frontals central boss present (1)
- SAM-PK-6240: badly preserved, unprepared

Bradysaurus:

- NHMUK R1971: frontal central boss present (1)
- NHMUK R49426: frontal central boss present (1)

Note: New character, Bunostegos cranial paper.

58. Boss ornamentation: dermal bosses of skull bones have no central pointed horn (0); dermal bosses of cranial bones have a central long, pointed horn (1).

Embrithosaurus:

- SAM-PK-8034: bosses of skull bones have no central pointed horn (0)

Nochelesaurus:

- SAM-PK-6239: bosses of skull bones have no central pointed horn (0) but bosses are more distinct than *B.baini, Embrithosaurus*
- SAM-PK-6238: bosses of skull bones have no central pointed horn (0) but bosses are distinct than (although most are badly eroded down or smoothed over this specimen)
- SAM-PK-6240: bosses of skull bones have no central pointed horn (0) but bosses are distinct.

Bradysaurus:

- NHMUK R1971: bosses of skull bones have no central pointed horn (0)
- NHMUK R49426: bosses of skull bones have no central pointed horn (0)

Note: Jalil and Janvier (2005) new character, separates Arganaceras and Elginia from the other pareiasaurs.

Lower Jaw: (characters 59-64)

59. Jaw articulation, position: anterior to occiput (0); even with occiput (1).

Embrithosaurus:

- SAM-PK-8034: jaw articulation anterior to occiput (0)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: jaw articulation anterior to occiput (0)
- SAM-PK-6240: jaw articulation anterior to occiput (0)

Bradysaurus:

- NHMUK R1971: jaw articulation anterior to occiput (0)
- NHMUK R49426: jaw articulation anterior to occiput (0)

Note: Jaw articulation anterior to occiput in all pareiasaurs except Sanchuansaurus and some outroups according to Turner et al. (2015) data matrix scores.

60. Mandibular symphysis: splenial is excluded from the mandibular symphysis (0); splenial forms the ventral portion of the mandibular symphysis (1).

Embrithosaurus:

- SAM-PK-8034: splenial forms the ventral portion of the mandibular symphysis (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: splenial forms the ventral portion of the mandibular symphysis (1)
- SAM-PK-6240: splenial forms the ventral portion of the mandibular symphysis (1)

Bradysaurus:

- NHMUK R1971: splenial forms the ventral portion of the mandibular symphysis (1)
- NHMUK R49426: splenial forms the ventral portion of the mandibular symphysis (1)

Note: Lee (1995): Splenial forms the ventral portion of the mandibular symphysis in all adequately known pareiasaurs.

61. Angular, boss: absent, ventral surface of the angular is smooth (0); boss is present (1).

Embrithosaurus:

- SAM-PK-8034: angular boss present (1)

Nochelesaurus:

- SAM-PK-6239: angular boss present (1)
- SAM-PK-6238: angular boss present (1)
- SAM-PK-6240: angular boss present (1)

Bradysaurus:

- NHMUK R1971: angular boss present (1)
- NHMUK R49426: angular boss present (1)

62. Angular, boss, form: low and rounded (0, prev. 1); well developed with a prominent, pointed tubercle (1, prev. 2).

Embrithosaurus:

- SAM-PK-8034: angular boss well developed (1)

Nochelesaurus:

- SAM-PK-6239: angular boss well developed (1)
- SAM-PK-6238: angular boss well developed (1)
- SAM-PK-6240: angular boss well developed (1)

Bradysaurus:

- NHMUK R1971: angular boss well developed (1)
- NHMUK R49426: angular boss well developed (1)

63. Articular, retroarticular process, dorsal projection: without a projection, tapers gradually to end (0); small projection (“dorsal lump” of Lee, 1997a) present at the very posterior end of the retroarticular process (1).

Embrithosaurus:

- SAM-PK-8034: small projection present (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: small projection present (1)
- SAM-PK-6240: small projection present (1)

Bradysaurus:

- NHMUK R1971: small projection present (1)
- NHMUK R49426: small projection present (1)

Note: Lee (1995): a small to moderate projection with a rounded end is present in all adequately known pareiasaurs.

64. Articular (region), lateral shelf: absent, the lateral surface of the articular region is smooth (0); present, there is a lateral extension of the surangular or articular, the lateral surface of the effected element extends dorsolaterally (1).

Embrithosaurus:

- SAM-PK-8034: lateral surface of articular/surangular extends dorsolaterally (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- **SAM-PK-6238: lateral surface of articular/surangular extends dorsolaterally (1), changed from (?)**
- **SAM-PK-6240: lateral surface of articular/surangular extends dorsolaterally (1), changed from (?)**

Bradysaurus:

- NHMUK R1971: lateral surface of articular/surangular extends dorsolaterally (1)
- NHMUK R49426: lateral surface of articular/surangular extends dorsolaterally (1)

Dentition: (characters 65-73)

65. Teeth, labiolingual compression (anteroposteriorly expanded): teeth not labio-lingually compressed (0); teeth labio- lingually compressed, leaf-shaped, with small denticles on the tooth crown (1); labio- lingual compression very pronounced, giving the marginal teeth a fan shape (2).

Embrithosaurus:

- SAM-PK-8034: leaf-shaped, with small denticles (1)

Nochelesaurus:

- SAM-PK-6239: leaf-shaped, with small denticles (1)
- SAM-PK-6238: leaf-shaped, with small denticles (1)
- SAM-PK-6240: leaf-shaped, with small denticles (1)

Bradysaurus:

- NHMUK R1971: leaf-shaped, with small denticles (1)

- NHMUK R49426: leaf-shaped, with small denticles (1)

66. Teeth, cusp arrangement: three central cusps close together, more lateral cusps farther apart and spaced farther apart from each other than these central three (0); cusps regularly spaced along the tooth crown (1).

Embrithosaurus:

- SAM-PK-8034: three central cusps close together, more lateral cusps further apart and spaced further apart from each other (0)

Nochelesaurus:

- SAM-PK-6239: three central cusps close together, more lateral cusps further apart and spaced further apart from each other (0)
- SAM-PK-6238: three central cusps close together, more lateral cusps further apart and spaced further apart from each other (0)
- SAM-PK-6240: three central cusps close together, more lateral cusps further apart and spaced further apart from each other (0)

Bradysaurus:

- NHMUK R1971: three central cusps close together, more lateral cusps further apart and spaced further apart from each other (0)
- NHMUK R49426: three central cusps close together, more lateral cusps further apart and spaced further apart from each other (0)

67. Maxillary teeth, orientation: maxillary teeth oriented vertically, teeth point directly downwards (0); alveolar ridge inflected towards the palate, teeth oriented ventromedially (1).

Embrithosaurus:

- SAM-PK-8034: maxillary teeth oriented vertically, teeth point downwards (0)

Nochelesaurus:

- SAM-PK-6239: maxillary teeth oriented vertically, teeth point downwards (0)
- SAM-PK-6238: maxillary teeth oriented vertically, teeth point downwards (0)
- SAM-PK-6240: maxillary teeth oriented vertically, teeth point downwards (0)

Bradysaurus:

- NHMUK R1971: alveolar ridge inflected towards the palate, teeth oriented ventromedially (1)
- NHMUK R49426: alveolar ridge inflected towards the palate, teeth oriented ventromedially (1)

Note: only inwards in B. baini, P. nasicornis and Sanchaunsaurus.

68. Upper jaw teeth (premaxilla and maxilla), number on each side: 20 or more (0), 18 or less (1).

Embrithosaurus:

- **SAM-PK-8034: 18 or less (1), Van den Brandt *et al*. (2019) changed from (0)**

Nochelesaurus:

- **SAM-PK-6239: 18 or less (1), changed from (0) but mandibular teeth are 19.**
- SAM-PK-6238: less than or equal to 18 (1)
- SAM-PK-6240: less than or equal to 18 (1)

Bradysaurus:

- NHMUK R1971: (0) 20 or more.

69. Maxillary teeth, cusp number: conical, single cusp (0); 2–7 cusps on each maxillary tooth (1); 7–9 cusps (2); 9–11 cusps (3); more than 11 cusps (4).

Embrithosaurus:

- SAM-PK-8034: 7-9 cusps (2=1)

Nochelesaurus:

- **SAM-PK-6239: 7-9 cusps (2=1), changed from (1=0)**
- **SAM-PK-6238: 7-9 cusps (2=1), changed from (1=0)**
- SAM-PK-6240: 2–7 cusps on each maxillary tooth (1=0)

Bradysaurus:

- **SAM-PK-K11638: 7-9 cusps (2=1), changed from (1=0)**
- NHMUK R1971: 2–7 cusps on each maxillary tooth (1=0)

70. Mandibular teeth, cusp number: conical, without cusps (0); 2–7 cusps on each mandibular tooth (1); 7–9 cusps (2); 9–11 cusps (3); more than 11 cusps (4).

Embrithosaurus:

- SAM-PK-8034: 7-9 cusps (2)

Nochelesaurus:

- **SAM-PK-6239: 7-9 cusps (2), changed from (1)**
- **SAM-PK-6238: 7-9 cusps (2), changed from (1)**
- SAM-PK-6240: 2–7 cusps on each mandibular tooth (1)

Bradysaurus:

- NHMUK R1971: 2–7 cusps on each mandibular tooth (1)
- **SAM-PK-K11638: 7-9 cusps (2), changed from (1)**
- NHMUK R49426:

71. Mandibular teeth, lingual surface, shape: smooth (0); has a distinct, triangular lingual ridge, narrowing towards the crown of the tooth (1).

Embrithosaurus:

- SAM-PK-8034: smooth (0)

Nochelesaurus:

- **SAM-PK-6239: ridge (1), changed from (?)**
- SAM-PK-6238: has a distinct, triangular lingual ridge, narrowing towards the crown of the tooth (1).
- SAM-PK-6240: smooth (0)

Bradysaurus:

- NHMUK R1971: smooth (0)
- **NHMUK R49426: ridge (1), changed from (0)**

72. Marginal teeth, lingual surface, horizontal cingulum: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: cingulum absent (0)

Nochelesaurus:

- **SAM-PK-6239: cingulum present (1), changed from (?)**
- **SAM-PK-6238: cingulum present (1), changed from (?)**
- SAM-PK-6240: cingulum absent (0)

Bradysaurus:

- NHMUK R1971: cingulum absent (0)
- NHMUK R49426: cingulum absent (0)

73. Marginal teeth, lingual surface, cingulum, extent: on some maxillary teeth (0); on most maxillary teeth (1).

Embrithosaurus:

- SAM-PK-8034(?)cingulum absent on all marginal (maxillary and mandibular) teeth (?)

Nochelesaurus:

- SAM-PK-6239: (?)cingulum absent on all maxillary teeth (although insipient cingula present on certain mandibular teeth)
- SAM-PK-6238: (?)cingulum absent on all maxillary teeth (although insipient cingula present on certain mandibular teeth)
- SAM-PK-6240: (?)cingulum absent on all maxillary teeth

Bradysaurus:

- NHMUK: R1971: n/a as cingula absent on all marginal teeth (?)
- NHMUK R49426: n/a as cingula absent on all marginal teeth (?)

Note: Based on Honania work by Xu et al. (2015).

Palate: (characters 74-78)

74. Pterygoid, transverse flange, dentition: teeth present on the transverse flange of the pterygoid (0); no dentition on the transverse flange of the pterygoid (1).

Embrithosaurus:

- SAM-PK-8034: teeth present on the transverse flange of the pterygoid (0)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: no denticals preserved
- SAM-PK-6240: not preserved
- CGP-JA-109: teeth present on the transverse flange of the pterygoid (0)

Bradysaurus:

- NHMUK R1971: teeth present on the transverse flange of the pterygoid (0)
- NHMUK R49426: (?)

Note: Lee (1995:499): pterygoid transverse flange teeth present in all pareiasaurs.

75. Pterygoid, anterior extent: reaches level of choana (0); posterior to choana (1).

Embrithosaurus:

- SAM-PK-8034: posterior to choana (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: posterior to choana (1)
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: posterior to choana (1)
- NHMUK R49426: posterior to choana (1)

Note: Posterior to choana in all pareiasaurs according to Turner et al (2015) data matrix scores.

76. Pterygoid, quadrate ramus: merges smoothly into transverse flange without distinctive excavation (0); deep excavation on posterolateral surface (1).

Embrithosaurus:

- **SAM-PK-8034: deep excavation on posterolateral surface (1), changed from (?)**

Nochelesaurus:

- **SAM-PK-6239: deep excavation on posterolateral surface (1), changed from (?)**
- SAM-PK-6238:
- SAM-PK-6240: deep excavation on posterolateral surface (1)

Bradysaurus:

- NHMUK R1971: deep excavation on posterolateral surface (1)
- NHMUK R49426: deep excavation on posterolateral surface (1)

77. Palatal teeth: medial rows of palatal denticles parallel and close together and to the medial axis of the skull (0); medial rows of palatal denticles widely separated, converging anteriorly (1).

Embrithosaurus:

- SAM-PK-8034: converge anteriorly (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: converge anteriorly (1)
- SAM-PK-6240: not preserved

Bradysaurus:

- NHMUK R1971: converge anteriorly (1)
- NHMUK R49426: converge anteriorly (1)

78. Caniniform region: present (0); absent (1).

Embrithosaurus:

- SAM-PK-8034: absent (1)

Nochelesaurus:

- SAM-PK-6239: absent (1)
- SAM-PK-6238: absent (1)
- SAM-PK-6240: absent (1)

Bradysaurus:

- NHMUK R1971: absent (1)
- NHMUK R49426: absent (1)

Vertebrae (characters 79-86)

79. Atlas-axis fusion: pleurocentrum of the atlas and axial intercentrum fused (0); atlas pleurocentrum separate from the axial intercentrum (1).

Embrithosaurus:

- **SAM-PK-8034: altas pleurocentrum separate from the axial intercentrum (1), changed from (0)**

Nochelesaurus:

- SAM-PK-6239: not preserved
- **SAM-PK-6238: altas pleurocentrum separate from the axial intercentrum (1), changed from (?)**

Bradysaurus:

- **NHMUK R1971: altas pleurocentrum separate from the axial intercentrum (1), changed from (?)**

80. Presacral vertebrae, number: more than 20 presacral vertebrae (0); 20 presacral vertebrae (1); 19 or fewer presacral vertebrae (2).

Embrithosaurus:

- **SAM-PK-8034: 19 or fewer presacral vertebrae (2), changed from (1)**

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)

Bradysaurus:

- **NHMUK R1971: 19 or fewer presacral vertebrae (2), changed from (1)**
- NHMUK R49426: 19 or fewer presacral vertebrae (2)

81. Lumbar vertebrae: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: (0) absent

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- **SAM-PK-11948: (0) absent, changed from (?)**

Bradysaurus:

- NHMUK R1971: (0) absent
- NHMUK: R49426: (0) absent

82. Sacral vertebrae, number: two (0); three (1); four (2); five (3).

Embrithosaurus:

- SAM-PK-8034: four (2)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- **SAM-PK-11596: four (2), changed from (?) for *Nochelesaurus***

Bradysaurus:

- NHMUK R1971: four (2)
- NHMUK: R49426: four (2)

83. Caudal vertebrae, number (tail length): long, with more than 25 caudal vertebrae (0); short, less than 25 caudal vertebrae (1).

Embrithosaurus:

- SAM-PK-8034: long, with more than 25 caudal vertebrae (0)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- **SAM-PK-11596: long, with more than 25 caudal vertebrae (0), changed from (?)**

Bradysaurus:

- NHMUK R1971:long, with more than 25 caudal vertebrae (0)

84. Caudal vertebrae, lateral projections: generally present on the first five but never on more than 9 of the first (most anterior) caudal vertebrae (0); prominent lateral projections on at least the first 9 caudal vertebrae (1).

Embrithosaurus:

- SAM-PK-8034: prominent lateral projections on at least the first 9 caudal vertebrae (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- SAM-PK-11948: not accessible (?)

Bradysaurus:

- NHMUK R1971: prominent lateral projections on at least the first 9 caudal vertebrae (1)

85. Caudal vertebrae, lateral projections, shape: projections form an 'L', as their distal portions are recurved posteriorly parallel to the axis of the body (0); projections almost straight and directed laterally (1).

Embrithosaurus:

- SAM-PK-8034: projections almost straight and directed laterally (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- SAM-PK-11948: not accessible (?)

Bradysaurus:

- NHMUK R1971: projections form an 'L', as their distal portions are recurved posteriorly parallel to the axis of the body (0)

86. Caudal vertebrae, hemal arch, insertion: between two caudal vertebrae (0); articulate with only one centrum via a facet of articulation found on posteroventral projections of the centra (1).

Embrithosaurus:

- SAM-PK-8034: articulate with only one centrum via a facet of articulation found on posteroventral projections of the centra (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- SAM-PK-11948: not accessible (?)

Bradysaurus:

- NHMUK R1971: articulate with only one centrum via a facet of articulation found on posteroventral projections of the centra (1)

Scapulocoracoid: (characters 87-91)

87. Scapula, blade, length: less than two times the glenoid fossa diameter (0), between two and three times the glenoid fossa diameter (1), greater than or equal to three times the glenoid fossa diameter (2).

Embrithosaurus:

- SAM-PK-8034: between two and three times glenoid diameter (1)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: between two and three times glenoid diameter (1)

Bradysaurus:

- NHMUK R1971: between two and three times glenoid diameter (1)

88. Scapula, blade, shape: straight preaxial and postaxial margins expanding gradually (0); preaxial and postaxial margins are curved, expansion pronounced dorsally at the distal end (flared) (1).

Embrithosaurus:

- SAM-PK-8034: expansion pronounced dorsally, flared (1)

Nochelesaurus:

- SAM-PK-6239: not well preserved
- **SAM-PK-6238, SAM-PK-11948: expansion gradual, straight preaxial and postaxial margins (0), changed from (?)**

Bradysaurus:

- NHMUK R1971:expansion pronounced dorsally, flared (1)

89. Acromion process: absent (0), present (1).

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- SAM-PK-6239: present (1)
- SAM-PK-6238: present (1)

Bradysaurus:

- NHMUK R1971: present (1)

90. Posterior coracoid, dorsal edge: almost horizontal, meets the posterior border of the scapula at an angle of less than 135^0 (0); dorsal edge of the posterior coracoid is oriented posteroventrally, forms an angle of more than 135^0 with the posterior border of the scapula (1).

Embrithosaurus:

- SAM-PK-8034: less than 135^0 (0)

Nochelesaurus:

- SAM-PK-6239: not reserved
- SAM-PK-6238: less than 135^0 (0)

Bradysaurus:

- NHMUK R1971: less than 135^0 (0)

91. Cleithrum: present (0); absent (1).

Embrithosaurus:

- SAM-PK-8034: present (0)

Nochelesaurus:

- SAM-PK-6239: present (0)
- SAM-PK-6238: present (0)

Bradysaurus:

- NHMUK R1971:present (0)

Humerus: (characters 92-104)

92. Humerus, torsion: the planes of proximal and distal expansion makes an angle of greater than or equal to 60^0 (0), less than or equal to 45^0 (1), less than or equal to 20^0 (2).

Embrithosaurus:

- **SAM-PK-8034: the planes of proximal and distal expansion makes an angle of greater than or equal to 60^0 (0), changed from (1)**

Nochelesaurus:

- SAM-PK-6239: 20^0= less than to equal to 20 (2)
- SAM-PK-6238: $30\text{-}40^0$= less than or equal to 45^0 (1)

Therefore *Nochelesaurus* = between 20 and 45^0 (1)

Bradysaurus:

- NHMUK R1971: damaged
- **SAM-PK-5624: the planes of proximal and distal expansion makes an angle of greater than or equal to 60^0 (0) $70\text{-}80^0$**
- **SAM-PK-3718: the planes of proximal and distal expansion makes an angle of greater than or equal to 60^0 (0) 70^0**

Note: Therefore *Bradysaurus baini* = $70\text{-}80^0$ (0), changed from (?)

93. Ectepicondyle, form: narrow and rounded (0); preaxially expanded wide rectangular flange (1).

Embrithosaurus:

- SAM-PK-8034: wide preaxially expanded flange (1).

Nochelesaurus:

- SAM-PK-6239: wide preaxially expanded flange (1).
- SAM-PK-6238: wide preaxially expanded flange (1).

Bradysaurus:

- NHMUK R1971: wide preaxially expanded flange (1).

94. Ectepicondylar foramen: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: present (1).

Nochelesaurus:

- SAM-PK-6239: present (1).
- SAM-PK-6238: present (1).

Bradysaurus:

- NHMUK R1971: present (1).

95. Entepicondyle, form: postaxially expanded wide rectangular flange (0); narrow and rounded (1).

Embrithosaurus:

- SAM-PK-8034: postaxially expanded wide rectangular flange (0)

Nochelesaurus:

- SAM-PK-6239: postaxially expanded wide rectangular flange (0)
- SAM-PK-6238: not preserved, but highly likely to be the same as SAM-PK-6239 (0)

Bradysaurus:

- NHMUK R1971: not preserved
- Other specimens: postaxially expanded wide rectangular flange (0)

96. Entepicondylar foramen, form: completely enclosed (0); an 'open groove' (1).

Embrithosaurus:

- SAM-PK-8034: completely enclosed (0).

Nochelesaurus:

- SAM-PK-6239: completely enclosed (0).
- SAM-PK-6238: completely enclosed (0).

Bradysaurus:

- NHMUK R1971: completely enclosed (0) partially preserved

97. Entepicondylar foramen, location: exposed in distal dorsal (extensor) view (0); ventral (flexor) view (1)

Embrithosaurus:

- SAM-PK-8034: exposed in distal dorsal (extensor) view (0)

Nochelesaurus:

- SAM-PK-6239: exposed in distal dorsal (extensor) view (0)
- SAM-PK-6238: exposed in distal dorsal (extensor) view (0)

Bradysaurus:

- NHMUK R1971: exposed in distal dorsal (extensor) view (0) partially preserved

98. Epicondylar distal projection: epicondyles do not project (far) past the radial and ulnar articulation surfaces (0); project past the radial and ulnar articulation surfaces, appearing 'forked' (1).

Embrithosaurus:

- SAM-PK-8034: epicondyles do not project (far) (0)

Nochelesaurus:

- SAM-PK-6239: epicondyles do not project (far) (0)
- SAM-PK-6238: epicondyles do not project (far) (0)

Bradysaurus:

- **NHMUK R1971: project past the radial and ulnar articulation surfaces, appearing 'forked' (1), changed from (0)**

99. Entepicondyle and ectepicondyle relative size: equal (0); ectepicondyle reduced (1).

Embrithosaurus:

- **SAM-PK-8034: equal (0); changed from (1)**

Nochelesaurus:

- **SAM-PK-6239: equal (0); changed from (?)**
- **SAM-PK-6238: equal (0); changed from (?)**

Bradysaurus:

- NHMUK R1971: equal (0).

100. Radial condyle of the humerus, location: entirely ventral (0); more terminally, encroaches onto the distal end of the humerus (1).

Embrithosaurus:

- SAM-PK-8034: location: entirely ventral (0)

Nochelesaurus:

- SAM-PK-6239: location: entirely ventral (0)
- SAM-PK-6238: location: entirely ventral (0)

Bradysaurus:

- NHMUK R1971: location: entirely ventral (0)

101. Humerus, ulnar articulation surface, form: groove bordered posteriorly by a faint ridge (0); groove bordered posteriorly by a prominent tubercle (1).

Embrithosaurus:

- SAM-PK-8034: ulnar groove posterior border prominant rim, but no tubercle(0)

Nochelesaurus:

- SAM-PK-6239: ulnar groove posterior border prominant rim but no tubercle (0)
- SAM-PK-6238: ulnar groove posterior border prominant rim but no tubercle (0)

Bradysaurus:

- NHMUK R1971: ulnar articulation groove posterior border EXTREMELY prominant ridge, but no tubercle(0)

102. Humerus, intercondylar depression, transverse ridge (intercondylar ridge border): on the distal dorsal end of the humerus, a transverse ridge separating the ulnar fossa (intercondylar depression) from the articulation (olecranon fossa) surface is absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- **SAM-PK-6239: present (1), changed from (0)**
- **SAM-PK-6238: present (1), changed from (0)**

Bradysaurus:

- **NHMUK R1971: definitely present, very prominent (1) changed from (0)**

103. Humerus, ulnar fossa (intercondylar depression), depth: shallow depression (0); deep fossa (1)

Embrithosaurus:

- SAM-PK-8034: shallow depression (0)

Nochelesaurus:

- **SAM-PK-6239: deep fossa (1), changed from 0**
- **SAM-PK-6238: deep fossa (1) , changed from 0**

Bradysaurus:

- NHMUK R1971: very deep fossa (1)

104. Humerus, ulnar fossa (intercondylar depression), width: ulnar fossa is much wider than the olecranon process (0); ulnar fossa is 'narrow', same width as olecranon process (1).

Embrithosaurus:

- SAM-PK-8034: ulnar fossa is wider than olecranon process (0)

Nochelesaurus:

- SAM-PK-6239: ulnar fossa is wider than olecranon process (0)
- SAM-PK-6238: ulnar fossa is wider than olecranon process (0)

Bradysaurus:

- NHMUK R1971: ulnar fossa is wider than olecranon process (0)

Ulna: (characters 105, 106)

105. Ulna, olecranon process, articulation surface: oriented medially (0); oriented terminally (1).

Embrithosaurus:

- SAM-PK-8034: oriented medially (anteriorly) (0)
- CGP CBT 112: oriented medially (anteriorly) (0)
- FMNH UR 2443: oriented medially (anteriorly) (0)

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: oriented medially (anteriorly) (0)

Bradysaurus:

- NHMUK R1971: oriented medially (anteriorly) (0)

106. Ulna, olecranon process, size: well developed, greatly expanded past the most preaxial surface of the proximal articulation surface (0); reduced, nearly level with preaxial surface of the proximal articulation surface (1).

Embrithosaurus:

- SAM-PK-8034: reduced, nearly level with preaxial surface of the proximal articulation surface (1)
- CGP CBT 112: well developed, greatly expanded past the most preaxial surface of the proximal articulation surface (0)
- FMNH UR 2443: well developed, greatly expanded past the most preaxial surface of the proximal articulation surface (0)

(I have used well developed, greatly expanded past the most preaxial surface of the proximal articulation surface (0) for *Embrithosaurus*).

Nochelesaurus:

- SAM-PK-6239: not preserved
- SAM-PK-6238: reduced, nearly level with preaxial surface of the proximal articulation surface (1)
- Other specimens: well developed, greatly expanded past the most preaxial surface of the proximal articulation surface (0)

(I have used well developed, greatly expanded past the most preaxial surface of the proximal articulation surface (0) for *Nochelesaurus*).

Bradysaurus:

- NHMUK R1971: well developed, greatly expanded past the most preaxial surface of the proximal articulation surface (0)

Manus: (character 107)

107. Manus, phalangeal formula: 23452, not reduced (0); 23332 reduced (1).

Embrithosaurus:

- 23332 reduced (1).

Nochelesaurus:

- **23332 reduced (1), changed from (?)**

Bradysaurus:

- **23332 reduced (1), changed from (?)**

Sacral Ribs: (character 108)

108. Sacral ribs, second and third: dorsoventral compression is slight (0); strong and sheet-like (1).

Embrithosaurus:

- SAM-PK-8034: second and third: dorsoventral compression is slight (0);

Nochelesaurus:

- **Second and third: dorsoventral compression is slight (0), changed from (?)**

Bradysaurus:

- NHMUK R1971: second and third: dorsoventral compression is slight (0);

Pelvis: (characters 109-119)

109. Ilium, crista sacralis: weakly developed (0); well developed (1).

Embrithosaurus:

- SAM-PK-8034: well developed (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)

Bradysaurus:

- NHMUK R1971: well developed (1)

110. Ilium, blade, expansion: not or only slightly anteriorly (0); well anteriorly (1).

Embrithosaurus:

- SAM-PK-8034: well anteriorly (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- **other *Nochelesaurus* specimens: well anteriorly (1), changed from (?)**

Bradysaurus:

- NHMUK R1971: well anteriorly (1)

111. Ilium, anterior margin, lateral eversion: flat or slightly everted (0); surface strongly everted, oriented almost horizontal (1).

Embrithosaurus:

- SAM-PK-8034: flat or only slightly everted (0).

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- other *Nochelesaurus* specimens (?)

Bradysaurus:

- **NHMUK R1971: surface strongly everted, oriented almost horizontal (1), changed from (0)**

112. Ilium, posterior process: long (0); strongly reduced (1).

Embrithosaurus:

- SAM-PK-8034: strongly reduced (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- **other *Nochelesaurus* specimens: strongly reduced (1), changed from (?)**

Bradysaurus:

- NHMUK R1971: strongly reduced (1)

113. Ilium, shaft, orientation: vertical or posterodorsally inclined (0); anterodorsally inclined, forming an angle with the vertical of more than 20^0 (1); inclined even further anteriorly, forming an angle of more than 45^0 with the vertical (2).

Embrithosaurus:

- **SAM-PK-8034: (1) anterodorsally inclined, forming an angle with the vertical of more than 20^0, changed from (0).**

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- other *Nochelesaurus* specimens (?)

Bradysaurus:

- **NHMUK R1971: (2) inclined even further anteriorly, forming an angle of more than 45^0 with the vertical , changed from (0).**

114. Acetabulum, dorsal buttress: not well developed (0); strongly developed (1).

Embrithosaurus:

- SAM-PK-8034: strongly developed (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- **other *Nochelesaurus* specimens: strongly developed (1), changed**

from (?)

Bradysaurus:

- NHMUK R1971: strongly developed (1)

115. Acetabulum, anterior shape: round (0), notched (1).

Embrithosaurus:

- **SAM-PK-8034: notched (1), changed from (0)**

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- other *Nochelesaurus* specimens (?)

Bradysaurus:

- **NHMUK R1971: notched (1), changed from (0)**

116. Pubis, process on the anterior border: absent (0); present (1). ('lateral pubic process' of Walker, 1973, Gaffney, 1990).

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- **other *Nochelesaurus* specimens: present (1), changed from (?)**

Bradysaurus:

- NHMUK R1971: present (1)

117. Pubis, median process: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- **other *Nochelesaurus* specimens: present (1), changed from (?)**

Bradysaurus:

- NHMUK R1971: present (1)

118. Pelvic symphysis, length: long (0), short (1)

Embrithosaurus:

- SAM-PK-8034: anteroposteriorly short (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- other *Nochelesaurus* specimens (?)

Bradysaurus:

- NHMUK R1971: anteroposteriorly long (0)

119. Pelvic symphysis, dorsoventral thickness: thin (0), thick (1).

Embrithosaurus:

- SAM-PK-8034: thick (1)

Nochelesaurus:

- SAM-PK-6239: not preserved (?)
- SAM-PK-6238: not preserved (?)
- other *Nochelesaurus* specimens (?)

Bradysaurus:

- NHMUK R1971: thin (0)

Femur: (characters 120-125)

120. Femur, head, preaxial expansion: no curvature (0); slight (1); strong (2).

Embrithosaurus:

- SAM-PK-8034: slight (1)

Nochelesaurus:

- SAM-PK-6239: slight (1)

Bradysaurus:

- NHMUK R1971: slight (1)

121. Femur, trochanter major: absent (0); present (1).

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- SAM-PK-6239: present (1) but very small

Bradysaurus:

- NHMUK R1971: present (1)

122. Femur, trochanter major, form: small, slightly thickened (0); large, more distinct (1).

Embrithosaurus:

- SAM-PK-8034: large, more distinct (1)

Nochelesaurus:

- **SAM-PK-6239: small, slight thickening (0), changed from (1)**

Bradysaurus:

- NHMUK R1971: small, slight thickening (0)

123. Femur, postaxial flange, length: limited to proximal region (0); extends entire length of femur (1).

Embrithosaurus:

- SAM-PK-8034: extends entire length of femur (1)

Nochelesaurus:

- SAM-PK-6239: extends entire length of femur (1)

Bradysaurus:

- NHMUK R1971: extends entire length of femur (1)

124. Femur, postaxial flange, width: narrows in the middle of the length of the femur (0); consistently wide, appearing straight (1).

Embrithosaurus:

- **SAM-PK-8034: consistently wide, appearing straight (1), changed from (0).**

Nochelesaurus:

- SAM-PK-6239: consistently wide, appearing straight (1).

Bradysaurus:

- NHMUK R1971: consistently wide, appearing straight (1)

125. Femur, internal trochanter, shape: in ventral view, appears straight (0); proximally curved preaxially (1).

Embrithosaurus:

- SAM-PK-8034: proximally curved preaxially (1)

Nochelesaurus:

- SAM-PK-6239: appears straight (0)

Bradysaurus:

- **NHMUK R1971: proximally curved preaxially (1), changed from (?)**

Tibia: (character 126)

126. Cnemial crest: cnemial crest of the tibia (longitudinal ridge on the dorsal (lateral or external) surface of the tibia) well developed and prominent (0); ridge and accompanying groove much reduced (1).

Embrithosaurus:

- SAM-PK-8034: well developed and prominent (0)

Nochelesaurus:

- SAM-PK-6239: well developed and prominent (0)
- SAM-PK-6238: well developed and prominent (0)

Bradysaurus:

- NHMUK R1971:well developed and prominent (0)

Tarsus: (character 127)

127. Astragalus and calcanium: separate or sutured (0); fused, with the presence of the obturator foramen (1).

Embrithosaurus:

- SAM-PK-8034: fused, with the presence of the obturator foramen

(1)

Nochelesaurus:

- **SAM-PK-6239: fused, with the presence of the obturator foramen (1), changed from (?)**

Bradysaurus:

- NHMUK R1971:fused, with the presence of the obturator foramen (1)

Pes: (characters 128-131)

128. Pes, phalangeal formula: 23454 or 23453 (0); 23343 (1).

Embrithosaurus:

- SAM-PK-8034: (?)
- other *Embrithosaurus* specimens: 23343 (1).

Nochelesaurus:

- SAM-PK-6239: (?)

Bradysaurus:

- NHMUK R1971: (?)

129. Pes, fifth digit: large, always longer than the first pedal digit (0); reduced, slender, shorter than the first pedal digit (1).

Embrithosaurus:

- SAM-PK-8034: (?)
- other *Embrithosaurus* specimens: reduced, slender, shorter than the first pedal digit (1).

Nochelesaurus:

- SAM-PK-6239: (?)

Bradysaurus:

- NHMUK R1971: (?)

130. Pes, metapodial (metacarpal and metatarsal), shape: slender, close to two times as long as wide (0); robust, approximately as wide as long (1).

Embrithosaurus:

- SAM-PK-8034: robust, approximately as wide as long (1).

Nochelesaurus:

- SAM-PK-6239: (?)

Bradysaurus:

- NHMUK R1971: robust, approximately as wide as long (1).

131. Pes, non-terminal phalanges, shape: slender, 50% longer than wide (0); short, as long as wide (1); even shorter and more massive, about two times as wide as long (2).

Embrithosaurus:

- SAM-PK-8034: even shorter and more massive, about two times as wide as long (2)

Nochelesaurus:

- SAM-PK-6239: (?)

Bradysaurus:

- NHMUK R1971: even shorter and more massive, about two times as wide as long (2)

Osteoderms: (characters 132-139)

132. Osteoderms, body coverage: Osteoderms absent on the body (0); present (1). (T:105)

Embrithosaurus:

- SAM-PK-8034: present (1)

Nochelesaurus:

- SAM-PK-6239: present (1)

Bradysaurus:

- NHMUK R1971: present (1)

133. Osteoderms, body coverage, extent: osteoderms form only a longitudinal band closely overlying the vertebral column (0); cover entire dorsal surface of the body including flanks (1).

Embrithosaurus:

- SAM-PK-8034: Osteoderms form only a longitudinal band closely overlying the vertebral column (0)

Nochelesaurus:

- SAM-PK-6239: Osteoderms form only a longitudinal band closely overlying the vertebral column (0)

Bradysaurus:

- NHMUK R1971: Osteoderms form only a longitudinal band closely overlying the vertebral column (0)

134. Osteoderms, appendages: no osteoderms over the appendages (0); fore and hind limbs covered with numerous conical osteoderms (1).

Embrithosaurus:

- SAM-PK-8034: no osteoderms over the appendages (0)

Nochelesaurus:

- SAM-PK-6239: no osteoderms over the appendages (0)

Bradysaurus:

- NHMUK R1971: no osteoderms over the appendages (0)

135. Osteoderm, appearance: dorsal surface of the osteoderms smooth, convex, without a central boss (0); possess a distinct rounded central boss (1); central boss on osteoderm capped by a small conical spine (2).

Embrithosaurus:

- SAM-PK-8034: possess a distinct rounded central boss (1)

Nochelesaurus:

- **SAM-PK-6239: possess a distinct rounded central boss (1), changed from dorsal surface of the osteoderms smooth, convex, without a central boss (0)**

Bradysaurus:

- NHMUK R1971: dorsal surface of the osteoderms smooth, convex, without a central boss (0)

136. Osteoderm, ornamentation: external surface of the osteoderms smooth and without ornamentation (0); osteoderms ornamented with fine, straight, regularly spaced ridges radiating out from a central boss to the edge (1); ridges fewer, larger, lumpier, and less regularly spaced (2).

Embrithosaurus:

- **SAM-PK-8034: ridges fewer, larger, lumpier, and less regularly spaced (2), changed from (0)**

Nochelesaurus:

- **SAM-PK-6239: (?), changed from external surface of the osteoderms smooth and without ornamentation (0)**

Bradysaurus:

- NHMUK R1971: external surface of the osteoderms smooth and without ornamentation (0)

137. Osteoderm, dimension: round and small, with a dimension no larger than diameter of the centra of the dorsal vertebrae (0); osteoderms large, with a maximal length the same as or larger than the dorsal vertebral centra (1).

Embrithosaurus:

- SAM-PK-8034: (0)

Nochelesaurus:

- SAM-PK-6239: (0)

Bradysaurus:

- NHMUK R1971: (0)

138. Osteoderm, position: osteoderms do not touch, separated by a space (0); osteoderms more densely packed, often touching one another, but touching only on the shoulder and pelvic regions, never sutured or articulated over the trunk (1); osteoderms overlapping, articulated or

sutured, forming a continuous layer on the dorsal surface of the body (2).

Embrithosaurus:

- SAM-PK-8034: (0)

Nochelesaurus:

- SAM-PK-6239: (0)

Bradysaurus:

- NHMUK R1971: (0)

139. Gastralia: present (0); absent (1).

Embrithosaurus:

- **SAM-PK-8034: (1), changed from (?)**

Nochelesaurus:

- SAM-PK-6239: (1)

Bradysaurus:

- NHMUK R1971: (1)

APPENDIX C: DATA MATRIX

Character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Millerettidae	0	?	?	0	?	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Owenetta	0	?	0	0	?	0	0	?	?	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	?
Babashkyricus	1	?	?	?	?	?	0	?	?	1	?	0	0	0	0	0	?	1	1	0	0	1	?	1	0	0	0	?	1	0	0	1	0	?	0	1	0	1	0	0
Bamesensis	1	?	?	?	?	?	?	?	?	1	?	?	0	0	0	0	?	1	1	0	0	1	?	1	0	0	0	?	1	1	0	1	0	1	0	1	0	0	0	0
Rhipaeosaurus	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	0	?	?	?	?	?
Nycteroleter	1	?	?	?	?	?	?	?	?	1	?	?	0	0	0	0	?	1	1	0	0	1	0	1	0	0	0	?	1	0	0	1	0	1	0	1	0	1	0	0
Emeroleter	1	?	?	1	0	?	?	?	?	1	?	?	0	0	0	0	?	1	1	0	0	1	?	1	0	0	0	?	1	1	0	1	0	1	0	1	0	0	0	0
Macroleter	1	0	1	1	0	1	0	0	0	1	?	?	0	0	0	0	?	1	1	0	0	1	?	1	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	0
Bradysaurus	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	1	0	2	1	1	1	1	1	1	2	1	1	1	0	0	1	0	0	1	0	0	1	1	1	?
Nochelesaurus	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	0	2	1	1	1	1	1	1	2	1	1	1	0	0	0	0	1	1	0	0	1	1	1	?
Embrithosaurus	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	1	0	2	?	1	1	1	1	1	2	1	1	1	0	0	1	0	0	1	0	0	1	1	1	?
Deltavjatia	1	?	?	1	1	1	0	1	1	0	1	1	1	0	0	1	1	2	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	1	1	0	1
Shihtienfenia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sanchuansaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	?	?	?	?	?	?	?
Honania	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	0	0	?	?	?	?	?	1	?	?
P.peringueyi	1	1	?	1	1	1	0	?	?	0	1	1	1	0	0	1	1	2	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	1	1	0	1
P.nasicornis	1	1	?	1	1	1	0	?	?	0	1	1	1	0	0	1	1	2	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	1	1	0	1
Pareiasaurus	1	1	?	1	1	1	0	?	?	0	1	1	1	1	?	1	1	2	1	1	0	1	?	1	1	1	1	1	0	0	1	0	1	1	0	0	1	1	?	?
Scutosaurus	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0	1	1	0	1
Parasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	1	1	?	?	?	?	?	?	?	?	0	0	?	1	?	?
E.mirabilis	1	1	?	?	?	1	0	?	?	0	1	?	?	?	?	?	?	2	1	?	0	1	1	?	1	1	1	1	0	0	1	?	1	?	1	0	2	1	0	1
Provelosaurus	?	?	?	?	?	1	0	?	?	0	1	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1	0	0	0	0	0	1	0	0	1	?	?	?
Anthodon	1	?	?	?	?	?	?	?	?	0	1	1	1	0	?	1	1	2	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	1	1	?	?
Pumiliopareia	1	?	?	?	?	?	?	?	?	0	1	1	1	0	?	1	1	2	?	1	0	0	?	1	0	1	1	1	0	0	0	0	0	?	0	0	1	1	?	?
Nanoparia	1	?	?	?	?	?	?	?	?	0	1	1	1	0	?	1	1	2	1	1	0	1	?	1	0	1	1	1	0	0	0	0	0	1	0	0	1	1	0	1
Arganaceras	?	?	?	1	1	?	0	1	1	0	1	?	2	1	1	1	1	2	?	1	0	1	?	1	?	?	?	?	1	0	0	?	0	1	1	1	0	1	1	0	1
Obirkovia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bunostegos	1	1	1	?	?	1	1	?	?	0	1	1	1	0	0	1	0	2	1	1	0	1	1	1	2	1	1	1	0	0	0	0	0	1	1	1	0	2	0	0	1
E.wuyongae	?	?	?	1	1	1	0	?	1	0	?	?	2	1	1	1	0	?	?	?	0	1	?	?	?	?	?	1	?	?	?	?	?	1	?	0	2	1	0	1

Character No.	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Millerettidae	0	0	0	0	0	0	0	0	0	0	0	?	0&1	0	0	0	?	?	0	?	0	?	0	0	0	?	0	0	0	0	0	0	?	1	0	0	?	0&1	0	0
Owenetta	?	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	?	0	0	0	?	0	?	0	?	0	0	0	0	0	0	?	0	1	1	?	0	1	0
Babashkyricus	0	?	?	0	?	1	?	0	0	1	1	1	0	1	0	0	0	?	?	?	?	?	?	?	0	?	0	0	?	?	0	0	?	0	0	1	?	?	?	?
Bamesensis	0	?	?	0	0&1	1	0	0	0	1	1	1	0	1	0	0	0	?	?	?	?	?	?	?	0	?	0	0	0	?	0	0	?	0	0	0	0	0	?	?
Rhipaeosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	?	?	?	1	?	0	?	?	?	0	?	?	?	0
Nycteroleter	0	0	0	0	0	0	0	?	0	1	1	1	0	1	0	0	0	?	1	0	0	?	?	?	0	0	0	0	0	0	0	0	?	0	0	1	?	1	?	?
Emeroleter	0	?	?	0	0	0	0	0	0	1	1	1	0	1	0	0	0	?	1	?	0	?	?	?	0	0	0	0	0	0	0	0	?	0	?	0	0	1	?	0
Macroleter	0	1	1	0	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	0	?	0	0	0	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0
Bradysaurus	?	1	1	1	1	0	1	0	0	1	1	0	0	1	1	1	1	0	0	1	1	1	1	1	1	0	1	0	1	2	1	0	?	1	1	1	1	1	1	2
Nochelesaurus	?	1	1	1	1	0	1	0	0	2	1	0	0	1	1	1	1	0	0	1	1	1	1	1	1	0	0	1	1	2	1	1	?	1	1	1	1	1	1	?
Embrithosaurus	?	1	1	2	1	0	1	0	0	1	1	0	0	1	1	1	1	0	0	1	1	1	1	1	1	0	0	1	1	2	0	0	?	1	1	1	1	1	1	2
Deltavjatia	0	1	1	2	1	0	1	1	0	2	1	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	0	0	2	3	0	1	0	1	1	1	0	1	?	2
Shihtienfenia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	0	1	1	?	?	?	4	1	1	1	?	?	?	?	1	?	?
Sanchuansaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	1	1	1	0	2	?	?	1	1	?	?	?	?	1	?	?
Honania	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	1	0&1	?	?	2	4	0	1	1	?	?	?	?	1	?	?
P.peringueyi	0	1	1	2	1	0	1	1	1	2	1	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	0	1	2	4	1	0	?	1	1	1	0	1	?	2
P.nasicornis	0	1	1	2	1	0	1	1	1	2	1	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	2	4	1	0	?	1	1	1	0	1	?	?
Pareiasaurus	0	1	1	2	1	0	1	1	1	2	1	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1	0	1	2	4	?	?	?	1	1	?	0	1	0	?
Scutosaurus	0	1	1	2	1	0	1	1	1	2	1	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	0	1	2	4	1	1	0	1	1	1	0	1	?	2
Parasaurus	?	1	?	2	?	?	?	0	?	?	1	0	0	1	?	?	?	?	?	?	?	?	?	?	1	1	?	?	2	?	0	1	?	?	?	?	?	?	?	?
E.mirabilis	1	1	1	1	1	?	1	1	1	3	0	0	0	1	1	1	0	1	0	?	?	?	?	?	1	1	0	1	2	?	?	?	?	?	?	?	?	0	1	?	?
Provelosaurus	?	1	1	2	1	0	1	1	1	2	1	0	0	1	1	1	1	0	0	?	?	?	?	?	1	1	0	1	2	?	?	?	?	?	?	?	?	1	?	?
Anthodon	?	1	1	2	1	0	1	1	1	2	1	0	0	1	1	1	1	0	0	1	1	0	1	1	2	1	0	1	3	4	?	0	?	1	1	?	0	1	?	2
Pumiliopareia	?	1	1	2	1	0	1	1	1	2	1	0	0	1	1	1	1	0	0	1	1	0	?	?	2	1	0	1	3	4	0	?	?	?	1	?	0	1	?	?
Nanoparia	0	1	1	?	1	0	1	?	1	?	1	0	0	1	1	1	1	0	0	?	?	?	?	?	1	?	0	1	?	?	?	0	?	1	1	1	0	1	?	?
Arganaceras	1	1	1	2	1	0	1	1	1	3	1	0	0	1	1	1	0	1	0	?	?	?	?	1	1	1	0	1	2	?	?	1	1	?	1	?	?	1	?	?
Obirkovia	?	?	?	?	?	?	?	1	?	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bunostegos	?	1	1	2	1	0	1	1	0	2	1	0	0	1	1	1	0	0	0	?	?	?	?	?	1	1	0	0	1	?	?	?	?	1	1	?	0	1	?	?
E.wuyongae	1	1	1	1	1	?	1	1	0	2	0	0	0	1	1	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Character No.	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Millerettidae	0	0	0	0	?	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
Owenetta	?	1	0	0	0	0	0	?	0	0	0	0	0	0	1	?	?	0	?	?	?	0	?	?	0	0	0	0	0	0	0	1	0	0	?	?	?	0	0	1
Babashkyricus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bamesensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rhipaeosaurus	?	?	?	?	?	?	?	?	0	0	?	0	1	0	?	0	0	?	?	?	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	?	?	?	1
Nycteroleter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Emeroleter	1	1	0	?	?	?	1	0	1	?	0	0	?	0	?	0	?	?	?	?	?	?	?	?	1	1	0	0	?	?	?	?	0	?	?	?	?	?	?	1
Macroleter	1	1	?	?	?	?	0	?	0	0	0	0	?	1	?	0	0	0	?	0	0	0	?	?	?	?	0	0	?	1	?	?	0	?	0	?	?	?	?	1
Bradysaurus	0	2	0	1	0	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	1	1	2	1	1	1	1	0	0	1
Nochelesaurus	0	2	0	?	?	?	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	?	1	?	1	?	1	?	1	1	?	?	1
Embrithosaurus	0	2	0	1	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1
Deltavjatia	0	2	0	?	1	1	1	1	1	1	1	1	1	1	0	0	0	0	?	0	0	?	1	1	0	1	1	0	?	1	0	1	1	1	?	?	?	?	?	1
Shihtienfenia	0	?	?	?	?	?	2	0	1	0	0	1	1	1	1	0&1	1	?	0	?	0	1	1	1	0	0	?	0	1	1	1	1	0	1	0	?	?	?	?	1
Sanchuansaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Honania	?	2&3	?	?	?	?	2	?	1	1	1	1	1	?	?	1	0	0	?	?	?	0	?	?	?	?	?	?	1	1	0	1	1	1	0	?	?	?	?	1
P.peringueyi	0	2	1	?	?	?	2	0	1	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	0	0	?	1	1	1	1	1	2	1	1	1	1	1	1	2
P.nasicornis	?	2	?	?	?	?	?	?	1	?	?	1	0	?	1	?	?	1	?	0	0	?	?	?	0	0	1	1	1	1	1	1	2	1	1	1	1	1	1	2
Pareiasaurus	0	2	?	?	?	?	1	0	1	1	1	1	1	1	0	0	0	0	?	0	0	1	0	1	0	0	1	0	1	1	1	1	1	1	0	1	1	1	1	1
Scutosaurus	0	?	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	?	0	0	1	?	?	0	0	1	0	1	1	1	1	1	1	0	1	1	1	1	1
Parasaurus	0	2	?	?	?	?	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	?	1	1	1	0	1	?	?	?	1
E.mirabilis	0	?	?	?	1	?	?	?	1	1	1	?	?	1	?	0	0	0	?	?	?	1	?	?	?	?	?	?	1	1	1	1	1	1	?	?	?	?	?	1
Provelosaurus	0	2	?	?	1	?	1	?	1	?	1	2	0	?	?	0	1	?	?	1	1	?	?	?	0	0	?	0	?	0	?	0	1	0	?	?	?	?	?	?	1
Anthodon	0	3	?	?	1	?	1	0	1	1	1	2	0	1	0	0	1	0	0	1	1	1	1	1	1	1	?	0	1	0	0	1	0	1	0	1	1	1	1	0
Pumiliopareia	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nanoparia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Arganaceras	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Obirkovia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bunostegos	?	2	?	?	?	?	1	1	1	0	0	0	?	1	?	?	1	1	1	0	?	1	1	1	0	0	?	0	1	1	0	1	1	1	0	1	1	0	1	2
E.wuyongae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Character No.	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139
Millerettidae	0	?	0	?	0	0	0	0	0	0	0	0	?	0	?	?	?	?	0
Owenetta	0	?	0	?	?	?	0	?	?	0	0	0	?	0	?	?	?	?	?
Babashkyricus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bamesensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rhipaeosaurus	0	?	0	?	0	0	1	0	0	0	0	?	?	?	?	?	?	?	?
Nycteroleter	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Emeroleter	0	?	?	?	?	1	1	0	0	0	0	?	?	?	?	?	?	?	0
Macroleter	?	?	?	?	?	0	1	0	?	1	1	0	?	0	?	?	?	?	1
Bradysaurus	1	0	1	1	1	0	1	?	?	1	2	1	0	0	0	0	0	0	1
Nochelesaurus	1	0	1	1	0	0	1	?	?	?	?	1	0	0	1	?	0	0	1
Embrithosaurus	1	1	1	1	1	0	1	1	1	1	2	1	0	0	1	2	0	0	1
Deltavjatia	1	1	1	1	0	0	1	1	0	1	2	1	0	0	1	0	0	0	1
Shihtienfenia	1	1	1	0	1	?	1	?	?	?	?	1	?	?	1	2	0	?	?
Sanchuansaurus	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Honania	1	0	1	1	1	0	?	?	?	1	?	?	?	?	?	?	?	?	?
P.peringueyi	1	1	1	0	1	0	?	?	?	1	2	1	1	1	1	2	1	1	1
P.nasicornis	?	?	1	0	1	0	1	?	?	1	2	1	1	1	1	2	1	1	1
Pareiasaurus	1	1	1	0	1	0	1	?	?	?	?	1	1	1	1	2	1	1	?
Scutosaurus	1	1	1	0	1	0	1	?	?	1	2	1	1	1	2	2	1	1	1
Parasaurus	1	1	?	?	?	0	1	?	?	1	1	?	?	?	?	?	?	?	1
E.mirabilis	?	?	1	0	1	0	?	?	?	1	2	1	1	1	2	2	1	1	1
Provelosaurus	?	?	1	0	?	0	?	?	?	?	?	1	1	?	1	1	1	1	?
Anthodon	1	1	0	?	1	1	?	?	?	?	?	1	1	?	1	1	1	2	1
Pumiliopareia	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	1	1	2	1
Nanoparia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Arganaceras	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Obirkovia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bunostegos	1	0	0	?	1	?	?	?	?	?	?	?	?	?	1	1	0	?	?
E.wuyongae	?	?	?	?	?	?	?	?	?	?	?	1	1	?	2	2	1	?	?

APPENDIX D: LOCALITY AND STRATIGRAPHIC DATA

Count	Collection Number	Genus	Species	District	Locality (Farm and District)	Member Range	Biozone	GPS/Centroid S	GPS/Centroid E
1	**AMNH FARB 2451 (SAM-PK-9148)**	Embrithosaurus	schwarzi	Prince Albert	Welgemoed, Prince Albert District	Moordenaars	Tap - Upper	-32,7833	21,9667
2	**AMNH FARB 2450 (SAM-PK-9128)**	Embrithosaurus	schwarzi	Prince Albert	Voelfontein, Prince Albert District	lower Moordenaars	Tap - Upper	-32,6833	21,7500
3	**AMNH FARB 5567**	Embrithosaurus	schwarzi	Prince Albert	Leeu Gamka area (Fraserburg Road)	Moordenaars	Tap - Upper	-32,7752	21,9777
4	**AMNH FARB 23880**	Embrithosaurus	schwarzi		Tapinocephalus AZ				
5	**AK 90-1/ CGP/1/853**	Embrithosaurus	schwarzi						
6	**CGP CBT 112**	Embrithosaurus	schwarzi	Sutherland	Portugals River 218	Upper Moordenaars	Tap - Upper	-32,5476	20,9060
7	**GSP R338/CGP/1/796**	Embrithosaurus	schwarzi						
8	**RMS 566/ CGP/1/795**	Embrithosaurus	schwarzi	Fraserburg	BORD VOL WATER, 313, FRASERBERG, NORTHERN CAPE	-	Tap - Upper	-31,6708	21,9278
9	**BP/1/1777**	Embrithosaurus	schwarzi	Prince Albert	Stinkfontein 7	mid-Moordenaars	Tap - upper	-32,6333	21,9833
10	**BP/1/7241**	Embrithosaurus	schwarzi	Beaufort West	Wolwehoek, Hendriks Kraal 298, Beaufort West	Karelskraal Member	Tap - upper	-32,3309	22,0949
11	**BP/1/8014**	Embrithosaurus	schwarzi	Laingsburg	Deesweesfontein, Deesweez Fontein 51	Lower? Moordenaars	Tap - Upper	-32,8922	21,2417
12	**FMNH No data pareiasaur**	Embrithosaurus	schwarzi		No locality data				
13	**FMNH UR 2442**	Embrithosaurus	schwarzi	Prince Albert	Vogelfontein 1, Sewefontein (=E part of Vogelfontein): about 1 mi	lower Moordenaars	Tap - Upper	-32,6833	21,7500
14	**FMNH UR 2443**	Embrithosaurus	schwarzi	Beaufort West	Hottentotsrivier	upper Moordenars	Tap - Upper	-32,4275	21,9107
15	**FMNH UR 2486**	Embrithosaurus	schwarzi	Prince Albert	Abrahamskraal Formation, Western Cape	mid-Moordenaars	Tap - upper	-32,6333	21,9833
16	**NHMUK R7782**	Embrithosaurus	schwarzi	Beaufort West	Hottentots River	upper Moordenars or possibly Karelskraal	Tap - Upper	-32,3833	21,9667
17	**SAM-PK-1207**	Embrithosaurus	schwarzi	Prince Albert	Stinkfontein 7	mid-Moordenaars	Tap - upper	-32,6667	22,0000
18	**SAM-PK-1882**	Embrithosaurus	schwarzi		Unknown				
19	**SAM-PK-3030**	Embrithosaurus	schwarzi	Beaufort West	Hottentots River 296	upper Moordenars or possibly Karelskraal	Tap - Upper	-32,3833	21,9667
20	**SAM-PK-4345**	Embrithosaurus	schwarzi	Beaufort West	Riet Kuil 307	upper Moordenaars	Tap - Upper	-32,4333	22,1167
21	**SAM-PK-4348**	Embrithosaurus	schwarzi	Prince Albert	Wilger Fontein 59	lower Moordenaars	Tap - Upper	-32,8167	21,9167
22	**SAM-PK-4352**	Embrithosaurus	schwarzi	Prince Albert	Veldmans River 9 (Leeu Gamka)	mid Moordenaars	Tap - Upper	-32,7833	21,9667
23	**SAM-PK-5000**	Embrithosaurus	schwarzi	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
24	**SAM-PK-5127**	Embrithosaurus	schwarzi	Beaufort West	Rietfontein 306 (Leeurivier)	mid to upper Moordenaars	Tap - Upper	-32,4333	22,1667
25	**SAM-PK-5590**	Embrithosaurus	schwarzi	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
26	**SAM-PK-6242**	Embrithosaurus	schwarzi	Prince Albert	Rietfontein 56 (Zwarts Siding)	Upper Moordenaars	Tap - Upper	-32,9000	21,8333
27	**SAM-PK-6535**	Embrithosaurus	schwarzi	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
28	**SAM-PK-8034**	Embrithosaurus	schwarzi	Beaufort West	Hogeveld 270 (Hogeveld Lot A)	upper Swaersk. to lower Moord.	Tap - lower/upper boundary	-32,6167	21,5667
29	**SAM-PK-9098**	Embrithosaurus	schwarzi	Beaufort West	Van Der Byls Kraal 265 (Knoffelfontein)	lower Moordenaars	Tap - upper	-32,6667	21,5500
30	**SAM-PK-9105**	Embrithosaurus	schwarzi	Prince Albert	Melkbosch Fontein 75 (Melkbosfontein)	Moordenaars	Tap - Upper	-32,9167	21,7000
31	**SAM-PK-9116**	Embrithosaurus	schwarzi	Prince Albert	Vogelfontein 1 (Voelfontein)	lower Moordenaars	Tap - Upper	-32,6833	21,7500
32	**SAM-PK-9128**	Embrithosaurus	schwarzi	Prince Albert	Vogelfontein 1 (Voelfontein)	lower Moordenaars	Tap - Upper	-32,6833	21,7500
33	**SAM-PK-9148**	Embrithosaurus	schwarzi	Prince Albert	Kruitfontein 33 (Welgemoed)	Moordenaars	Tap - Upper	-32,7833	21,9667
34	**SAM-PK-9165**	Embrithosaurus	schwarzi	Beaufort West	Van Der Byls Kraal 265 (Kruisvlei)	Swaerskraal-lower Moordenaars	Tap - lower/upper boundary	-32,6000	21,5167
35	**SAM-PK-9355**	Embrithosaurus	schwarzi	Sutherland	Roggenkloof 132	Upper Moordenaars	Tap - Upper	-32,5333	20,7333
36	**SAM-PK-11940**	Embrithosaurus	schwarzi	Laingsburg	Vereniging, Drooge Heuvel 55	Swaerskraal-lower Moordenaars	Tap - Upper	-32,9500	21,3833
37	**SAM-PK-12140**	Embrithosaurus	schwarzi	Prince Albert	Rietfontein 56	Upper Moordenaars	Tap - Upper	-32,8833	21,9000
38	**SAM-PK-12252**	Embrithosaurus	schwarzi	Fraserburg	Gannakraal 422 (Beukesplaas)	Karelskraal	Tap - Upper	-32,1000	21,2333
39	**SAM-PK-K00324**	Embrithosaurus	schwarzi	Beaufort West	Zeekoevalley 282 (Zeekoeivlei)	lower Moordenaars	Tap - Upper	-32,6167	21,8000
40	**SAM-PK-K11637**	Embrithosaurus	schwarzi				Tap		
41	**AMNH FARB 5324**	Nochelesaurus	alexanderi	Prince Albert	Leeu Gamka area (Fraserburg Road)	Moordenaars	Tap - Upper	-32,7752	21,9777
42	**CBT 114/ CGP/1/812**	Nochelesaurus	alexanderi	Sutherland	DE VREEDE 133	Upper Moordenaars	Tap - Upper	-32,5250	20,8517
43	**CGP JA 109**	Nochelesaurus	alexanderi						
44	**RMS 565/ CGP/1/866**	Nochelesaurus	alexanderi	Fraserburg	BORD VOL WATER, 313, FRASERBERG, NORTHERN CAPE	-	Tap - Upper	-31,7083	21,7833
45	**RMS 1005/ CGP/1/821**	Nochelesaurus	alexanderi	Prince Albert	Rietfontein 12	Moordenaars	Tap - Upper	-32,9397	22,3806
46	**BP/1/297**	Nochelesaurus	alexanderi	Beaufort West	Kleinwaterval, Spreeuw Fontein 26, Prince Albert	upper Abrahamskraal fm	Tap	-32,9667	22,3333
47	**BP/1/4859**	Nochelesaurus	alexanderi	Laingsburg	De Skeur, Riethoek 28, Laingsburg District	lower-mid Moordenaars	Tap - Upper	-32,8000	21,2500
48	**BP/1/7165**	Nochelesaurus	alexanderi	Prince Albert	Jan Willems Fontein 32 Farm (Beleie), Prince Albert District	Moordenaars	Tap - Upper	-32,8469	22,0558
49	**BP/1/7252**	Nochelesaurus	alexanderi	Beaufort West	Wolwehoek, Hendriks Kraal 298, Beaufort West	lower Karelskraal Member	Tap - upper	-32,3309	22,0949
50	**BP/1/8006**	Nochelesaurus	alexanderi	Laingsburg	Kransrivier 24	Swaerskraal	Tap - lower	-32,8186	21,3258

Count	Collection Number	Genus	Species	District	Locality (Farm and District)	Member Range	Biozone	GPS/Centroid S	GPS/Centroid E
51	**BP/1/8011**	Nochelesaurus	alexanderi	Laingsburg	De List 19	Koornplaats	Tap - lower	-32,7589	21,3978
52	**FMNH Field no 15**	Nochelesaurus	alexanderi	Prince Albert	Stinkfontein 7, 2 mi N of dam, 1mi W of River, Moordenaars Member, Abrahamskraal Formation, Western Cape	mid-Moordenaars	Tap - upper	-32,6333	21,9833
53	**FMNH UR 2436**	Nochelesaurus	alexanderi		Stinkfontein 7, Stinkfontein: N bounday of farm	mid-Moordenaars	Tap - upper	-32,6333	21,9833
54	**FMNH UR 2437**	Nochelesaurus	alexanderi	Prince Albert	Stinkfontein 7, Stinkfontein : About 3 mi E of spring	mid-Moordenaars	Tap - upper	-32,6333	21,9833
55	**FMNH UR 2476**	Nochelesaurus	alexanderi		Myburg's	upper Moordenars	Tap - Upper	-32,4419	21,9342
56	**FMNH UR 2480**	Nochelesaurus	alexanderi	Prince Albert	Stinkfontein 7: 3 mi N of dam	mid-Moordenaars	Tap - upper	-32,6333	21,9833
57	**FMNH UR 2481**	Nochelesaurus	alexanderi	Prince Albert	Stinkfontein 7: about 1 mi N of dam, W of road to Hottentotsrivier	mid-Moordenaars	Tap - upper	-32,6333	21,9833
58	**SAM-PK-3717**	Nochelesaurus	alexanderi	Beaufort West	Rietfontein 306 (Leeurivier)	mid to upper Moordenaars	Tap - Upper	-32,4333	22,1667
59	**SAM-PK-4324**	Nochelesaurus	alexanderi	Beaufort West	Leeuwkraal 309 (Uitkyk)	mid-Moordenaars	Tap - Upper	-32,7000	22,0833
60	**SAM-PK-5012**	Nochelesaurus	alexanderi	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
61	**SAM-PK-5015**	Nochelesaurus	alexanderi	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
62	**SAM-PK-5019**	Nochelesaurus	alexanderi	Prince Albert	Blauwkranse 30	Upper Moordenaars-Karelskraal	Tap - Upper	-32,9667	21,9833
63	**SAM-PK-6238**	Nochelesaurus	alexanderi	Beaufort West	Bushmans Kop 302 (Boesmanskop)	upper Moord to upper Karelsk.	Tap - Upper	-32,3500	22,2333
64	**SAM-PK-6239**	Nochelesaurus	alexanderi	Beaufort West	Bushmans Kop 302 (Boesmanskop)	upper Moord to upper Karelsk.	Tap - Upper	-32,3500	22,2333
65	**SAM-PK-6239A**	Nochelesaurus	alexanderi	Beaufort West	Bushmans Kop 302 (Boesmanskop)	upper Moord to upper Karelsk.	Tap - Upper	-32,3500	22,2333
66	**SAM-PK-6240**	Nochelesaurus	alexanderi	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
67	**SAM-PK-8944**	Nochelesaurus	alexanderi	Beaufort West	Klein Koedoes Kop 310	mid Moord	Tap - upper	-32,5500	22,1667
68	**SAM-PK-9089**	Nochelesaurus	alexanderi	Beaufort West	Klein Koedoes Kop 310	mid Moord	Tap - upper	-32,5500	22,1667
69	**SAM-PK-9114**	Nochelesaurus	alexanderi	Prince Albert	Sevenfontein 5 (Sewefontein)	lower Moordenaars	Tap - upper	-32,6667	21,8333
70	**SAM-PK-9115**	Nochelesaurus	alexanderi	Prince Albert	Vogelfontein 1 (Voelfontein)	lower Moordenaars	Tap - Upper	-32,6833	21,7500
71	**SAM-PK-9137**	Nochelesaurus	alexanderi	Prince Albert	Vogelfontein 1 (Voelfontein)	lower Moordenaars	Tap - Upper	-32,6833	21,7500
72	**SAM-PK-9169**	Nochelesaurus	alexanderi	Beaufort West	Van Der Byls Kraal 265 (Knoffelfontein)	lower Moordenaars	Tap - upper	-32,6667	21,5500
73	**SAM-PK-11559**	Nochelesaurus	alexanderi	Beaufort West	Flagfontein 308 (Vlaefontein)	Upper Moordenaars	Tap - Upper	-32,5167	22,0667
74	**SAM-PK-11596**	Nochelesaurus	alexanderi	Beaufort West	farm Delivershoek (1942 catalogue) (now called Rondom)	?			
75	**SAM-PK-11930**	Nochelesaurus	alexanderi	Laingsburg	Dikboome, Krans Rivier 24	Swaerskraal	Tap - lower	-32,8833	21,3667
76	**SAM-PK-11948**	Nochelesaurus	alexanderi	Fraserburg	Paarde Grass Valley 241 (Roxana)	upper Abrahamskraal fm	Tap - upper	-31,6667	21,8500
77	**SAM-PK-12047**	Nochelesaurus	alexanderi	Laingsburg	Klipfontein 31	Moordenaars-Karelskraal	Tap - Upper	-32,7833	21,1500
78	**SAM-PK-12057**	Nochelesaurus	alexanderi	Beaufort West	Elandsfontein 257 (Leeuwkraal)	Swaerskraal-lower Moordenaars	Tap - lower/upper boundary	-32,4667	21,5167
79	**SAM-PK-12076**	Nochelesaurus	alexanderi	Beaufort West	Varsfontein 254	upper Swaersk. to lower Moord.	Tap - lower/upper boundary	-32,5333	21,5500
80	**SAM-PK-12129**	Nochelesaurus	alexanderi	Prince Albert	Wilger Fontein 59 (Wilgerfontein)	lower Moordenaars	Tap - Upper	-32,8167	21,8333
81	**SAM-PK-K07999**	Nochelesaurus	alexanderi	Beaufort West	Klein Koedoes Kop 310	mid Moord	Tap - upper	-32,5500	22,1667
82	**SAM-PK-K08000**	Nochelesaurus	alexanderi	Beaufort West	Klein Koedoes Kop 310	mid Moord	Tap - upper	-32,5500	22,1667
83	**SAM-PK-K10898**	Nochelesaurus	alexanderi	Beaufort West	Flagfontein 308 (Vlaefontein)	Upper Moordenaars	Tap - Upper	-32,5167	22,0667
84	**AM 3748**	Bradysaurus	baini	Beaufort West	Hottentots River, Beaufort West District	upper Moordenars	Tap - Upper	-32,3667	21,8833
85	**AMNH FARB 2452**	Bradysaurus	baini		Orangefontein, Sutherland District, Tapinocephalus AZ	?			
86	**AMNH FARB 5323**	Bradysaurus	baini	Prince Albert	Leeu Gamka area (Fraserburg Road)	Moordenaars	Tap - Upper	-32,7752	21,9777
87	**47/ CGP/1/863**	Bradysaurus	baini						
88	**CDB 7**	Bradysaurus	baini	Fraserburg	Groot Fontein 311	upper Abrahamskraal fm	Tap - Upper	-31,8431	21,6736
89	**CGP/1/2269**	Bradysaurus	baini				Tap		
90	**CGP/1/2268**	Bradysaurus	baini				Tap		
91	**MP 47/CMARL**	Bradysaurus	baini	Beaufort West	Duikerfontein, Beaufort West	upper Abrahamskraal fm	Tap - Upper	-31,6123	22,3530
92	**RMS 1096/ CGP/1/810**	Bradysaurus	baini	Prince Albert	Rietfontein 12	lower to mid Moord	Tap - Upper	-32,9533	22,3864
93	**RMS 1258**	Bradysaurus	baini	Prince Albert	Varsch Fontein 27	Moordenaars	Tap - Upper	-32,9547	22,2919
94	**RMS 1296**	Bradysaurus	baini	Prince Albert	Farm 57	lower to mid Moord	Tap - Upper	-32,8581	21,9033
95	**BP/1/347**	Bradysaurus	baini	Merweville	Buffelsvlei, Buffels Valley 268, Beaufort West	upper Koornp to lower Moord	Tap - lower?	-32,7333	21,5167
96	**BP/1/1574**	Bradysaurus	baini	Prince Albert	De Bad 286	lower Moordenaars	Tap - Upper	-32,5500	21,8000
97	**BP/1/1577**	Bradysaurus	baini	Prince Albert	De Bad 286	lower Moordenaars	Tap - Upper	-32,5500	21,8000
98	**BP/1/2233**	Bradysaurus	baini	Prince Albert	Kleinwaterval, Spreeuw Fontein 26, Prince Albert	upper Abrahamskraal fm	Tap	-32,9667	22,3333
99	**BP/1/4848**	Bradysaurus	baini	Laingsburg	Schoppel Maay Kraal 54 (Schoppelmaaikraal)	lower Moordenaars	Tap - Upper	-32,8833	21,3333
100	**BP/1/4857**	Bradysaurus	baini	Laingsburg	Schoppel Maay Kraal 54 (Schoppelmaaikraal)	lower Moordenaars	Tap - Upper	-32,8833	21,3333

Count	Collection Number	Genus	Species	District	Locality (Farm and District)	Member Range	Biozone	GPS/Centroid S	GPS/Centroid E
101	**BP/1/5414**	Bradysaurus	baini	Laingsburg	Banksdrif, Koornplaats 41, Laingsburg District	upper Koornplaats	Tap - lower	-32,8167	20,9667
102	**BP/1/5430**	Bradysaurus	baini						
103	**BP/1/7054**	Bradysaurus	baini	Beaufort West	Rietfontein 269	lower Moordenaars	Tap - Upper	-32,7361	21,6025
104	**BP/1/7082**	Bradysaurus	baini	Beaufort West	Springfontein, Rondom 247	upper Moordenaars	Tap - Upper	-32,4011	21,4643
105	**BP/1/7213**	Bradysaurus	baini	Sutherland	Witfontein 85, Sutherland	lower part of the Karelskraal	Tap - Upper	-32,3883	20,9346
106	**BP/1/7870**	Bradysaurus	baini	Laingsburg	Banksdrif, Koornplaats 41, Laingsburg District	upper Koornplaats	Tap - lower	-32,8103	20,9586
107	**BP/1/7886**	Bradysaurus	baini	Laingsburg	Blounek, Koornplaats 41, Lainsburg	mid/upper koornplaats	Tap - lower	-32,8100	20,9589
108	**BP/1/7953**	Bradysaurus	baini	Sutherland	Die Puts, Kuilenburg 96, Sutherland District	upper Moordenars	Tap - Upper	-32,4000	20,9297
109	**BP/1/8020**	Bradysaurus	baini	Laingsburg	De Skeur, Riethoek 28, Laingsburg District	mid Moordenaars	Tap - Upper	-32,8058	21,2222
110	**FMNH Field no 49**	Bradysaurus	baini		Member, Abrahamskraal Formation, Western Cape	upper Moordenars	Tap - Upper	-32,4087	21,9165
111	**FMNH Field no 29**	Bradysaurus	baini	Prince Albert	Sevefontein 5 (=E part of Vogelfontein), 1/2 mi W of house	lower Moordenaars	Tap - upper	-32,6667	21,8333
112	**FMNH UC 1525**	Bradysaurus	baini		Hottentotsrivier 296, Hottentot River, 3/4 mi E of Myburg farm	upper Moordenars	Tap - Upper	-32,4097	21,9800
113	**FMNH UC 1526**	Bradysaurus	baini		Hottentotsrivier 296, Hottentot River, 2 mi W of Myburg farm ,	upper Moordenars	Tap - Upper	-32,4097	21,9800
114	**FMNH UC 1533**	Bradysaurus	baini	Prince Albert	Stinkfontein 7, Stinkfontein: on the Leeuw River,	mid-Moordenaars	Tap - upper	-32,6333	21,9833
115	**FMNH UR 2439**	Bradysaurus	baini		Hottentotsrivier 296, 1/2 mi SW of Myburg's, Hottentotsrivier	upper Moordenars	Tap - Upper	-32,4097	21,9800
116	**FMNH UR 2461**	Bradysaurus	baini	Prince Albert	Western Cape	mid-Moordenaars	Tap - upper	-32,6333	21,9833
117	**FMNH UR 2476**	Bradysaurus	baini		Myburg's	upper Moordenars	Tap - Upper	-32,4419	21,9339
118	**FMNH UR 2484**	Bradysaurus	baini	Prince Albert	Stinkfontein 7, Stinkfontein: 1 mi NW of dam	mid-Moordenaars	Tap - upper	-32,6333	21,9833
119	**NHMUK R1970**	Bradysaurus	baini	Beaufort West	Tamboersfontein 291, Beaufort West	mid Moordenaars	Tap - Upper	-32,4416	21,8696
120	**NHMUK R1971**	Bradysaurus	baini	Beaufort West	Die Bad 286, Beaufort West	lower to mid Moordenaars	Tap - Upper	-32,5339	21,8251
121	**NHMUK R4066**	Bradysaurus	baini	Beaufort West	Hottentotsrivier, Hottentots River 296, Beaufort West	upper Moordenars	Tap - Upper	-32,3853	21,9736
122	**NHMUK R49426**	Bradysaurus	baini	Beaufort West	Palmietfontein 229, Beaufort West	Karelskraal	Tap - Upper	-32,3403	21,7984
123	**SAM-PK-745**	Bradysaurus	baini	Prince Albert	Goeiemoed 90 (Prince Albert Road)	Moordenaars or Karelskraal	Tap - Upper	-32,9833	21,7000
124	**SAM-PK-3533**	Bradysaurus	baini	Beaufort West	Hottentots River 296	Moordenaars or Karelskraal	Tap - Upper	-32,3833	21,9667
125	**SAM-PK-3718**	Bradysaurus	baini	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
126	**SAM-PK-4346**	Bradysaurus	baini	Prince Albert	Kruitfontein 33 (Welgemoed)	Moordenaars	Tap - Upper	-32,7833	21,9667
127	**SAM-PK-4347**	Bradysaurus	baini	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
128	**SAM-PK-4350**	Bradysaurus	baini	Beaufort West	Rietfontein 306 (Leeurivier)	mid to upper Moordenaars	Tap - Upper	-32,4333	22,1667
129	**SAM-PK-4351**	Bradysaurus	baini	Prince Albert	Kruitfontein 33 (Grootkruidfontein)	Moordenaars	Tap - Upper	-32,7333	21,9500
130	**SAM-PK-4999**	Bradysaurus	baini	Beaufort West	Grootfontein 252	upper Moordenaars-Karelskraal	Tap - Upper	-32,3667	22,3833
131	**SAM-PK-5002**	Bradysaurus	baini	Prince Albert	Vogelfontein 1	lower Moordenaars	Tap - Upper	-32,6833	21,7500
132	**SAM-PK-5011**	Bradysaurus	baini	Prince Albert	Kruitfontein 33 (Grootkruidfontein)	Moordenaars	Tap - Upper	-32,7333	21,9500
133	**SAM-PK-5013**	Bradysaurus	baini	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
134	**SAM-PK-5597**	Bradysaurus	baini	Prince Albert	Jan Willems Fontein 32	Moordenaars	Tap - Upper	-32,8167	22,0333
135	**SAM-PK-5624**	Bradysaurus	baini	Prince Albert	Kruitfontein 33 (Grootkruidfontein)	Moordenaars	Tap - Upper	-32,7333	21,9500
136	**SAM-PK-8941**	Bradysaurus	baini	Beaufort West	Mynhardts Kraal 311	mid Moordenaars	Tap - Upper	-32,5333	22,4000
137	**SAM-PK-9095**	Bradysaurus	baini	Prince Albert	Veldmans River 9	mid Moordenaars	Tap - Upper	-32,7500	22,0833
138	**SAM-PK-9104**	Bradysaurus	baini	Prince Albert	Melkbosch Fontein 75 (Melkbosfontein)	Moordenaars	Tap - Upper	-32,9167	21,7000
139	**SAM-PK-9121**	Bradysaurus	baini	Prince Albert	Vogelfontein 1 (Voelfontein)	lower Moordenaars	Tap - Upper	-32,6833	21,7500
140	**SAM-PK-9136**	Bradysaurus	baini	Prince Albert	Vogelfontein 1 (Voelfontein)	lower Moordenaars	Tap - Upper	-32,6833	21,7500
141	**SAM-PK-9142**	Bradysaurus	baini	Beaufort West	Zeekoevalley 282 (Zeekoeivlei)	lower Moordenaars	Tap - Upper	-32,6167	21,8000
142	**SAM-PK-9143**	Bradysaurus	baini	Beaufort West	Zeekoevalley 282 (Zeekoeivlei)	lower Moordenaars	Tap - Upper	-32,6167	21,8000
143	**SAM-PK-9170**	Bradysaurus	baini	Prince Albert	Melkbosch Fontein 75 (Melkbosfontein)	Moordenaars	Tap - Upper	-32,9167	21,7000
144	**SAM-PK-11487**	Bradysaurus	baini	Beaufort West	Mynhardts Kraal 311	mid Moordenaars	Tap - Upper	-32,5333	22,4000
145	**SAM-PK-12014**	Bradysaurus	baini	Beaufort West	Rietfontein 269	lower Moordenaars	Tap - Upper	-32,7333	21,5667
146	**SAM-PK-12048**	Bradysaurus	baini	Laingsburg	Dwars Rivier 14	upper Koornplaats to lower Moordenaars	Tap - lower?	-32,7500	21,0833
147	**SAM-PK-12090**	Bradysaurus	baini	Prince Albert	Blaaw Draay 3 (Die Vlei)	mid Moord	Tap - Upper	-32,6833	21,9000
148	**SAM-PK-12115**	Bradysaurus	baini	Prince Albert	Farm 57 (Palmietfontein)	mid Moord	Tap - Upper	-32,8333	21,9000
149	**SAM-PK-12128**	Bradysaurus	baini	Prince Albert	Wilger Fontein 59 (Wilgerfontein)	lower Moordenaars	Tap - Upper	-32,8167	21,8333
150	**SAM-PK-12133**	Bradysaurus	baini	Prince Albert	Wilger Fontein 59 (Deelfontein)	lower Moordenaars	Tap - Upper	-32,8167	21,8333

Count	Collection Number	Genus	Species	District	Locality (Farm and District)	Member Range	Biozone	GPS/Centroid S	GPS/Centroid E
151	**SAM-PK-12216**	Bradysaurus	baini	Laingsburg	Schoppel Maay Kraal 54 (Schoppelmaaikraal)	lower Moordenaars	Tap - Upper	-32,8667	21,3333
152	**SAM-PK-12222**	Bradysaurus	baini	Laingsburg	De List 19	Koornplaats/Swaerskraal	Tap - lower	-32,7500	21,3000
153	**SAM-PK-12251**	Bradysaurus	baini	Fraserburg	Gannakraal 422 (Beukesplaas)	Karelskraal	Tap - Upper	-32,1000	21,2333
154	**SAM-PK-K00196**	Bradysaurus	baini	Prince Albert	Jan Willems Fontein 32 (Magdelena)	mid Moordenaars	Tap - Upper	-32,8000	22,0667
155	**SAM-PK-K00325**	Bradysaurus	baini	Laingsburg	Dikboome 53 (Bosluiskraal)	lower Moordenaars	Tap - Upper	-32,8667	21,3667
156	**SAM-PK-K11638**	Bradysaurus	baini				Tap		
157	**GPIT-RE-1602**	Bradysaurus	baini	Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper	-32,9333	22,0000
158	**113/ CGP/1/811**	Bradysaurus/Embrithosaurus							
159	**BP/1/7266**	Bradysaurus/Embrithosaurus		Beaufort West	Wolwehoek, Hendriks Kraal 298, Beaufort West	Karelskraal Member	Tap - upper		S32 18.574, E22 07.554
160	**BP/1/8050**	Bradysaurus/Embrithosaurus		Laingsburg	Deesweesfontein, Deesweez Fontein 51	Lower? Moordenaars	Tap - Upper		S32 53.381, E21 14.508
161	**SAM-PK-9144**	Bradysaurus/Embrithosaurus		Beaufort West	Zeekoevalley 282 (Zeekoeivlei)	lower Moordenaars	Tap - Upper		32 deg 37 min 00.0 sec S, 21 deg 48 min 00,0 sec E
162	**SAM-PK-12043**	Bradysaurus/Embrithosaurus		Beaufort West	Rietfontein 269	lower Moordenaars	Tap - Upper		32 deg 44 min 00,0 sec S, 21 deg 34 min 00,0 sec E
163	**SAM-PK-12068**	Bradysaurus/Embrithosaurus		Beaufort West	Bovenste Schoenmakers Winkel 279 (Skoenmaker)	Swaerskraal-lower Moordenaars	Tap - lower/upper boundary		32 deg 29 min 00,0 sec S, 21 deg 44 min 00,0 sec E
164	**BP/1/1040**	Bradysaurus/Nochelesaurus		Prince Albert	Antjiesfontein, Prince Albert District	upper Abrahamskraal fm	Tap - upper		S32.95, E22.4666666666667
165	**BP/1/1783**	Bradysaurus/Nochelesaurus		Prince Albert	Stinkfontein 7	mid-Moordenaars	Tap - upper		S32.6333333333333, E21.9833333333333
166	**BP/1/7247**	Bradysaurus/Nochelesaurus		Beaufort West	Brakleegte 297, Beaufort West	Moordenaars/Karelskraal Member	Tap - upper		S32 20.781, E22 05.131
167	**FMNH Field no 44**	Bradysaurus/Nochelesaurus		Beaufort West	Member, Abrahamskraal Formation, Western Cape	upper Moordenars	Tap - Upper		S32.424633, E21.937134
168	**SAM-PK-1204**	Bradysaurus/Nochelesaurus		Beaufort West	Bushmans River 312 (Letjesbos)	mid-upper Moordenaars	Tap - Upper		32 deg 34 min 00.0 sec S, 22 deg 16 min 00,0 sec E
169	**SAM-PK-5008**	Bradysaurus/Nochelesaurus		Prince Albert	Vogelfontein 1	lower Moordenaars	Tap - Upper		32 deg 41 min 00,0 sec S, 21 deg 45 min 00,0 sec E
170	**SAM-PK-9001**	Bradysaurus/Nochelesaurus		Beaufort West	Klein Koedoes Kop 310	mid Moord	Tap - upper		32 deg 33 min 00.0 sec S, 22 deg 10 min 00,0 sec E
171	**AMNH FARB 5568**	Embrithosaurus/Nochelesaurus			Tapinocephalus AZ				
172	**RMS 1030/ CGP/1/855**	Embrithosaurus/Nochelesaurus		Prince Albert	SPREEUW FONTEIN 26	upper Abrahamskraal fm	Tap - upper		S32,58,04, E 22,20,48
173	**RMS 1304/ CGP/1/820**	Embrithosaurus/Nochelesaurus		Prince Albert	Rietfontein 56	Upper Moordenaars	Tap - Upper		S32.870833, E21.952778
174	**BP/1/1772**	Embrithosaurus/Nochelesaurus		Prince Albert	Stinkfontein 7	mid-Moordenaars	Tap - upper		S32.6333333333333, E21.9833333333333
175	**BP/1/5418**	Embrithosaurus/Nochelesaurus		Laingsburg	Banksdrif, Koornplaats 41, Laingsburg District	upper Koornplaats	Tap - lower		S32.8167, E20.9667
176	**BP/1/5435**	Embrithosaurus/Nochelesaurus		Laingsburg	Rietfontein, Swaerskraal 40	Lower Moordenaars	Tap - upper		S32.8666666666667, E21.1166666666667
177	**BP/1/7037**	Embrithosaurus/Nochelesaurus		Beaufort West	Elandsfontein 257	lower Moordenaars	Tap - upper		S32 31.234, E21 25.437
178	**SAM-PK-1208**	Embrithosaurus/Nochelesaurus		Prince Albert	Ganze Kraal 25 (Ganskraal)	Moordenaars-Karelskraal	Tap - Upper		33 deg 01 min 00,0 sec S, 22 deg 26 min 00,0 sec E
179	**SAM-PK-8933**	Embrithosaurus/Nochelesaurus		Beaufort West	Leeufontein 273 (Leeuwfontein)	upper Swaersk. to lower Moord.	Tap - lower/upper boundary		32 deg 37 min 00,0 sec S, 21 deg 38 min 00,0 sec E
180	**SAM-PK-12231**	Embrithosaurus/Nochelesaurus		Laingsburg	Dikboome 53 (Bosluiskraal)	lower Moordenaars	Tap - Upper		32 deg 52 min 00.0 sec S, 21 deg 22 min 00,0 sec E
181	**AM Unnumbered skull**	Unidentifiable							
182	**AM 4068**	Unidentifiable							
183	**AMNH FARB Unknown Number (P. strubeni holotype)**	Unidentifiable		Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper		32 deg 57 min 00,0 sec S, 21 deg 59 min 00,0 sec E
184	**AMNH FARB 2231**	Unidentifiable			Tapinocephalus AZ				
185	**AMNH FARB 2232**	Unidentifiable			Tapinocephalus AZ				
186	**AMNH FARB 2233**	Unidentifiable			Tapinocephalus AZ				
187	**AMNH FARB 2234**	Unidentifiable			Tapinocephalus AZ				
188	**AMNH FARB 2235**	Unidentifiable			Tapinocephalus AZ				
189	**AMNH FARB 3897**	Unidentifiable		Prince Albert	Abrahams Kraal 29	Moordenaars	Tap - Upper		32 deg 57 min 00,0 sec S, 21 deg 59 min 00,0 sec E
190	**AMNH FARB 5604**	Unidentifiable							
191	**AMNH FARB 23878**	Unidentifiable			Tapinocephalus AZ				
192	**AMNH FARB 23879**	Unidentifiable			Spitzkop, Laingsberg District, Tapinocephalus AZ				
193	**AMNH FARB 24169**	Unidentifiable			Tapinocephalus AZ				
194	**AMNH FARB 24170**	Unidentifiable							
195	**A 109/ CGP/1/858**	Unidentifiable							
196	**CBT 9**	Unidentifiable							
197	**GM 64**	Unidentifiable			ROODE POORT, 328, FRASERBERG, NORTHERN CAPE				S31,46,50, E22,11,55
198	**JP 56/ CGP/1/847**	Unidentifiable			KAFFIRS BERG, 112, PEARSTON, EASTERN CAPE				S32,51,36, E25,09,37
199	**RMS 1095**	Unidentifiable		Prince Albert	Rietfontein 12	Moordenaars	Tap - Upper		S32 55' 46", E22 22' 07"
200	**RMS 1257**	Unidentifiable		Prince Albert	Varsch Fontein 27	Moordenaars	Tap - Upper		S32, 56, 50, E22,16,28

Count	Collection Number	Genus	Species	District	Locality (Farm and District)	Member Range	Biozone	GPS/Centroid S	GPS/Centroid E
201	**S 260**	Unidentifiable		Beaufort West	Riet Kuil 307	upper Moordenaars	Tap - Upper		S32,27,24, E22,04,47
202	**BP/1/298**	Unidentifiable		Beaufort West	Kleinwaterval, Spreeuw Fontein 26, Prince Albert	upper Abrahamskraal fm	Tap		S32.9667, E22.3333
203	**BP/1/1578**	Unidentifiable		Prince Albert	De Bad 286	lower Moordenaars	Tap - Upper		S32.5500, E21.8000
204	**BP/1/1781**	Unidentifiable		Prince Albert	Stinkfontein 7	mid-Moordenaars	Tap - upper		S32.6333333333333, E21.9833333333333
205	**BP/1/1782**	Unidentifiable		Prince Albert	Stinkfontein 7	mid-Moordenaars	Tap - upper		S32.6333333333333, E21.9833333333333
206	**BP/1/4855**	Unidentifiable		Laingsburg	Schoppel Maay Kraal 54 (Schoppelmaaikraal)	lower Moordenaars	Tap - Upper		S32.3833, E25.0000
207	**BP/1/5620**	Unidentifiable		Laingsburg	Swaerskraal 40	Lower Moordenaars	Tap - upper		S32.8666666666667, E21.1166666666667
208	**BP/1/5644**	Unidentifiable			Wayside, Klipplaat District	?Tapinocephalus Z, Note: '60 m above Ecca-Beaufort contact'.			S32 57.26, E24 27.31
209	**BP/1/5858**	Unidentifiable			Sandheuwel, Middelpos District	?Tapinocephalus Z, Note: '60 m above Ecca-Beaufort contact'.			S31 51.062, E20 20.043
210	**BP/1/6870**	Unidentifiable		Beaufort West	Rietfontein 269	lower Moordenaars	Tap - Upper		S32 43.225, E21 34.961
211	**BP/1/6871**	Unidentifiable		Beaufort West	Rietfontein 269	lower Moordenaars	Tap - Upper		S32 42.739, E21 35.3864
212	**BP/1/6976**	Unidentifiable		Beaufort West	Rietfontein 269	lower Moordenaars	Tap - Upper		S32 43 786, E21 36.496
213	**BP/1/7014**	Unidentifiable			Jakkalsfontein, Beaufort West District	Tapinocephalus			S32 55.284, E21 36.777
214	**BP/1/7019**	Unidentifiable		Beaufort West	Bullekraal 254, Beaufort West District	mid-Moordenaars	Tap - Upper		S32 26.656, E21 26.036
215	**BP/1/7035**	Unidentifiable		Beaufort West	Elandsfontein 257	lower Moordenaars	Tap - upper		S32 30.595, E21 26.462
216	**BP/1/7036**	Unidentifiable		Beaufort West	Elandsfontein 257	lower Moordenaars	Tap - upper		S32 31.248, E21 25.563
217	**BP/1/7167**	Unidentifiable		Sutherland	Puntkraal portion of Uitvlug 90, Sutherland district	Uppermost Moordenaars Member.	Tap-upper		S32 25.266, E21 04.716
218	**BP/1/8024**	Unidentifiable		Laingsburg	Kransrivier 24	lower Moordenaars	Tap - upper		S32 49.200, E21 18.777
219	**BP/1/8025**	Unidentifiable		Laingsburg	De List 19	Swaerskraal	Tap - lower		S32 46.846, E21 22.868
220	**FMNH UR 2465**	Unidentifiable			Formation, Western Cape	upper Moordenars or possibly Karelskraal	Tap - Upper		32 deg 23 min 00.0 sec S, 21 deg 58 min 00,0 sec E
221	**NHMUK R1714 (43525)**	Unidentifiable		Prince Albert	Jan Willems Fontein 32	Moordenaars	Tap - Upper		32 deg 49 min 00.0 sec S, 22 deg 02 min 00,0 sec E
222	**SAM-PK-3434**	Unidentifiable		Prince Albert	Jan Willems Fontein 32	Moordenaars	Tap - Upper		32 deg 49 min 00.0 sec S, 22 deg 02 min 00,0 sec E
223	**SAM-PK-8934**	Unidentifiable		Beaufort West	Leeufontein 273 (Leeuwfontein)	upper Swaersk. to lower Moord.	Tap - lower/upper boundary		32 deg 37 min 00.0 sec S, 21 deg 38 min 00,0 sec E
224	**SAM-PK-9118**	Unidentifiable		Prince Albert	Vogelfontein 1 (Voelfontein)	lower Moordenaars	Tap - Upper	-32,6833	21,7500
225	**SAM-PK-9156**	Unidentifiable		Prince Albert	Moordenaarskraal Noord 64				32 deg 46 min 00.0 sec S, 21 deg 35 min 00,0 sec E
226	**SAM-PK-9168**	Unidentifiable		Beaufort West	Van Der Byls Kraal 265 (Knoffelfontein)	lower Moordenaars	Tap - upper		32 deg 40 min 00.0 sec S, 21 deg 33 min 00,0 sec E
227	**SAM-PK-12015**	Unidentifiable		Beaufort West	Buffels Valley 268 (Buffelsvlei)				32 deg 45 min 00.0 sec S, 21 deg 27 min 00,0 sec E
228	**SAM-PK-12054**	Unidentifiable		Laingsburg	Klipfontein 31	Moordenaars-Karelskraal	Tap - Upper		32 deg 47 min 00.0 sec S, 21 deg 09 min 00,0 sec E
229	**SAM-PK-12071**	Unidentifiable		Beaufort West	Varsfontein 254 (Papkuil)				32 deg 31 min 00,0 sec S, 21 deg 29 min 00,0 sec E
230	**SAM-PK-12072**	Unidentifiable		Beaufort West	Varsfontein 254 (Papkuil)				32 deg 31 min 00,0 sec S, 21 deg 29 min 00,0 sec E
231	**SAM-PK-12077**	Unidentifiable		Beaufort West	Varsfontein 254				32 deg 32 min 00.0 sec S, 21 deg 33 min 00,0 sec E
232	**SAM-PK-12080**	Unidentifiable		Beaufort West	Hendriks Kraal 298 (Grantham)	Karelskraal	Tap - Upper		32 deg 16 min 00,0 sec S, 22 deg 10 min 00,0 sec E
233	**SAM-PK-12116**	Unidentifiable		Prince Albert	Farm 57 (Palmietfontein)	mid Moord	Tap - Upper		32 deg 50 min 00.0 sec S, 21 deg 54 min 00,0 sec E
234	**SAM-PK-12127**	Unidentifiable		Prince Albert	Rietfontein 56	Upper Moordenaars	Tap - Upper		32 deg 53 min 00.0 sec S, 21 deg 54 min 00,0 sec E
235	**SAM-PK-12137**	Unidentifiable		Prince Albert	Wilger Fontein 59 (Maraisdal)	lower Moordenaars	Tap - Upper		32 deg 48 min 00,0 sec S, 21 deg 55 min 00,0 sec E
236	**SAM-PK-K00197**	Unidentifiable		Prince Albert	Rietfontein 56 (Paradys)	Upper Moordenaars	Tap - Upper		32 deg 53 min 00.0 sec S, 21 deg 58 min 00,0 sec E
237	**SAM-PK-K04506**	Unidentifiable		Victoria West	Melton Wold 158				31 deg 27 min 00,0 sec S, 22 deg 45 min 00,0 sec E
238	**SAM-PK-K07665**	Unidentifiable		Prince Albert	Varsch Fontein 27 (Varsfontein)	Moordenaars	Tap - Upper		32 deg 52 min 00.0 sec S, 22 deg 05 min 00,0 sec E
239	**SAM-PK-K07916**	Unidentifiable		Prince Albert	Kweekkraal 92 (Combrinckskraal)	?			33 deg 02 min 00.0 sec S, 21 deg 59 min 00,0 sec E
240	**SAM-PK-K10547**	Unidentifiable		Laingsburg	Spitskop 20	Swaerskraal	Tap - lower		32 deg 45 min 00,0 sec S, 21 deg 19 min 00,0 sec E

APPENDIX E: CRANIO-DENTAL TABLES

Tables of comparative cranio-dental characters of *Embrithosaurus schwarzi*, *Nochelesaurus alexanderi* and *Bradysaurus baini*. Bold text indicates that a character that is unique to that particular species, regular text indicates that a character that is shared by more than one species.

UPPER JAW DENTITION	***Embrithosaurus***	***Nochelesaurus***	***B. baini***
1. Tooth orientation	Vertical	Vertical	**Medially inflicted inwards, horizontal - all specimens (NHMUK R1971, NHMUK R1970, SAM-PK-5002, SAM SAM-PK-K11638, SAM-PK-9121, CGP/1/2269)**
2. Tooth shape	• **9 cusped teeth: Dorsoventrally shortened and mesiodistally widened (SAM-PK-8034, SAM-PK-9098), no central trident** or: • **7 cusped teeth: Dorsoventrally elongated and mesiodistally narrower (CGP CBT 112)**	Dorsoventrally elongated and mesiodistally narrower, central trident, all specimens	Dorsoventrally elongated and mesiodistally narrower, central trident, all specimens
3. Cusp numbers	• 9 (SAM-PK-8034, SAM-PK-9098) • 7 (CGP CBT 112)	• 7-8 (SAM-PK-6239, 8th due to additional, low basal cusp near **mesial** margin on certain teeth) • 7 (SAM-PK-6240) • **5,7 (BP/1/7165)**	• 7 (NHMUK R1971, SAM-PK-5002, SAM-PK-3718) • **7-8 (NHMUK R49426)** • 8-9 (SAM-PK-K11638, 1st and ^{2nd} left Pm and 1st right Pm • 9 (BP/1/7082)
4. Cusp arrangement	SAM-PK-8034, SAM-PK-9098: • Irregularly arranged, but more regularly than co-occurring taxa. • **No central trident.** • 5 central cusps close together, with no gaps between central 3 cusps and very small gaps to first lateral cusps either side.	SAM-PK-6239: • Irregularly arranged. • Central elongated, narrow trident, with 3 close cusps with no gaps between. • mesial and distal margins with 2 or more cusps with large gaps between	NHMUK R1971, SAM-PK-K11638: • Irregularly arranged. • Central elongated, narrow trident, with 3 close cusps with no gaps between. • mesial and distal margins with 2 (NHMUK R1971) or 3 (SAM-PK-K11638) cusps with large gaps between.

	• mesial and distal margins with 2 cusps with large gaps between (SAM-PK-8034) or: CGP CBT 112: • Irregularly arranged. • Central elongated, narrow trident, with 3 close cusps with no gaps between. • mesial and distal margins with 2 or more cusps with large gaps between		
5. Cusp symmetry	Symmetrical mesial and distal cusp arrangements on all teeth (SAM-PK-8034, CGP CBT 112)	**Non- symmetrical mesial and distal cusp arrangements due to extra, low, basal, marginal mesial cusp on certain teeth (SAM-PK-6239, SAM-PK-6238)**	Symmetrical mesial and distal cusp arrangements on all teeth (NHMUK R1971, SAM-PK-5002, SAM-PK-K11638l).
6. Medial cusps	No medial cusps (SAM-PK-8034, CGP CBT 112)	No medial cusps	No medial cusps
7. Lingual surface features	Inaccessible (SAM-PK-8034, CGP CBT 112)	**Three to five high, distinct, vertical ridges**	• **SAM-PK-K11638: low, smooth bulge** • Inaccessible: NHMUK R1971
8. Lingual surface: cingulum	Inaccessible (SAM-PK-8034, CGP CBT 112)	No cingulum	• SAM-PK-K11638: no cingulum • Inaccessible NHMUK R1971

Appendix E, Table 1: Comparison of upper jaw dental features (1-8) amongst South African middle Permian pareiasaurs.

LOWER JAW DENTITION	***Embrithosaurus***	***Nochelesaurus***	***B. baini***
9. Tooth orientation	Anterodorsally	Anterodorsally	Anterodorsally
10. Tooth shape	• **Dorsoventrally shortened and mesiodistally widened(SAM-PK-8034)** • CGP CBT 112 – not accessible	Dorsoventrally elongated, mesiodistally narrow (SAM-PK-6239)	• Dorsoventrally elongated, mesiodistally narrow (most specimens) • **Dorsoventrally shortened and mesiodistally widened((SAM-PK-K11638)**
11. Cusp numbers	• **9 (SAM-PK-8034)** • 7 (CGP CBT 112 – lower jaw not accessible, but presumable 7 cusps as per upper jaw teeth.	• **8-10 (SAM-PK-6239), Very small, very low additional mesial marginal cusp, and sometimes one to two additional unique medial cusps, near the distal margin.** • **7-8 (SAM-PK-6238) due to one extra marginal mesial, low, basal, cusp.** • 7 (SAM-PK-6240) • 9 (FMNH Field no 15)	• 7 (NHMUK R1971) • **7-8 (NHMUK R49426), due to one additional low, basal, VERY SMALL, distal marginal cusp!** • **9 (SAM-PK-K11638) due to symmetrical three marginal mesial and distal cusps, including a low, basal cusp, mesially and distally.**
12. Cusp arrangement	SAM-PK-8034: • Irregularly arranged. • Central trident with 3 close cusps with no gaps between • mesial and distal margins with 3 cusps with large gaps between (SAM-PK-8034) CGP CBT 112: • not accessible	SAM-PK-6239, SAM-PK-6238: • Irregularly arranged. • Central trident with 3 close cusps with no gaps between • **mesial and distal margins with 2 or more cusps with large gaps between**	Inaccessible holotype (NHMUK R1971) SAM-PK-K11638: • Irregularly arranged. • Central trident with 3 close cusps with no gaps between • mesial and distal margins with 3 cusps with large gaps between, including a low, basal, cusp on both the mesial and distal margins
13. Cusp symmetry	SAM-PK-8034: • Symmetrical mesial and distal cusp arrangements CGP CBT 112: • not accessible	**SAM-PK-6239, SAM-PK-6238, FMNH Field no 15:** • **Non- symmetrical mesial and distal cusp arrangements due to extra, low, basal, very small, mesial (anterior) cusp on certain mandibular teeth**	Inaccessible NHMUK R1971 SAM-PK-K11638: • Symmetrical mesial and distal cusp arrangements on all teeth **NHMUK R49426:** • **Non- symmetrical mesial and distal cusp arrangements due to extra, low, basal, very small, distal (posterior)**

			cusp on certain mandibular teeth
14. Medial cusps	SAM-PK-8034: • No medial cusps CGP CBT 112: • not accessible	**SAM-PK-6239:** • **One to-two medial cusps on incipient cingulum ridge, near distal margin, on certain teeth**	• Inaccessible NHMUK R1971 **SAM-PK-K11638:** • **One medial cusp, near distal margin (6th right dentary tooth** **NHMUK R49426:** • **One medial cusp, right dentary tooth**
15. Lingual surface	SAM-PK-8034: • Low, smooth, triangular bulge, lacking vertical ridges CGP CBT 112: • not accessible	**SAM-PK-6239:** • **three high, distinct, vertical ridges** **SAM-PK-6238, SAM-PK-6240:** • **one ridge**	NHMUK R1971, NHMUK R1970, SAM-PK-K11638: • Low, smooth, triangular bulge, lacking vertical ridges **NHMUK R49426:** • **Three high, distinct, vertical ridges**
16. Lingual surface: cingulum	SAM-PK-8034: • No cingulum CGP CBT 112: • not accessible	**SAM-PK-6239, SAM-PK-6238:** • **Incipient cingulum ridge on certain teeth**	NHMUK R1971: • No cingulum

Appendix E, Table 2: Comparison of lower jaw dental features (9-16) amongst South African middle Permian pareiasaurs.

CRANIAL FEATURES: SNOUT	*Embrithosaurus*	*Nochelesaurus*	*B. baini*
17. Snout dimensions (anteriorly)	SAM-PK-8034: • Wider than high	**SAM-PK-6239, SAM-PK-6238, SAM-PK-6240:** • **Square: as high as wide, narrower snout**	NHMUK R1971, SAM-PK-5002, NHMUK R49426, CGP/1/2269 (juvenile): • Wider than high
18. Maxillary boss	SAM-PK-8034, sub-adult: • Small, distinct, high, posterodorsal maxillary boss CGP CBT 112: • low, wide, maxillary boss (right side), distinct, high pointed maxillary boss (left side).	• **No maxillary boss**	NHMUK R1971: • swollen, high, rugose, posterodorsal maxillary boss, adult specimens SAM-PK-5002, SAM-PK-K11638: • a wider, lower, maxillary boss, adult/sub-adultspecimens CGP/1/2269 (juvenile), NHMUK R49426: • no maxillary boss, juvenile specimens
19. Posterodorsal maxillary-lacrimal ridge (bulging maxilla & lacrimal)	SAM-PK-8034, sub-adult: • Ridge formed by distinct maxillary boss, and several distinct lacrimal bosses. CGP CBT 112: • Ridge formed by low maxillary boss and swollen indistinct lacrimal boss complex	**SAM-PK-6239:** • **Ridge very low and indistinct, with only a sharp lateral edge.** • **No maxillary boss.** • **Maxillary ridge ends before the separate lacrimal boss complex,**	All specimens: • Ridge is bulbous, swollen and continuous NHMUK R1971, SAM-PK-5002: • Ridge carries a large maxillary boss in adults NHMUK R49426, CGP/1/2269 (juvenile): • Ridge carries no boss in juveniles
20. Premaxilla and maxilla shape	SAM-PK-8034, CGP CBT 112: • Maxillary teeth visible in lateral view. • Premaxilla and maxilla vertical, mediolaterally very narrow, less than 5 mm wider than the tooth row • Maxillary teeth vertically oriented and downwards pointing.	SAM-PK-6239, SAM-PK-6238: • Maxillary teeth visible in lateral view. • Premaxilla and maxilla vertical, mediolaterally very narrow, less than 5 mm wider than the tooth row. • Maxillary teeth vertically oriented and downwards pointing.	**NHMUK R1971, SAM-PK-5002:** • **Maxillary teeth not visible in lateral view.** • **Premaxilla and maxilla strongly convex, mediolaterally wide, up to 20mm wider than the tooth row.** • **Maxillary teeth horizontally to posteroventrally oriented and backwards pointing.**

Appendix E, Table 3: Comparison of cranial features of the snout (17-20) amongst South African middle Permian pareiasaurs.

CRANIAL FEATURES: DORSAL SKULL TABLE	***Embrithosaurus***	***Nochelesaurus***	***B. baini***
21. Overall cranial ornamentation	SAM-PK-8034, CGP CBT 112 • Lower bosses, less distinct, less pointed	All specimens: • **More distinct, higher bosses, more pointed**	NHMUK R1971, SAM-PK-5002, CGP/1/2269 (juvenile), NHMUK R49426: • Lower bosses, less distinct, less pointed. Adults and juveniles.
22. Orbital marginal bosses (prefrontal, postfrontal, postorbital)	Less distinct	**Very distinct**	Less distinct
23. Nasal tab-like processes	SAM-PK-8034: • **anterolateral tab above the nostrils very distinct** • posterolateral tab distinct • posteromedial tab less distinct	**SAM-PK-6239:** • **usually no anterolateral tab** • posterolateral tab distinct • posteromedial tab less distinct CGP JA 109: • **anterolateral tab above the nostrils very distinct**	**NHMUK R1971, CGP/1/2269 (juvenile):** • **anterolateral tab above the nostrils very distinct** • posterolateral tab distinct • posteromedial tab less distinct **SAM-PK-3718, SAM-PK-4350:** • **anterolateral tab not present**
24. Frontal central boss	**SAM-PK-8034:** • **Very small, indistinct, low, irregular**	SAM-PK-6239: • Large, distinct, high, circular, very regular	NHMUK R1971, SAM-PK-5002, SAN-PK-3718: • Large, wide, irregular, low A minority of specimens: • Large, distinct, high, circular, very regular
25. Prefrontal depression	**SAM-PK-8034:** • **Wide and distinct, shallow, bowl-shaped depression covers prefrontal, between the three lateral Prefrontal bosses and the medial prefrontal-frontal suture.**	Not present	Not present
26. Postfrontal shape	**SAM-PK-8034, NHMUK R7782, internal sutures:** • **Postfrontal mediolaterally elongated**	SAM-PK-6239, SAM-PK-6238: • Postfrontal roughly square, slightly longitudinally elongated, and posteriorly curved medially	SAM-PK-3718, CGP/1/2269 (juvenile): • Postfrontal roughly square, slightly longitudinally elongated, and posteriorly curved medially

27. Postparietal shape & bosses	SAM-PK-8034: • Postparietal transversely narrow, so no anterolateral swelling and no distinct posterolateral boss.	**SAM-PK-6239, SAM-PK-6238:** • **Postparietal transversely wide, includeing an indistinct anterolateral swelling and a distinct posterolateral boss**	SAM-PK-3718, CGP/1/2269 (juvenile): • Postparietal transversely narrow, so no anterolateral swelling and no distinct posterolateral boss.

Appendix E, Table 4: Comparison of cranial features of the dorsal skull table (21-27) amongst South African middle Permian pareiasaurs.

CRANIAL FEATURES: CHEEKS	***Embrithosaurus***	***Nochelesaurus***	***B. baini***
28. Mediolateral width of cheek flanges (posterior portions of the quadratojugal);	Mediolaterally wider cheek flanges: • SAM-PK-8034: 60 mm • CGP CBT 112: 70 mm	**Mediolaterally narrower cheek flanges:** • **SAM-PK-6239: 50 mm**	Mediolaterally wider cheek flanges: • NHMUK R1971: 65 mm • SAM-PK-5002: 50 mm Sub adult • SAM-PK-3718: 55 mm (mediolaterally crushed)
29. Cheek size	**Largest cheeks in the group, 30^0 to 40^0below the tooth row:** • **SAM-PK-8034 (left cheek 24^0, right cheek 34^0, average 29^0)** • **CGP CBT 112 (40^0 both sides)**	**Relatively large cheeks, up to 30^0below the tooth row:** • SAM-PK-6239: right cheek 33^0, no left cheek • SAM-PK-6238: right cheek 35^0 • SAM-PK-6240 (left 30^0, right 28^0, average 29^0)	**Highly variable cheeks: small (20^0) to large (30^0) below the tooth row:** • NHMUK R1971: left cheek 35^0, right cheek 20^0, **average 27.5^0** • Diagnostic small cheek flanges: SAM-PK-5002: right 20^0, left 25^0, **average 22.5^0** • SAM-PK-K11638: 20^0 both sides • CGP/1/2269 (juvenile): left 25^0, right 30^0, average 27.5^0. • NHMUK R49426: 30^0 both sides. • **SAM-PK-5624: 20-25^0** • **SAM-PK-3718** (right 26^0, left 30^0, **average 28^0**)
30. Vertical separation (gap) on the posterior edge of the cheek, between the dorsal-most quadratojugal boss and the large squamosal boss	No gap	**Gap present:** • **SAM-PK-6239, SAM-PK-6239A, JA-109 (not on SAM-PK-6238) small gap on SAM-PK-6240**	No gap present on most specimens: • NHMUK R1971, CGP/1/2269 (juvenile), SAM-PK-3718) Gap present on a minority of specimens: • e.g. SAM-PK-5002
31. Quadratojugal posterior edge bosses	Large, wide, low, bulbous, indistinct: • SAM-PK-8034, CGP CBT 112	**Horizontally flat, pointed and plate-like:** • **SAM-PK-6239, SAM-PK-6240, SAM-PK-9137** **Medium sized, round (as wide as high, 25-30 mm), pointed and distinct:** • **SAM-PK-6239A, SAM-PK-5019, SAM-PK-6238**	Large, wide, low, bulbous, indistinct: • Adult: NHMUK R1971, SAM-PK-3718, Sub-adult SAM-PK-9121, CGP/1/2269 (juvenile) Medium sized, round (as wide as high, 25-30 mm), pointed and distinct:

			• SAM-PK-5002, NHMUK R49426, SAM-PK-K11638, SAM-PK-5624.
32. Quadratojugal posterior edge corner boss	Corner boss big, bulbous, low: • SAM-PK-8034, CGP CBT 112	Corner boss distinct and very elongated, with proximal narrow neck and raised distal rim, pointed tip, and covered in more distinct rugose ridges • all specimens	Corner boss big, bulbous, low, • NHMUK R1971, CGP/1/2269 (juvenile) Corner boss smaller, pointier, longer and more distinct: • SAM-PK-5002, SAM-PK-K11638, SAM-PK-5008, SAM-PK-5624
33. Quadratojugal lateral surface ornamentation	SAM-PK-8034: • **Cheek flange flat** • 2-4 distinct, low to high, circular, ovoid, bosses arranged posterodorsally • bosses round to elongated or curved CGP CBT 112: • **Cheek flange flat** • distinct bosses, arranged almost vertically, posterodorsally, in two rows or ridges each side	SAM-PK-6239, SAM-PK-6238, SAM-PK-6240: • **Cheek flange flat** • 3-4 very distinct , small, low to high, circular to slightly ovoid, pointed, bosses arranged in an arc • bosses small and round (not elongated or curved)	NHMUK R1971, SAM-PK-5002, SAM-PK-3718: • **Cheek flange not flat , but ventrally swollen and bulging, forming a shelf** • **Few or no distinct, discrete bosses, instead has irregular rugose ridges, that thicken the lower lateral** quadratojugal. • bosses not elongated or curved CGP/1/2269 (juvenile), NHMUK R49426: • Cheek flange flat, with very, very low ornamentation of irregular rugose ridges

Appendix E, Table 5: Comparison of cranial features of the cheeks (28-33) amongst South African middle Permian pareiasaurs.

CRANIAL FEATURES: OCCIPUT and LOWER JAW	***Embrithosaurus***	***Nochelesaurus***	***B. baini***
34. Paroccipital process of the opisthotic - anteroposterior expansion	Distal portion of the process is anteroposteriorly short, 55 mm • SAM-PK-8034:	Distal portion of the process is anteroposteriorly short, 50-55 mm • SAM-PK-6239, SAM-PK-6240	**Distal portion of the process is anteroposteriorly very expanded** • **NHMUK R1971: 80 mm** • **SAM-PK-3718: 75 mm** • **SAM-PK-5624:60-80 mm** • **SAM-PK-5002 Sub-adult:60 mm**
35. Paroccipital process of the opisthotic – posterior process	Dorsomedially elongated (40 mm dorsomedially long, 20 mm mediolaterally wide), posteriorly projecting (10-15 mm) knob-like process, on the medial edge of the posterodorsal corner of the paroccipital process • SAM-PK-8034: • NHMUK R7782	**Dorsolaterally elongated posterior process absent (20 mm, 10 mm, 10 mm), but posteroventral edge of the distal paroccipital process is dorsolaterally elongated and swollen (20 mm long, 10 mm wide, 10 mm high)** • **SAM-PK-6239,** • **CGP JA-109,** • **SAM-PK-6240**	**Dorsomedially elongated**, posteriorly projecting knob-like process, on the medial edge of the posterodorsal corner of the paroccipital process • NHMUK R1971: 60 mm dorsomedially long, 30 mm wide, 30 mm high • SAM-PK-5002: 40 mm long,30 mm wide, 25 mm high • SAM-PK-5624: 45 mm long, 25 mm wide, 10-20 high • SAM-PK-3718: 50 mm long,30 mm wide, 25 high
36. Angular boss	SAM-PK-8034 sub-adult: • long, slender, small, gracile, slightly distally tapering. SAM-PK-3030: • large angular boss with a “tennis ball-like” rim, distal end thick. SAM-PK-9098 Juvenile: • Pareiasaurian claw shape: mediolaterally narrow, proximal swollen/bulged rim, distally tapering. CGP CBT 112: • very large, robust, wide, extending ventrally to a very thick, pronounced, swollen “tennis ball-like” rim covered with ridges.	SAM-PK-6238: • Long, slender, small to medium for an adult, conical, distally tapering SAM-PK-6240 Juvenile : • small, very blunt, stubby knob at tip SAM-PK-8944, SAM-PK-5019: • Large, Pareiasaurian claw shape due to a swollen rim proximally, not distally.	NHMUK R1971: • Long, slender, small (for an adult specimen), CGP/1/2269 (juvenile): • very small, short and stubby SAM-PK-4347, BP/1/1577: • Pareiasaurian claw shape: large, bulged, swollen rim proximally.

	NHMUK R7782: • oversized very long, very sharp and pointed, conical shaped elongated.		

Appendix E, Table 6: Comparison of cranial features of the occiput and lower jaw (34-36) amongst South African middle Permian pareiasaurs.

APPENDIX F: KEY COMPARATIVE FEATURES

Bradysaurus baini key comparative features

Cranial features:

Upper jaw teeth:

- Mediolaterally wide and curved premaxilla and maxilla (20 mm wider than the tooth row), accommodating horizontally to posteroventrally oriented, backwards pointing upper jaw teeth that are not visible in lateral view;
- Seven to nine cusps on the maxillary teeth;
- Maxillary teeth with smooth, bulged lingual surface;
- Shares with *Embrithosaurus* symmetrical mesial and distal marginal cusp arrangements;
- Shares with some specimens of *Embrithosaurus* maxillary teeth with irregularly arranged marginal cusps, with a central 3-cusped trident;

Lower jaw teeth:

- Mandibular teeth with seven to nine cusps;
- Seven or nine cusped mandibular teeth have a symmetrical arrangement;
- Nine cusped mandibular teeth including a very low, very small, cusp at base of the mesial and distal margins;
- Eight cusped mandibular teeth with non-symmetrically arranged marginal cusps, due to a very low, very small, cusp at base of the distal margin of each tooth, with the mesial margin lacking corresponding low, basal cusp;
- Mandibular teeth dorsoventrally elongated and mesiodistally narrow, (dorsoventrally shortened and mesiodistally widened on a minority of specimens);
- Shares with some specimens of *Embrithosaurus* mandibular teeth lingual surface with a low smooth triangular bulge;

- Shares with some specimens of *Nochelesaurus* mandibular teeth lingual surface with three ridges;
- Shares with *Embrithosaurus* the absence of a cingulum on the lingual surface;

Snout:

- Shares with *Embrithosaurus* a wider than high snout;
- Maxilla with a wide, swollen, high, rugose, posterodrosal maxillary boss in adult specimens, lower in juveniles, but always with a wide, swollen maxillary-lacrimal ridge continuous with the swollen lacrimal boss complex;

Dorsal skull table:

- Shares with *Embrithosaurus* lower, generally less distinct cranial ornamentation (especially on the prefrontal, postfrontal and postorbital) and some specimens of *Bradysaurus,* share the presence of a distinct anterolateral tab-like process above the external naris;
- Some *Bradysaurus* specimens share a frontal with a high, distinct central boss with *Nochelesaurus*, other specimens have Large, wide, low, irregular frontal central boss.
- Shares with *Nochelesaurus* a roughly square postfrontal, slightly longitudinally elongated, and posteriorly curved medially;
- Shares with *Embrithosaurus* a transversely narrow postparietal;

Cheeks:

- Shares with *Embrithosaurus* mediolaterally wider cheek flanges and the absence of a gap on the posterior cheek between the dorsal-most quadraojugal boss and the large squamosal boss (in most specimens of *Bradysaurus*);

- cheek flange highly variable, extending below the tooth row from small (20^0), the smallest in the group of pareiasaurs to large (30^0);
- Some *Bradysaurus* specimens shares with *Embrithosaurus* specimens wide, low, bulbous (wider than high) posterior cheek bosses and a bulbous corner cheek boss;
- Some *Bradysaurus* specimens shares with *Nochelesaurus* specimens posterior cheek bosses that are smaller medium sized, as wide as high, more distinct and pointed;
- Shares with *Nochelesaurus* a flat lateral surface of the quadratojugal cheek flange, with distinct bosses arranged posterodorsally;
- Lateral surface of the quadratojugal not flat, but ventrally swollen and bulging, forming a shelf in adults, covered with irregular rugose ridges;

Occiput:

- An anteroposteriorly long distal paraoccipital process of the opisthotic
- Highly variable angular boss, but typically smaller than those of *Embrithosaurus* or *Nochelesaurus*.
- Shares with *Embrithosaurus* a paroccipital process of the opisthotic with a dorsomedially elongated, posteriorly projecting, knob-like process, on the medial edge of the posterodorsal corner (smaller in *Embrithosaurus;*

Postcranial features

Scapulocoracoid:

- Short, wide scapula blade, distally flared, similar to *Embrithosaurus*, very different from the longer, anteroposteriorly narrower, only moderately distally flared, scapula blade of most specimens of *Nochelesaurus*;

Clavicles:

- Posteroventral process on the ventral margin of the clavicle low (10 -15 mm) and wide (110 mm), and lacking the distinct notch just medial to the process seen in *Embrithosaurus*;

Humerus:

- Shares with *Embrithosaurus* highly twisted proximal and distal expansions of the humerus, forming an angle of 60-80^0 apart;
- Shares with *Embrithosaurus* and *Nochelesaurus* a humerus with triangular intercondylar fossa demarcated by a gently concavely curved, distinct swollen ridge (intercondylar ridge border) on the dorsal distal margin, preventing the fossa from reaching round onto the distal side of the humerus;
- Shares with *Nochelesaurus* a deep intercondylar fossa, at 40-50 mm (*Nochelesaurus*: 35 -50 mm), corresponding with a large and prominent olecranon process of the ulna;
- Humerus with two epicondyles that do project distally far beyond the radial and ulnar articulation surfaces, appearing “forked”;
- Shares with *Nochelesaurus* a massive, robust “heart shaped” delto-pectoral crest, 90 mm anteroposteriorly, with a notch on the ventrodistal corner and with a ventral surface lacking the long, central, ventral groove of *Embrithosaurus*;
- Shares with *Nochelesaurus the* presence of a short, curved, crescent-shaped, insertion point for muscle attachment on the humeral shaft of the dorsal proximal humerus (Absent in *Embrithosaurus*);
- Wider distal humerus (290 mm holotype) than *Nochelesaurus* or *Embrithosaurus*;
- Wider proximal humerus (305 mm holotype), than *Nochelesaurus* or *Embrithosaurus*;

Radius:

- Shares with *Embrithosaurus* a radius with the proximal end mediolaterally slightly wider than the distal end and a more symmetrical distal and proximal radius;
- Shares with *Nochelesaurus* the presence of a distinct, vertical, ridge on the medial side of the distal portion of the radius, extending from the swollen base of the radius, tapering dorsally and almost reaches midway up the shaft;

Ulna:

- Shares with *Nochelesaurus* a dorsoventrally very long ulna (370 mm), due to an extended proximal postaxial bar and proximal articulation surface;
- Shares with *Nochelesaurus* the presence of an oblique ridge on the proximal articulation surface;
- Presence of a high, convex, and highly variable 15 – 45 mm high olecranon processes;
- Anterodorsal ulna constricted or "pinched in", medially and laterally, which meet;
- Shares with *Nochelesaurus*, ulna with posterodorsal limiting ridge;

Femur (general):

- Shares with *Embrithosaurus* a postaxial shaft that is notable bulged/convex;
- Shares with *Embrithosaurus* a moderately distally extended lateral condyle, beyond the distal edge of the medial condyle, (20-45 mm) compared to the much longer condition present in most specimens of *Nochelesaurus* of up to 70 mm;
- Shares with *Embrithosauus* a generally anteroposteriorly wider Femur across the distal condyles compared to *Nochelesaurus*;

Femur (major trochanter):

- Posterior projection of the major trochanter short (10 mm); longer than *Nochelesaurus* (<5 mm), shorter than *Embrithosaurus* (20-30 mm).
- Shares with *Nochelesaurus* the absence of a deep notch (so no notch or only a shallow notch) proximal and/or distal to the major trochanter, on the postaxial flange, separating the major trochanter from the postaxial shaft;

Femur (internal trochanter):

- Proximal region of internal trochanter very strongly curved with a concave preaxial (anterior) side and a convex postaxial (posterior) side, compared to the gently/moderate curvature of *Embrithosaurus* and the complete lack of curvature or very slight curvature of *Nochelesaurus;*
- Shares with *Embrithosaurus* the proximal region of internal trochanter extends far ventrally (30-40 mm) beyond the proximal postaxial shaft the femur, compared to the very low condition of *Nochelesaurus* (10 mm);
- Shares with *Embrithosaurus* the proximal edge of internal trochanter emerges perpendicularly (90^0) out of the femur;
- A wide proximal internal trochanter (narrow in most specimens of *Nochelesaurus* and *Embrithosaurus)*;
- Shares with *Embrithosaurus* proximal region of internal trochanter positioned further from the preaxial (anterior) border of the femur and not close or parallel to the border as in *Nochelesaurus*;
- Distal portion of internal trochanter narrow (not wide and rugose as it is in *Embrithosaurus*) and with a smaller, very short anterior (preaxial) process/projection compared to *Embrithosaurus* (anterior process not present in *Nochelesaurus*)*;*

Tibia:

- Shares with *Nochelesaurus*, a smaller angle (40^0) between the lateral and medial facets of the proximal articulation surface of the tibia, which is 60^0 in *Embrithosaurus*;
- Distal tibia morphology shared with *Nochelesaurus*:
    - ventromedially expanded and projecting distal tibia
    - ventrolaterally upturned distal tibia
    - mediolaterally wider distal tibia than *Embrithosaurus*
- Shares with *Nochelesaurus* an elongated rugose ridge, just dorsal to a vertical depression, on the lateral edge of the shaft of the tibia;

Pelvis:

- Pelvis low and wide, shallow u-shaped, in anterior or posterior view;
- Posterior half of iliac blade generally flat and thin and vertically oriented and dorsal margins of the posterior process, curve medially inwards (convex);
- Anterior half of iliac blades deeply concave (laterally) due to curved (everted) anterior process sharply upwards, and laterally outwards from the sagittal plane;
- Iliac blades oriented parallel to sagittal plane, posteriorly;
- Iliac blades strongly curved anteriorly, diverging anteriorly, to orient roughly 45^0 off the sagittal plane;
- Shalf of pelvis horizontally oriented, only 30^0 above the vertical plane;
- Acetabulum round to anteroposteriorly elongated (oval);
- Puboischiatic plate mediolateral wide;
- Puboischiatic plate anteroposteriorly long;
- Dorsal surface of puboischiatic plate horizontally very flat and wide between the iliac blades (not concave);
- Pelvic symphysis dorsoventrally not as thick as in *Embrithosaurus*;

- Keel on ventral puboischiatic plate mediolaterally much narrower than *Embrithosaurus*, and only covers a minority of the wide, flat, plate ventrally. Keel extends dorsolaterally upwards at a shallower angle than in *Embrithosaurus*;
- Median pubic process squared, short (10 mm), projecting only ventrally (not anteroventrally far as in *Embrithosauus*) and without a deep notch either side;

Vertebrae:

- Parapophysial and diapophysial articulations fuse into a single vertical flange, creating a transverse process with a single lateral facet from the 5th vertebrae backwards; NHMUK R1971, or the 4th backwards NHMUK R49426 (This occurs from the 6th vertebrae backwards in *Embrithosaurus* and *Nochelesaurus*);
- Second sacral rib (20th vertebra) is the largest in the sacrum and the first sacral rib (19th vertebra) is second largest (NHMUK R1971, NHMUK R49426). In *Embrithosaurus*, the first sacral rib (19th vertebra) is massively large and the second one (20th vertebra) much smaller.
- Caudal vertebra lateral projections “L-shaped” (straight in *Embrithosaurus*);

Osteoderms:

- Anterior dorsal osteoderms (6th-9th vertebrae) large (45-55 mm), low (18-20 mm high), evenly, smoothly and strongly convex dorsal surface due to a lack of a distinct central boss and lacking a flat, thin periphery. Anterior dorsal osteoderms with a large, indistinct or incipient central boss, 25 mm wide (very slightly thickened centre, or a very slightly raised central region), ornamentation very light, consisting of very fine (1 mm wide), very short (2-4 mm long), straight to slightly curved, radial ridges, with

very shallow, very thin depressions or troughs in between, very small, very shallow, circular pits on a minority of the scutes;

- Posterior dorsal osteoderms (10^{th}-19^{th} vertebrae) small, (25-30 mm wide), flat, low and thin, “disc like”, smoothly/evenly convex dorsal surface. Posterior dorsal osteoderms, mostly with a central, well defined, circular hollow, (6-8 mm wide) surrounded by very light ornamentation, similar to the anterior dorsal ostederms: very fine (1 mm wide), very short (2-4 mm long), straight to slightly curved , raised ridges, with shallow, very thin depressions or troughs in between, and very small, very shallow, circular pits on a minority of the scutes;
- Shares with *Embrithosaurus*, presence of a few, high, evenly smoothly convex, small “stud like” osteoderms.

Embrithosaurus schwarzi key comparative features

Cranial features:

Upper jaw teeth:

- Shares with *Nochelesaurus* vertically oriented, mediolaterally narrow, premaxilla and maxilla, only slightly wider (by <5 mm) than the tooth row, accommodating downwards pointing, vertically oriented maxillary teeth;
- Nine cusped teeth, dorsoventrally shortened, mesiodistally widened, lacking a long central trident and with marginal cusps arranged more regularly around the tooth crown than in co-occurring taxa;
- Seven cusped teeth with dorsoventrally elongated, mesiodistally narrower, with a long, central, three cusped trident;
- Shares with *Bradysaurus* symmetrical mesial and distal marginal cusp arrangements;

Lower jaw teeth:

- Nine cusped teeth, dorsoventrally shortened, mesiodistally widened;
- Seven cusped teeth dorsoventrally elongated, mesiodistally narrow;
- Shares with some *Bradysaurus* specimens a symmetrical mesial and distal marginal cusp arrangement;
- Shares with some *Bradysaurus* specimens a low, smooth, triangular bulge on the lingual surface;
- Shares with *Bradysaurus* the absence of a cingulum on the lingual surface;

Snout:

- Shares with *Bradysaurus* a wider than high snout;

- Presence of a small, distinct, maxillary boss and a posterodoral maxillary-lacrimal ridge outlining the external naris, formed by the distinct maxillary boss and several distinct or indistinct lacrimal bosses;

Dorsal skull table:

- Shares with *Bradysaurus* lower, generally less distinct cranial ornamentation (especially on the prefrontal, postfrontal and postorbital) and the presence of a distinct anterolateral tab-like process above the external naris (*Bradysaurus*: most specimens);
- Small, indistinct frontal central boss;
- Wide depression on the prefrontal on some specimens;
- Postfrontal mediolaterally elongated;
- Shares with *Bradysaurus* a transversely narrow postparietal;

Cheeks:

- Shares with *Bradysaurus* mediolaterally wider cheek flanges and the absence of a gap on the posterior cheek between the dorsal-most quadraojugal boss and the large squamosal boss;
- Cheek size largest of co-occurring pareiasaurs 30^{0}-$40^{0;}$
- Shares with some *Bradysaurus* specimens wide, low, bulbous posterior cheek bosses and a bulbous corner cheek boss;
- Shares with *Nochelesaurus* a flat lateral surface of the quadratojugal cheek flange, with distinct bosses arranged posterodorsally;

Occiput:

- Shares with *Nochelesaurus* an anteroposteriorly short distal paraoccipital process of the opisthotic and a highly variable angular boss, but typically large and elongated with either a proximal swollen rim (reminiscent of a pareiasaurian terminal claw) or a midway swollen rim;

- Shares with *Bradysaurus* a paroccipital process of the opisthotic with a dorsomedially elongated, posteriorly projecting, knob-like process, on the medial edge of the posterodorsal corner (larger in *Bradysaurus*)*;*

Postcranial features

Scapulocoracoid:

- Short, wide scapula blade, distally flared, similar to *Bradysaurus*, very different from the longer, anteroposteriorly narrower, only moderately distally flared scapula blade of most specimens of *Nochelesaurus*;

Clavicle:

- Presence of a large posteroventral process on the clavicle, high (20 mm), wide (80 mm) and a distinct, deep notch just medial to the posteroventral process;

Humerus:

- Shares with *Bradysaurus* highly twisted proximal and distal expansions of the humerus, forming an angle of 60-80^{0}apart;
- Shares with *Bradysaurus* and *Nochelesaurus* a humerus with triangular intercondylar fossa demarcated by a gently concavely curved, distinct swollen ridge (intercondylar ridge border) on the dorsal distal margin, preventing the fossa from reaching round onto the distal side of the humerus;
- Humerus with shallow intercondylar fossa, (20 mm deep) unlike the deeper fossa in *Nochelesaurus* (35 -50 mm) and *Bradysaurus baini*: (40-50 mm)
- Shares with *Nochelesaurus* a humerus with two epicondyles that do not project distally far beyond the radial and ulnar articulation surfaces;

- Narrower (60-70 mm) delto-pectoral crest than *Bradysaurus* and *Nochelesaurus* (90 mm), with long, shallow groove on the ventral surface and lacking the notch that *Nochelesaurus* and *Bradysaurus* have at the ventrodistal corner;
- Humerus lacks the short, curved, crescent-shaped, insertion point for muscle attachment on the humeral shaft of the dorsal proximal humerus, seen in *Nochelesaurus* and *Bradysaurus*;

Radius:

- Shares with *Bradysaurus* a radius with the proximal end mediolaterally slightly wider than the distal end and a more symmetrical distal and proximal radius;

Ulna:

- Sub-adult (SAM-PK-8034: holotype) ulna short and without an olecranon process, and with proximal articular surface consisting of a shallow groove on the anterior, dorsal and posterior sides of the ulna, with distinct lateral and medial olecranon crests, and lacking an anterodorsal limiting ridge and a posterolateral limiting ridge;
- Adult specimens (CGP CBT 112, AMNH FARB 2451, SAM-PK-9148, SAM-PK-4352, FMNH UR 2443) with a long ulna and a large, prominent olecranon process (10-40 mm dorsoventrally high, extending anteriorly 10-20 mm), formed anterodorsally by two overhanging, concavely curved projections from the lateral and medial surfaces that meet each other anteriorly, forming an anterodorsal limiting ridge ("lip-like" overhanging ledge), with presence of a posterolateral limiting ridge;

Femur (general):

- Shares with *Bradysaurus* a postaxial shaft that is notable bulged/convex;

- Shares with *Bradysaurus* a moderately distally extended lateral condyle, beyond the distal edge of the medial condyle, (20-45 mm) compared to the much longer condition present in most specimens of *Nochelesaurus* of up to 70 mm;
- Shares with *Bradysaurus* a generally anteroposteriorly wider Femur across the distal condyles compared to *Nochelesaurus*;

Femur (major trochanter):

- Posterior projection of the major trochanter of the femur very long (20-30 mm), longer than *Nochelesaurus* (<5 mm), and *Bradysaurus* (10 mm).
- Presence of a deep notch proximal and/or distal to the major trochanter, on the postaxial flange, separating the major trochanter from the postaxial shaft (notch very slight or not present in *Bradysaurus* or *Nochelesaurus*)

Femur (internal trochanter):

- Proximal region of internal trochanter gently or moderately curved, with a concave preaxial (anterior) side and a convex postaxial (posterior) side, compared to the very strong curvature of *Bradysaurus* and the complete lack of curvature or very slight curvature of *Nochelesaurus;*
- Shares with *Bradysaurus baini* the proximal region of internal trochanter extends far ventrally (30-40 mm) beyond the proximal postaxial shaft the femur, compared to the very low condition of *Nochelesaurus* (10 mm);
- Shares with *Bradysaurus baini* the proximal edge of internal trochanter emerges perpendicularly (90^0) out of the femur;
- Proximal internal trochanter variable from narrow (most specimens) to thickened, wide and rugose (CGP CBT 112, BP/1/7241, SAM-PK-9116);
- Shares with *Bradysaurus baini* proximal region of internal trochanter positioned further from the preaxial (anterior) border of the femur and therefore not parallel or close to the border as in *Nochelesaurus;*

- Distal portion of internal trochanter wide and rugose, with a large anterior (preaxial) process/projection (SAM-PK-8034, CGP CBT 112), not present in *Nochelesaurus* and smaller in *Bradysaurus baini*.

Tibia:

- Shaft of the tibia very constricted and narrow (45mm mediolaterally), much narrower than *Nochelesaurus* (70-72 mm) or *Bradysaurus* (75mm);
- Large, 60^0, angle between the medial and lateral facets of the proximal articulation surface of the tibia, larger than the 40^0 in specimens of *Nochelesurus* and *Bradysaurus*;

Pelvis:

- Pelvis high and narrow, v-shaped, in anterior or posterior view;
- Iliac blades mediolateral narrow, anteriorly and dorsally;
- Iliac blades almost perfectly flat and straight, lateral surface flat to very slightly and gently concave overall;
- Iliac blades oriented almost perfectly dorsoventrally (vertically), except for the anteroventral margin of the anterior process, which is very slightly curved or everted upwards and outwards;
- Iliac blades oriented 45 -60^0 off the sagittal midline plane, diverging anteriorly;
- Shaft of pelvis vertically oriented, only slightly forwardly leaning off the vertical to orient anterodorsally 30^0 off the vertical plane;
- Acetabulum perfectly round and smaller in diameter than in *Bradysaurus;*
- Puboischiatic plate mediolateral narrow;
- Puboischiatic plate anteroposteriorly short;
- Dorsal surface of puboischiatic plate narrow and strongly and evenly concavely curved, (not flat);
- Pelvic symphysis dorsoventrally thicker than in *Bradysaurus baini*;

- Keel on ventral puboischiatic thick and covers most ventral surface of the puboischiatic plate and extends dorsolaterally upwards at a 50^0 angle above a horizontally flat plane;
- Median pubic process large and distinct, “tongue” shaped (rounded edges), extending anteroventrally far (50 mm), and with a deep notch either side;

Vertebrae:

- Shares with *Nochelesaurus*, parapophysial and diapophysial articulations fuse into a single vertical flange, creating a transverse process with a single lateral facet from the 6^{th} vertebrae backwards; SAM-PK-8034 (In *Bradysaurus* this occurs from the 5^{th} vertebrae backwards; NHMUK R1971, or the 4^{th} backwards NHMUK R49426);
- First sacral rib (19^{th} vertebra) is the largest, second sacral rib (20^{th} vertebra) is second largest (SAM-PK-8034). In *Bradysaurus baini*, the second sacral rib (20^{th} vertebra) is the largest and the first one (19^{th} vertebra) is much smaller;
- Caudal vertebra lateral projections straight (“L shaped” in *Bradysaurus*);

Osteoderms:

- Anterior dorsal osteoderms large (40-50 mm in diameter), roughly pentagonal, with straight to concave edges, relatively low (only 15-20 mm high). Anterior dorsal osteoderms with very distinct, very high well-defined, central boss, accounting for most of the height (+- 15 mm) of the relatively low boss (15-20 mm), small to medium in diameter(20-35 mm wide) compared to the width of the boss (40-50 mm) and irregularly shaped (L-shaped or E-shaped), comprising one to more thickened rugose tab-like swellings or ridges;
- Anterior dorsal osteoderm peripheries very flat, thin, disc-like, very low (5-7 mm high), covered with low, irregularly placed and numbered,

straight, thin, radiating ridges which radiate our laterally from the sides of each central boss towards the edges,

- Shares with *Bradysaurus*, presence of a few, high, evenly smoothly convex, small “stud like” osteoderms.

Nochelesaurus alexanderi key comparative features

Cranial features:

Upper jaw teeth:

- Shares with *Embrithosaurus* vertically oriented, mediolaterally narrow, premaxilla and maxilla, only slightly wider (by <5 mm) than the tooth row, resulting in downwards pointing, vertically oriented maxillary teeth;
- Seven or eight cusped teeth, dorsoventrally elongated, mesiodistally narrower, with a long, central, three cusped trident;
- Eight cusped teeth with an additional low, basal cusp, near the mesial margin, creating a non-symmetrical mesial and distal marginal cusp arrangement;
- Maxillary teeth lingual surface with three-five distinct vertical ridges and with no cingulum;
- Shares with *Bradysaurus* maxillary teeth with irregularly arranged marginal cusps, with a central 3-cusped trident;

Lower jaw teeth:

- Mandibular teeth with seven to ten cusps;
- Eight to ten cusped teeth have non-symmetrical marginal cusp arrangement, due to very low, very small, cusp at base of the mesial margin of each tooth, with the distal margin lacking corresponding low, basal cusp;
- Seven cusped teeth dorsoventrally elongated, mesiodistally narrow;
- Non-symmetrical mesial and distal marginal cusp arrangement;

- Mandibular teeth lingual surface with one -three distinct vertical ridges (certain *Bradysaurus* specimens also have three ridges on the lingual surface;
- Certain mandibular teeth with lingual surface with incipient horizontal cingulum above the base and with certain teeth carrying medially placed cusp(s) on the cingulum, near the distal margin;

Snout:

- Relatively narrow snout, only very slightly wider than high or as high as wide;
- Maxilla lacking a central maxillary boss, but with a distinct, low, posterodorsally oriented maxillary-lacrimal ridge that does not reach the lacrimal boss complex;

Dorsal skull table:

- More distinct overall cranial ornamentation than *Bradysaurus* or *Embrithosaurus* (especially on the prefrontal, postfrontal and postorbital;
- Absence of a distinct anterolateral tab-like process above the external naris on most specimens;
- Shares with some specimens of *Bradysaurus* a frontal with a distinct, high, central boss;
- Shares with *Bradysaurus* a roughly square postfrontal, slightly longitudinally elongated, and posteriorly curved medially;
- Postparietal transversely wide and rectangular;

Cheeks:

- Narrow cheek flange;
- Large cheek flange extending about 30^0 below the tooth row;
- Presence of flat, vertical separation (gap) on the posterior edge of the cheek, between the dorsal-most quadratojugal boss and the large

squamosal boss, through which the horizontal squamosal-quadratojugal suture passes;

- Posterior edge of the quadratojugal (cheek flange) with more distinct bosses that vary from horizontally flat and plate-like to medium sized, round (as wide as high) pointed bosses (medium bosses shared with some specimens of *Bradysaurus*);
- Cheek corner boss of the quadratojugal large and elongated, with proximal narrow neck and raised distal rim, pointed tip, and more distinct rugose ridges;
- Boss on the posterior edge of the squamosal projects posterolaterally high above the lateral surface of the cheek, and sometimes includes dorsal and ventral sharp projections; sometimes;
- Shares with *Embrithosaurus*: lateral surface of the quadratojugal cheek flange flat, with distinct bosses arranged posterodorsally;

Occiput:

- Distal portion of the paroccipital process of the opisthotic lacking the dorsomedially elongated, posterior process of *Bradysaurus* and *Embrithosaurus*, and is instead low and smooth, with or without a dorsolaterally elongated and gently swollen posteroventral edge;
- Shares with *Embrithosaurus* an anteroposteriorly short distal paraoccipital process of the opisthotic and a highly variable angular boss, but typically large and elongated with either a proximal swollen rim (reminiscent of a pareiasaurian terminal claw) or a midway swollen rim;

Postcranial features

Scapulocoracoid:

- Long scapula blade in most specimens, in comparison with *Embrithosaurus* and *Bradysaurus;*

- Mid scapula blade anteroposteriorly constricted and very narrow in most specimens, much narrower than *Embrithosaurus* and *Bradysaurus*;
- Dorsal scapula blade narrow, little anteroposterior distal flaring, preaxial and postaxial margins are very straight and only very slightly curved in most specimens; compared to the dorsal flaring in *Embrithosaurus* and *Bradysaurus;*
- Medial process of scapula blade larger and higher than in *Embrithosaurus* and *Bradysaurus*;
- Glenoid fossa anteroposteriorly shorter than *Embrithosaurus* and *Bradysaurus;*
- Subscapular fossa groove slightly smaller in all dimensions than in *Embrithosaurus*, and much smaller than *Bradysaurus.*

Clavicle:

- Posteroventral process on the ventral margin of the clavicle low (10 mm) and wide (90 mm), much smaller than the same feature on *Embrithosaurus*, and lacking the distinct notch just medial to the process seen in *Embrithosaurus*.

Humerus:

- Little twisting or torsion between the proximal and distal expansions of the humerus, only 20-40^{0}apart, the two ends therefore appearing on nearly the same plane;
- Shares with *Bradysaurus* and *Embrithosaurus* a humerus with triangular intercondylar fossa demarcated by a gently concavely curved, distinct swollen ridge (intercondylar ridge border) on the dorsal distal margin, preventing the fossa from reaching round onto the distal side of the humerus;

- Shares with *Bradysaurus baini* a deep intercondylar fossa (*Nochelesaurus*: 35 -50 mm; *Bradysaurus baini*: 40-50 mm) corresponding with a large and prominent olecranon process of the ulna;
- Shares with *Embrithosaurus* a humerus with two epicondyles that do not project distally far beyond the radial and ulnar articulation surfaces (in most, but not all specimens of *Nochelesaurus*);
- Certain specimens with a distinct tubercle on the swollen postaxial margin of the intercondylar fossa (Holotype: SAM-PK-6239, SAM-PK-6238, FMNH UR 2436, FMNH UP 2480);
- Shares with *Bradysaurus baini* a massive, robust "heart shaped" delto-pectoral crest, 90 mm anteroposteriorly, with a notch on the ventrodistal corner and with a ventral surface lacking the long, central, ventral groove of *Embrithosaurus*;
- Shares with *Bradysaurus baini* the presence a short, curved, crescent-shaped, insertion point for muscle attachment on the humeral shaft of the dorsal proximal humerus. Absent in *Embrithosaurus*;

Radius:

- Ventrolaterally expanded and projecting distal radius, creating a non-symmetrical radius, resulting in the distal expansion being wider than the proximal expansion of the radius;
- Shares with *Bradysaurus baini* the presence of a distinct, vertical, ridge on the medial side of the distal portion of the radius, extending from the swollen base of the radius, tapering dorsally and almost reaches midway up the shaft;

Ulna:

- Shares with *Bradysaurus baini* and certain *Embrithosaurus* specimens a dorsoventrally very long ulna (370 mm), due to an extended proximal postaxial bar and proximal articulation surface;

- Shares with *Bradysaurus baini* the presence of an oblique ridge on the proximal articulation surface;
- Shares with *Embrithosaurus* the presence of medial and lateral olecranon crests, with very shallow, wide groove between the crests. Crests smaller and only located anteriorly in *Nochelesaurus*;
- Presence of a low, convex, olecranon process;
- Anterodorsal ulna constricted or "pinched in", concavely curved projection of the lateral surface;
- Shared with *Bradysaurus baini*, the presence of a limiting ridge on the posterodorsal edge of the ulna;

Femur (general):

- Postaxial shaft straight and not notable bulged/convex (bulged and convex in *Embrithosaurus* and *Bradysaurus)*;
- Lateral condyle of most specimens extends distally much further (up to 70 mm) beyond the distal edge of the medial condyle than in co-occurring taxa (*Embrithosaurus* 30-45 mm, *Bradysaurus* 20-30 mm);
- Femur generally anteroposteriorly narrower across the distal condyles compared to *Embrithosaurus* and *Bradysaurus*;

Femur (major trochanter)

- Posterior projection of the major trochanter very short (< 5 mm), and hardly protrudes beyond the postaxial (posterior) shaft of the femur;
- Shares with *Bradysaurus* the absence of a deep notch (so no notch or only a shallow notch) proximal and/or distal to the major trochanter, on the postaxial flange, separating the major trochanter from the postaxial shaft;

Femur (internal trochanter)

- Internal trochanter straight or very slightly curved (proximally gently or moderately curved in *Embrithosaurus* and strongly curved in *Bradysaurus*).
- Internal trochanter dorsoventrally very short, or low, extending only 10 mm beyond the shaft the femur; compared to the much high conditions present in *Embrithosaurus* and *Bradysaurus* (30-40 mm);
- Proximal edge of internal trochanter emerges obliquely from the femur (perpendicular in *Embrithosaurus* and *Bradysaurus*);
- Shares with most specimens of *Embrithosaurus* a narrow proximal internal trochanter (wide in *Bradysaurus*);
- Proximal region of internal trochanter positioned close to the preaxial (anterior) border of the femur and aligned or parallel to the border (farther away in *Embrithosaurus* and *Bradysaurus*).
- Absence of an anterior process/projection on the distal portion of internal trochanter, present in *Embrithosaurus* and *Bradysaurus*;

Tibia:

- Distal tibia morphology shared with *Bradysaurus baini*:
    - ventromedially expanded and projecting distal tibia
    - ventrolaterally upturned distal tibia
    - mediolaterally wider distal tibia than *Embrithosaurus*
- Shares with *Bradysaurus baini*, a smaller angle (40^0) between the lateral and medial facets of the proximal articulation surface of the tibia which is 60^0 in *Embrithosaurus*;
- Shares with *Bradysaurus baini* an elongated rugose ridge, just dorsal to a vertical depression, on the lateral edge of the shaft of the tibia;

Vertebrae:

- Shares with *Embrithosaurus*, parapophysial and diapophysial articulations fuse into a single vertical flange, creating a transverse process with a

single lateral facet from the 6th vertebra backwards; SAM-PK-8034 (In *Bradysaurus* this occurs from the 5th vertebra backwards; NHMUK R1971, or the 4th backwards NHMUK R49426);

Osteoderms:

- Osteoderms large (45-55 mm wide) relatively high (30-40 mm), strongly convex,
- Osteoderms with a distinct, clearly delimited, knob-like, central boss, very high (15-20 mm) accounting for about half the height of the osteoderm, and very wide (25-40 mm), accounting for most of the width of the oseteoderm, round to irregularly shaped with tab-like, rugose edges, and small circular pits;
- Osteoderm periphery high and thick (15-20 mm), (not thin and flat as in *Embrithosaurus*) accounting for about half the height of the osteoderm, and generally smooth, besides for small, circular pits and low, and very few irregular, rugose ridges or tab-like processes, that are lower and less distinct than the tab-like processes on the central bosses. Osetoderms medium to large in width, very rugose, covered in rugose flattened, tab-like processes that cover most of the scute, in an almost radial star-like pattern (comprising five or six tabs), creating a very irregular central boss that is low. Scutes are not evenly or smoothly convex (SAM-PK-11596, SAM-PK-11948).