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Revista Brasileira de Paleontologia, 26(4):288–314, Outubro/Dezembro 2023
A Journal of the Brazilian Society of Paleontology
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doi:10.4072/rbp.2023.4.04

CRANIAL OSTEOLOGY AND A NEW DIAGNOSIS OF THE LATE PERMIAN PAREIASAUR *NANOPARIA LUCKHOFFI* (BROOM, 1936) FROM THE KAROO BASIN OF SOUTH AFRICA, AND A CONSOLIDATED PAREIASAURIAN PHYLOGENY

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ABSTRACT – Pareiasaurs were an enigmatic and diverse group of parareptilian herbivores of the middle and late Permian. *Nanoparia luckhoffi* was erected in 1936 but remains the least well-known member of four "dwarf" pareiasaurs that comprise Pumiliopareiasauria. After new preparation of the holotype, we present the first detailed cranial description of *Nanoparia luckhoffi* and a new diagnosis for the taxon based on seven autapomorphies: (1) an additional bone on the posterior margin of the cheek flange between the squamosal and quadratojugal; (2) a pyramidal-shaped parietal; (3) a very short, square lacrimal; (4) paired prepalatal foramina positioned anterolaterally on the internal premaxillary palatal flange; (5) notch on anteromedial border of the choana; (6) a ventral flange formed by the lateral margin of the internal tabulars; and (7) tabulars that extend posteriorly further than the supratemporals. We find evidence supporting a juvenile ontogenetic state for the holotype, including small skull; unossified open cranial sutures; an unossified dorsal braincase; and fewer marginal teeth than most pareiasaurs. An updated phylogeny recovers *Nanoparia* as a sister taxon to *Provelosaurus americanus* from Brazil and remains a constituent member of Pumiliopareiasauria.

Keywords: *Nanoparia*, Pumiliopareiasauria, Pareiasauria, Parareptilia, late Permian, Gondwana.

RESUMO – Os pareiassauros foram um enigmático e diverso grupo de pararrépteis herbívoros do Permiano médio e inferior. *Nanoparia luckhoffi* foi proposta em 1936, mas é um dos menos conhecidos pareiassauros "anões" que formam os Pumiliopareiasauria. Após nova preparação do holótipo, apresentamos a primeira descrição detalhada de *Nanoparia luckhoffi* e uma nova diagnose para o táxon, baseado em sete autapomorfias: (1) um osso adicional na margem posterior da aba temporal entre o esquamosal e o quadradojugal; (2) parietal com

formato piramidal; (3) lacrimal muito curto e com formato quadrado; (4) forame prepalatal posicionado anterolateralmente na vista interna da pré-maxila; (5) entalhe na borda anteromedial da coana; (6) aba ventral ao longo da margem lateral na vista interna dos tabulares; e (7) tabulares estendendo-se posteriormente mais do que os supratemporais. Encontramos evidência que apoia um estágio juvenil no holótipo, incluindo crânio pequeno, suturas cranianas abertas, não-ossificadas; neurocrânio não-ossificado; e menos dentes marginais do que a maioria dos pareiassauros. Uma filogenia atualizada mostra a *Nanoparia* como o táxon irmão de *Provelosaurus americanus* do Brasil, continuando como membro dos Pumiliopareiasauria.

Palavras-chave: *Nanoparia*, Pumiliopareiasauria, Pareiasauria, Parareptilia, Permiano superior, Gonduana.

INTRODUCTION

Pareiasaurs were an abundant, successful, and diverse group of specialised herbivorous parareptiles of the middle and late Permian (Boonstra, 1934; Lee, 1997a; Day *et al*., 2015; Smith *et al*., 2020). They were an important component of Permian terrestrial biodiversity and the clade achieved a high level of species richness and global distribution by the late Permian, before their ultimate demise at the Permo-Triassic boundary. Historic taxonomic confusion resulted in an overinflated number of species (Boonstra, 1934; Kuhn, 1969; Lee, 1994, 1997a) that persisted for about 100 years and hampered research of these reptiles until the seminal work of Lee (1994, 1997a) who resolved many taxonomic issues and reduced the number of recognised species from 49 to 17.

The taxonomic framework of Lee (1994, 1997a) enabled successive researchers to produce detailed species-level anatomical studies and more advanced palaeobiological studies. Palaeobiological studies include an ontogenetic study of *Deltavjatia* (Tsuji, 2010, 2013), bone microstructure, isotopic analyses, and histological studies of several species (Canoville *et al*., 2014; Rey *et al*., 2015, 2019; Canoville & Chinsamy, 2017) and volumetric body mass estimates for *Scutosaurus* (Romano *et al*., 2021) and *Bradysaurus* (Van den Brandt *et al*., 2023). New species described since the mid-1990s, comprise detailed cranial descriptions of *Arganaceras vacanti* (Jalil & Janvier, 2005), *Obirkovia gladiator* (Bulanov & Yashina, 2005), *Bunostegos akokanensis* (Sidor *et al*., 2003; Tsuji *et al*., 2013), *Elginia wuyongae* (Liu & Bever, 2018) and a brief cranial description of a tentative new elginid based on the first complete pareiasaur skull from China, *Shihtienfenia completus* (Wang *et al*., 2019). Detailed redescriptions of the crania of previously erected taxa include *Scutosaurus karpinskii* (Lee, 1994), *Pareiasuchus nasicornis* (Lee *et al*., 1997), *Deltavjatia rossica* (Tsuji, 2010, 2013), *Embrithosaurus schwarzi* (Van den Brandt *et al*., 2020), *Provelosaurus americanus* (Cisneros *et al*., 2005, 2021), and *Nochelesaurus alexanderi* (Van den Brandt *et al*., 2021b). The basal-most pareiasaurs from the middle Permian of South Africa have recently been taxonomically reassessed (Van den Brandt *et al*., 2020, 2021a, b, 2022) resulting in the proposal of a previously unrecognized basal monophyletic group, Bradysauria, comprising *Bradysaurus*, *Embrithosaurus* and *Nochelesaurus*.

The Beaufort Group of the Karoo Basin of South Africa holds the world's highest diversity of pareiasaurs with at least nine species in eight genera currently recognised, that can be split into two distinct stratigraphic and evolutionary cohorts: the basal group (Bradysauria) flourished only in the middle Permian (Guadalupian) and were locally replaced by a new set of pareiasaurs that flourished in the late Permian (Lopingian). Members of the basal Bradysauria (restricted to the *Tapinocephalus* Assemblage Zone (AZ)) comprise three large pareiasaurs, *Bradysaurus baini* (Seeley, 1892), *Embrithosaurus schwarzi* (Broom, 1903) and *Nochelesaurus alexanderi* (Haughton & Boonstra, 1929) (Day *et al*., 2015; Day & Rubidge, 2020; Van den Brandt *et al*., 2022). After a short stratigraphic hiatus, three small pareiasaurs, *Anthodon serrarius* (Owen, 1876), *Nanoparia luckhoffi* (Broom, 1936) and *Pumiliopareia pricei* (Broom & Robinson, 1948); two moderately-sized members of *Pareiasuchus*, *P. peringueyi* (Broom & Haughton, 1913) and *P. nasicornis* (Haughton & Boonstra, 1929); and the large *Pareiasaurus serridens* (Owen, 1876) appear and occupy stratigraphic intervals in the *Endothiodon, Cistecephalus* and *Daptocephalus* AZs of the Beaufort Group (Day & Smith, 2020; Smith, 2020; Smith *et al*., 2020; Viglietti, 2020). *Pareiasaurus serridens* was the most successful South African pareiasaur, ranging across all three Lopingian AZs of the Karoo (Smith, 2020). The three small species, *Anthodon serrarius*, *Nanoparia luckhoffi* and *Pumiliopareia pricei,* make up the South African members of Pumiliopareiasauria (sensu Jalil & Janvier, 2005) or "dwarf" pareiasaurs" (Lee, 1997, p. 283), along with the South American *Provelosaurus americanus* from Brazil (Araújo, 1985a, b; Lee, 1994, 1997a; Cisneros *et al*., 2005, 2021).

Nanoparia luckhoffi is known from only the holotype cranium, briefly described and dorsally figured by Broom (1936: fig. 1). After some additional preparation, Brink (1955) added a good ventral illustration (Brink, 1955: fig. 18). A detailed modern cranial description for *Nanoparia luckhoffi* does not exist and only brief comparative diagnoses have been provided for the taxon in larger pareiasaurian taxonomic reviews (Haughton & Brink, 1954; Brink, 1955; Kuhn, 1969; Lee, 1994, 1997a). Kuhn (1969: 76: Abb. 41.1) reproduced the dorsal figure of Broom (1936). Ivakhnenko (1987) placed *N. luckhoffi* within *Pareiasaurus.* With only these few brief descriptions, two figures published, and no postcrania preserved, *Nanoparia luckhoffi* is the least well-known member of Pumiliopareiasauria, and therefore an excellent candidate for a cranial redescription, which we present here, after extensive additional preparation of the holotype. We justify our phylogenetic score for each character, within each cranial element described, an unambiguous and transparent method employed by Benton (2016) in describing the crania of the Chinese pareiasaurs, and Van den Brandt *et al.* (2021a) in describing the postcrania of the three genera of Bradysauria.

Comparisons to the three other closely related members of Pumiliopareiasauria (*Anthodon serrarius*, *Pumiliopareia pricei* and *Provelosaurus americanus*) are emphasised in our description, followed by comparisons to co-occurring late Permian South African taxa: *Pareiasaurus serridens*, *Pareiasuchus nasicornis*, *Pareiasuchus peringueyi*, and all remaining pareiasaurs.

Using the two latest phylogenetic data matrices as input (Cisneros *et al*., 2021; and Van den Brandt *et al*., 2022) we here contribute a new consolidated pareiasaurian phylogenetic data matrix with updated character scores for all taxa (see Supplementary material, Appendix 1, Data Matrix) and updated character state definitions (see Supplementary material, Appendix 2, Character List).

Institutional abbreviations: BP, Evolutionary Studies Institute (formerly the Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; **CGP/GSP,** Council for Geosciences, Pretoria, South Africa; **FMNH**, Field Museum of Natural History, Chicago, U.S.A; **GSE**, Geological Survey, Edinburgh, Scotland; **NHMUK,** Natural History Museum, London, U.K; **PIN**, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **RC,** Rubidge Collection, Wellwood, Graaff-Reinet, South Africa; **SAM,** Iziko South African Museum, Cape Town, South Africa; **UFRGS**, Instituto de Geociências da Universidade Federal do Rio Grande do Sul, Brazil.

Historical background of the Pumiliopareiasauria, the "dwarf" pareiasaurs

Anthodon serrarius (Owen, 1876)

Holotype: NHMUK PV OR 47337, Etymology: Greek: *Anthos* [ανθός], flower; o*dous* [ὀδούς], tooth; Latin: *serratus*, serrated (Owen, 1876). *Anthodon serrarius* was erected by Owen (1876:14) based on a badly damaged partial skull with occluded lower jaw (NHMUK PV OR 47337) from the farm Stylkrant/z/s, Graaff-Reinet district, (Lydekker, 1890; Watson, 1914b) justifying his erection based on the semi-circular tooth crowns resembling a broad flower on a stem. Later publications included new specimens and added new information to our understanding of *Anthodon* (Haughton & Boonstra, 1929, 1930; Boonstra, 1932a,b, 1934; Findlay, 1970). Consequently, the genotype *Anthodon serrarius* has been recognised as valid in all major taxonomic works (Lydekker, 1890; Watson, 1914b; Haughton & Boonstra, 1929; Boonstra, 1934; Haughton & Brink, 1954; Kuhn, 1969; Lee, 1994, 1997a). Kuhn (1969) recognised up to six species: *Anthodon serrarius* (Owen, 1876), *Anthodon gregoryi* (Broom, 1930), *Anthodon nesemanni* (Broom, 1940), *Anthodon minusculus* (Haughton, 1932), *Anthodon (?) haughtoni* (von Huene, 1944), and *Anthodon rossicus* (Hartmann-Weinberg, 1933). Most recently, Lee (1994, 1997a) found only one species of *Anthodon* valid and produced the most recent diagnosis, descriptions and illustrations.

Nanoparia luckhoffi (Broom, 1936)

Holotype: RC 109, Etymology: Greek: *Nanos* [νάνος], dwarf; *pareia* [παρειά], cheek; *luckhoffi*, after the discoverer of the fossil, Mr R. Luckhoff (Broom, 1936). Erected by Broom in 1936 based on a small pareiasaur skull of length 152 mm, lacking a lower jaw, found by a Mr R. Luckhoff on the "Oudeberg Plateau", Graaff-Reinet district, Eastern Cape Province, South Africa. Broom (1936) briefly described the cranial proportions, ornamentation style, cranial elements and sutures, and marginal and palatal dentition and roughly illustrated the skull in dorsal view (Broom, 1936: fig. 1). Broom (1936:349) noted the possibility of the skull belonging to a juvenile individual due to it being "the smallest pareiasaurian skull ever found" with easily identifiable sutures, and also stating that it differs "so greatly from any other type previously found that one has no hesitation in describing it as the type of a new species". The basis for this statement was the presence of two additional cranial bones, labelled "A" and "B" by Broom. In his short paper, Broom (1936) also specified the cranial ornamentation as deeply pitted, with a well-developed boss at the centre of each element, and also especially mentioned large nostrils.

Broom & Robinson (1948) erected a second species of *Nanoparia* (*N. pricei*) for an even smaller skull (90 mm long), with an occluded lower jaw (BP/1/81), slightly larger than half the size of the holotype of *Nanoparia luckhoffi*, from the farm Sondagsriviershoek, also in the Graaff-Reinet district. This specimen also preserves a large flat plate containing most of the trunk of the animal, comprising articulated vertebrae, ribs and covering osteoderms. Broom & Robinson's (1948) very brief cranial description of *N. pricei* included interpretative drawings of the skull in dorsal and lateral view, and an illustration of three marginal teeth. Note that this specimen was later renamed under the new combination *Pumiliopareia pricei* (Lee 1997a) see below.

Pumiliopareia pricei (Broom & Robinson, 1948)

Holotype: BP/1/81, Etymology: Latin *Pumilio*, dwarf; Greek: *pareia*, [παρειά], cheek; *pricei*, Lee (1997a: 283), named after Dr Bernard Price (Broom & Robinson, 1948: 53). Declared the holotype of a new genus by Lee (1994, 1997a), noting this species as smallest known pareiasaur with several diagnostic autapomorphies, such as: unique, very densely spaced conical bosses; perfectly round orbits; only approximately 9 upper and 7 lower teeth per side; and very wide ribs.

After additional preparation of the holotype skulls of the two species of *Nanoparia* recognised at that time (*N. luckhoffi*, RC 109; and "*N. pricei"*, BP/1/81), Brink (1955) published a comparison of the differences between the two taxa and included one additional specimen of *N. luckhoffi* (RC 784). Brink (1955: fig.18) produced an accurate illustration of the palate of *N. luckhoffi* (RC 109) and a misleading figure of the then unprepared osteodermal arrangement pattern of *N. pricei* (BP/1/81; Brink 1955: fig. 17) resembling a "necklace" with a midline row of osteoderms above each vertebra, flanked by

unusually large gaps laterally either side where no osteoderms are present, until the distal-most lateral rib portions where osteoderms are present, an incorrectly interpreted osteoderm distribution pattern, corrected by Findlay (1970) after a more careful study of the material, to complete rows of scutes above and along each rib. Lee (1994, 1997a) re-assigned RC 784 as a juvenile *Pareiasuchus peringueyi*. Kuhn (1969:76, Abb.42.1), and other authors (*e.g*., von Huene 1944:27, Abb.19), have reproduced Broom's (1936) dorsal cranial illustration of *N. luckhoffi* (RC 109) and Lee (1994, 1997a) provided the most up to date diagnoses for *Nanoparia luckhoffi* and *Pumiliopareia pricei*.

***Provelosaurus americanus* (Araújo, 1985b)**

Holotype: UFRGS PV0231P, Etymology: Greek: *Pro* [προ], before; *velo* [βέλο], to cover; Latin: *saurus*, lizard; *americanus*, from South America (Lee, 1994, 1997a). Described as a new species, *Pareiasaurus americanus*, by Araújo (1985b), Lee (1994, 1997a) transferred it to a new genus, *Provelosaurus*, based on the taxon being intermediate between the primitive large pareiasaurs, and the small derived pareiasaurs. "*Pareiasaurus americanus*" was extensively studied in the 1980s (Araújo, 1985a, 1985b, 1986a, 1986b; Araújo-Barberena, 1987, 1989a, 1989b). Since Lee's (1994, 1997a) taxonomic revision, this taxon has been notably redescribed by Cisneros *et al.* (2005). Recently, the crania, postcrania, phylogenetic placement, stratigraphic occurrences and dating of this taxon were significantly updated using several new specimens described by Cisneros *et al.* (2021), making *Provelosaurus* the best-known member of Pumiliopareiasauria.

Brief phylogenetic background of the "dwarf" pareiasaurs

Phylogenetically, Lee (1994, 1995, 1996, 1997a, b) found the small South African pareiasaurs (*Nanoparia*, *Pumiliopareia*, *Anthodon*) and *Provelosaurus* from Brazil, to form a monophyletic group, to be the most derived pareiasaurs, and *Anthodon* to be the nearest relative to turtles. Jalil & Janvier (2005: figs. 52, 53) named a new clade, the Pumiliopareisauriae, for the grouping of *Anthodon serrarius* and *Pumiliopareia pricei* from South Africa, *Provelosaurus americanus* from Brazil, and Testudines, all united by five synapomorphies, which excluded *Nanoparia luckhoffi*. Tsuji and Müller, in their redescription of *Parasaurus geinitzi* (Tsuji & Müller, 2008) and in their broad phylogenetic diversity study of parareptilian clades (Tsuji & Müller, 2009) grouped *Provelosaurus*, *Anthodon*, *Pumiliopareia* and *Nanoparia* in a clade, and removed testudines from Parareptilia. Since this work by Tsuji & Müller (2008, 2009) most phylogenetic studies have retained the four constituent members of Pumiliopareisauriae, but with little revisions of character scores for *Anthodon*, *Pumiliopareia* and *Nanoparia* (Tsuji, 2013; Tsuji *et al*., 2013; Turner *et al*., 2015; Xu *et al*., 2015; Benton, 2016; Liu & Bever, 2018; Cisneros *et al*., 2021; Van den Brandt *et al*., 2022). Phylogenetic character scorings for *Provelosaurus* were recently significantly updated (Cisneros *et al*., 2021).

MATERIAL AND METHODS

Preparation

The skull of the holotype of *Nanoparia luckhoffi* (RC 109) was mechanically prepared historically in the mid-1930s by Robert Broom for his initial description (Broom, 1936). The specimen was prepared further by James Kitching in the 1950s (Brink, 1955). Most of the external surface of the skull is slightly overprepared and is, therefore, slightly damaged (Figures 1A–B). The right snout and anterior left cheek flange are partially reconstructed with light-coloured plaster (Figures 2A–B). Minor deposits of uncleared matrix have been retained on the exterior surface of the dorsal skull roof and the lateral cheek flanges, as they fill and make small circular pits, foramina, and grooves between ridges of ornamentation more obvious. Sutures are identifiable as narrow, grey, matrix filled, interdigitating lines. The posterior border of the cheeks, as well as the circumorbital bones (prefrontal, postfrontal, postorbital), retain minor deposits of the uncleared matrix.

For this project, extensive additional preparation using compressed air-driven pneumatic scribes fitted with a tungsten carbide tip was performed by Justin Arnols with extraordinary aplomb. Specifically, the palate and braincase were cleared of obscuring matrix to allow a detailed description of these regions for the first time (Figures 2C, 3). The internal surfaces of the postparietal, tabulars, supratemporals and squamosals are now almost fully accessible. A layer of protective matrix was retained around the rows of delicate palatal denticles.

Previous researchers (probably Robert Broom) have 'drawn' sutures directly on the external surface of the skull in black ink, a fairly typical historical practise. We were able to remove most of these ink lines with acetone. Our interpretation of cranial sutures closely agrees with most of the historic ink lines, except where noted (see pterygoid). After additional preparation, a very thin layer of protective B-72 Paraloid glue was applied to the skull, helping to expose external cranial sutures which in places retains a small amount of dark green-grey rock matrix. The cranial sutures of the holotype skull are open and unfused, and easier to identify than on most pareiasaur skulls, strongly suggesting a not yet fully matured individual. On the postparietal, parietals, tabulars, supratemporals, squamosals, jugals, and quadratojugals, we were able to confirm external sutures through direct extrapolation of newly revealed internal cranial sutures after preparation, confirming that most sutures pass directly perpendicularly through the bone, a method necessarily used by several previous pareiasaurian researchers (Lee, 1994; Jalil & Janvier, 2005; Liu & Bever, 2018; Watson, 1914a; Van den Brandt *et al*., 2020, 2021b).

Phylogenetic methods

Lee recognised 17–19 different pareiasaur taxa in the first cladistic phylogenetic analyses of the group (Lee, 1994, 1995, 1997a, b). At least 21 pareiasaur species are now sufficiently known to be confidently placed in the most recent phylogenetic analyses (Van den Brandt *et al*., 2020, 2022; Cisneros *et al*., 2021). Additionally, a few less well-

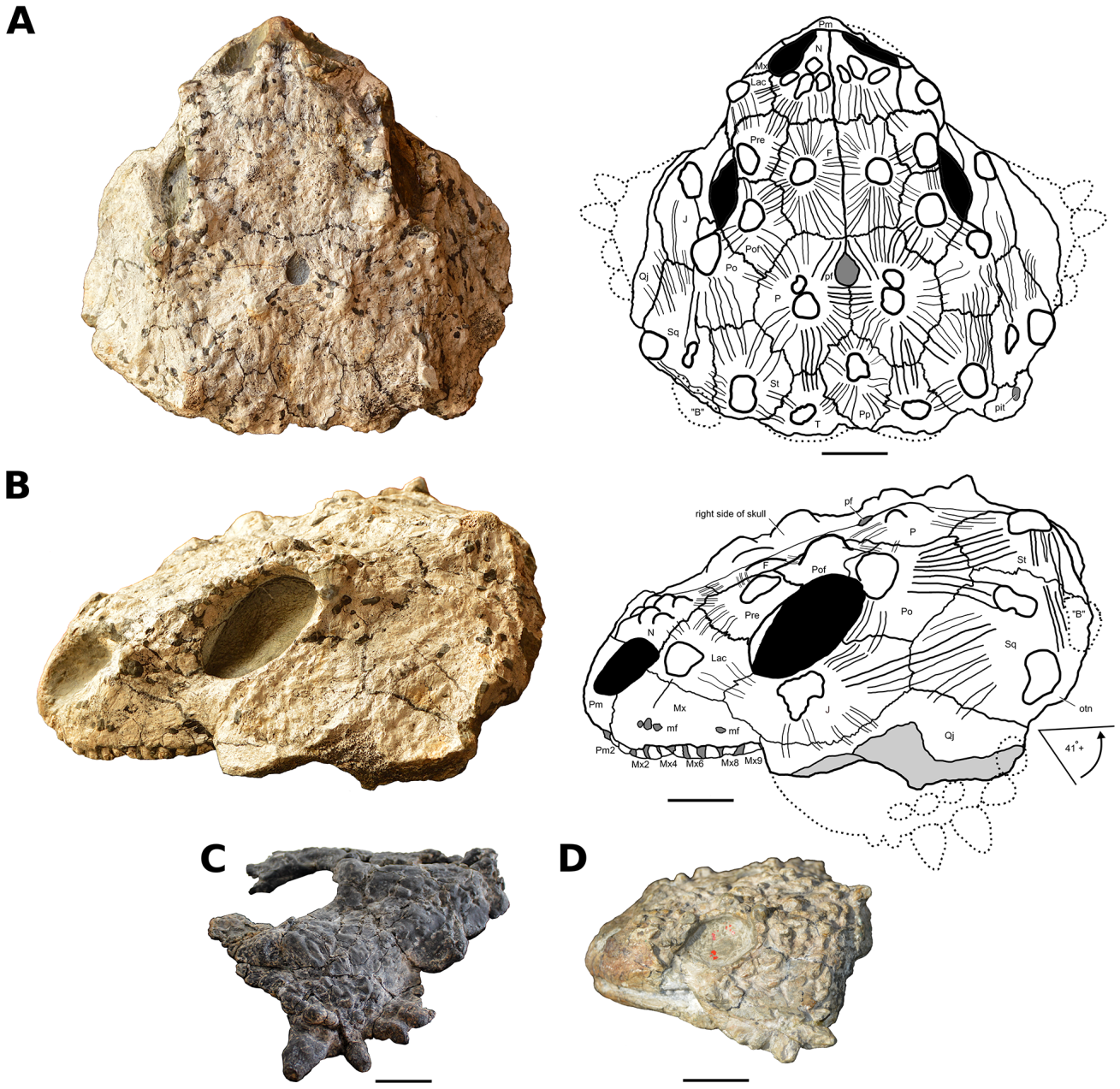

Figure 1. Photograph and interpretative drawing of the holotype skull of *Nanoparia luckhoffi* (RC 109), in (**A**) dorsal view, and (**B**) left lateral view. Photograph of *Provelosaurus americanus* (UFRGS-PV-0358-P) in left lateral view (**C**), and photograph of the holotype skull of *Pumiliopareia pricei* (BP/1/81) in left lateral view (**D**) (mirrored image of right of skull, as left cheek flange is damaged). **Abbreviations: "B"**, Element B; **F**, frontal; **J**, jugal; **Lac**, lacrimal; **mf**, maxillary foramen; **Mx**, maxilla; **Mxn**, maxillary tooth number; **N,** nasal; **otn**, otic notch; **P**, parietal; **pf**, pineal foramen; **Pm**, premaxilla; **Pmn**, premaxillary tooth number; **Po**, postorbital; **Pof**, postfrontal; **Pp**, postparietal; **Pre**, prefrontal; **Qj**, quadratojugal; **Sq**, squamosal; **St**, supratemporal; **T**, tabular. Scale bars: A–B, D = 20 mm; C = 50 mm.

known species comprising limited material and therefore limited anatomical information have been excluded from most phylogenetic analyses: *Anthodon* (?) *haughtoni* (von Huene, 1944; Maisch & Matzke, 2019); the "Welgevonden" pareiasaur (Lee, 1997a); the "Kupferschiefer" pareiasaur (Lee, 1997a); Pareiasauria gen. et sp. Indet. 1 and Pareiasauria gen. et sp. Indet. 2. (Jalili & Janvier, 2005); *Proelginia permiana* (Hartmann-Weinberg, 1937); *Scutosaurus tuberculatus* (Amalitzky, 1922); and *Scutosaurus itilensis* (Ivakhnenko, 1987).

As a result of close publication dates, the two most recent pareiasaurian phylogenetic contributions (Cisneros *et al*., 2021:142 characters; Van den Brandt *et al*., 2022: 139 characters), that both used Liu & Bever (2018) for their initial data matrix scores, and Turner *et al*. (2015) for character state definitions, have excluded each other's significant

character score updates for the individual taxa they studied, character state definition changes and polarity changes. The matrix of Van den Brandt *et al*. (2022) excluded the three novel characters added by Cisneros *et al*. (2021, characters 140–142).

We used the data matrix of Van den Brandt *et al*. (2022) containing 21 pareiasaurian species and eight non-pareiasaur parareptilian outgroups, for initial character scores (characters 1–139) and included the changes made in the data matrix of Cisneros *et al*. (2021) who re-coded 31 character states for *Provelosaurus americanus* (characters 33, 38–42, 60–62, 72, 73, 77, 80, 84, 95, 98, 100, 102–104, 113, 114, 118, 124, 125, 133–138, 140–142), two character states for *Shihtienfenia permica* (characters 90, 91), introduced three new characters (140–142), and reversed the polarity of character 79.

Based on our redescription, we re-assessed all coded cranial characters for *Nanoparia*, resulting in changes to eight-character scores (characters 6, 12, 15, 21, 23, 44, 50, 75). We also updated scores for character 31 for *Pareiasuchus nasicornis*, characters 48 and 49 for *Provelosaurus*, character 140 for *Bradysaurus* and *Nochelesaurus*, and character 142 for *Bradysaurus*, *Nochelesaurus*, and *Embrithosaurus*, (see Supplementary material, Appendix 1, Data Matrix).

We used the character list of Van den Brandt *et al*. (2022) and modified it by re-wording characters 25, 32 and 44; by including the three new characters of Cisneros *et al*. (2021), characters 140–142; and by introducing an additional character state (state 2) for character 47, "Quadratojugal, anterior extend: reaches or almost reaches the anterior margin of the orbit (2)" for *Nanoparia*, *Pumiliopareia*, *Provelosaurus* and *Pareiasuchus peringueyi* (see Supplementary material, Appendix 2, Character List).

The program Tree Analysis Using New Technology (TNT) version 1.5 was used to find the most parsimonious trees (Goloboff *et al*., 2008; Goloboff & Catalano, 2016). Considering the relatively large size of the data matrix (29 taxa and 142 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 retained as the root and all characters were run as unordered and equally weighted.

Key to interpretative line drawings

Sutures drawn in solid lines have been positively identified and both missing lateral quadratojugals and the left element "B", have been reconstructed with dotted lines (Figures 1, 2, 3). Light grey indicates the sides of bones (bone breaks), dark grey indicates small foramina or fenestrae, and black indicates deep and large matrix filled cavities such as the orbits and nares. Cranial bosses are in bold lines, cranial sutures in regular thickness, and rugose ridges are in the lightest lines. Patches of light-coloured plaster infill on the right snout (maxilla, lacrimal and jugal), and the hundreds of small circular matrix filled dark cranial pits, have not been illustrated as they would clutter the figures, hampering legibility.

When referring to the marginal dentition of *Nanoparia*, we have used a terminology modified from that proposed for 'non-mammals' by Smith & Dodson (2003). Therefore, teeth of the premaxilla are reported as Pmn, and teeth of the maxilla as Mxn, where n represents tooth position in the rostral-caudal direction (Figures 2B, 3, 4B). The abbreviations 'P' and 'M' are avoided to prevent possible confusion with premolars and molars in mammalian dental terminology.

The palatal teeth/denticles are mapped into four distinct regions (Figure 3, T1–T4). Although the individual palatal teeth are not numbered/referred to in this work, the framework proposed by Smith & Dodson (2003: figs. 1B, 3, 4) allows for this to be undertaken, and such practise may be useful in future studies of pareiasaurian dentition and palatal anatomy.

Comparative material

Anthodon serrarius: NHMUK PV OR 47337, holotype, severely damaged partial skull with occluded lower jaw, missing the anterior snout and a large portion of the posterior half of the skull, including the entire occiput; RC 785: skull with cheeks reconstructed in plaster, occluded posterior right lower jaw fragment, and three-four unprepared articulated cervical vertebrae with short rib fragments, and a partial median interclavicle.

Bradysaurus baini: NHMUK PV R 1971, holotype, skull with lower jaw, and most of the postcranium, on display at the Natural History Museum, London ("Fred"); CGP/1/2269, juvenile skull and occluded lower jaw, with the anterior one-third of the postcranium attached ("Toothless"); NHMUK PV R 1970, cranial material comprising most of the palate and braincase and a large partial snout with occluded lower jaw, most of the dorsal vertebrae; SAM-PK-5002, skull and lower jaw, and several postcranial elements; SAM-PK-5624, articulated skull and lower jaw, with almost complete skeleton on display at the Iziko South African Museum, Cape Town.

Elginia mirabilis: NHMUK PV R 2114, cast of holotype skull (GSE 4780-4788) without lower jaw.

Embrithosaurus schwarzi: SAM-PK-8034, holotype, skull with separate lower jaw, and most of the postcranium.

Nochelesaurus alexanderi: SAM-PK-6239, holotype, skull, a few vertebrae and partial fore-and-hind-limb elements; SAM-PK-6238, skull and a few postcranial elements.

Obirkovia gladiator: Unnumbered personal cast (MJVDB) of left quadratojugal of the holotype (PIN 4546/18).

Pareiasaurus serridens: NHMUK PV R 4063, holotype, skull cast (NHMUK R1710a), partial right lower jaw in three large fragments and two thin sections (NHMUK R1710); three large partially prepared blocks containing scapula and interclavicle, pelvis (previously registered as NHMUK PV OR 36251), and osteoderms on vertebrae; and three small unprepared blocks containing two articulated vertebrae, three to four unprepared vertebrae with ribs, and some vertebrae ("Blinkwater Monster"); BP/1/3653,

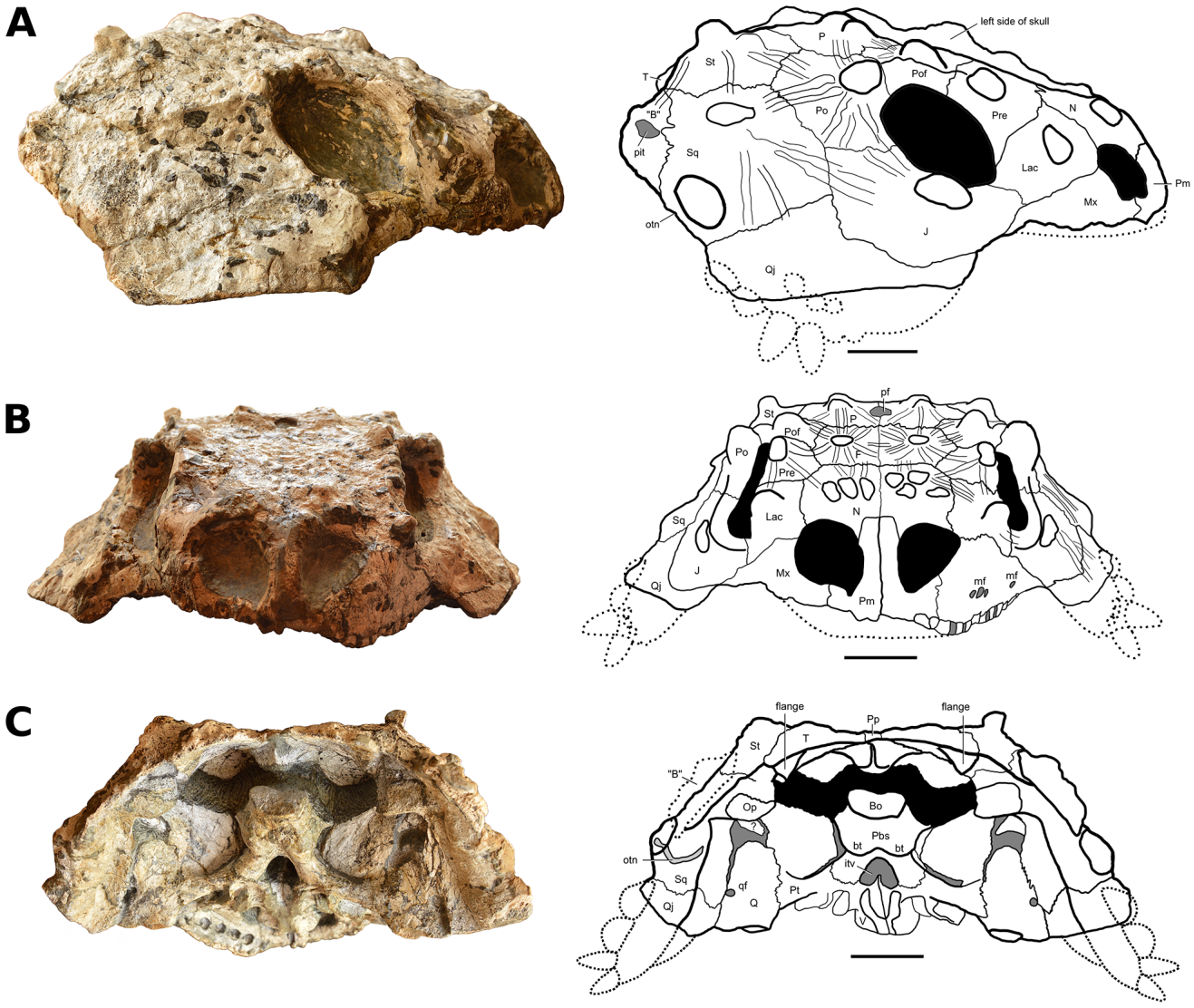

Figure 2. Photograph and interpretative drawing of the holotype skull of *Nanoparia luckhoffi* (RC 109) in (**A**) right lateral view, (**B**) anterior view, and (**C**) occipital view. Note that in (B), the anterior view, the postparietal and tabular bones are not visible as the skull curves steeply downwards behind the parietals on the posterior margin or occipital flange. **Abbreviations: "B"**, Element **B**; **Bo**, basioccipital; **bt**, tubera basispheniodales (basal tubera); **F**, frontal; **itv**, interpterygoid vacuity; **J**, jugal; **Lac**, lacrimal; **Mx**, maxilla; **N**, nasal; **otn**, otic notch; **P**, parietal; **Pbs**, parabasisphenoid; **Pm**, premaxilla; **Po**, postorbital; **Pof**, postfrontal; **Pre**, prefrontal; **Pt**, pterygoid; **Q**, quadrate; **qf**, quadrate foramen; **Qj**, quadratojugal; **Sq**, squamosal; **St**, supratemporal; **T**, tabular; **V**, vomer. Scale bars = 20 mm.

complete skull and occluded lower jaw and unprepared blocks containing anterior cervicals, osteoderms and portions of the shoulder girdle; SAM-PK-12000, partial large skull; SAM-PK-K10036, complete sub-adult skull with occluded lower jaw, and an almost complete articulated skeleton, notably preserving a virtually full "carapace" of several hundred articulated osteoderms, on display at the Iziko South African Museum in Cape Town ("Delilah"); RC 28, holotype skull of *Pareiasaurus rubidgei* ("Pete").

Pareiasaurus nasicornis: SAM-PK-3016, holotype, crushed skull and occluded lower jaw, partial forelimbs, pelvis, both hindlimbs, osteoderms.

Pareiasuchus peringueyi: SAM-PK-2337, holotype, skull and separate lower jaw, most of the vertebral column, ribs, osteoderms, partial shoulder and pelvic girdles, both forelimbs, left hindlimb.

Provelosaurus americanus: specimens curated at the Federal University of Rio Grande do Sul (UFRGS), Brazil, including the holotype (UFRGS-PV-0231-P), recently studied by JCC, see additional specimen numbers in Cisneros *et al.* (2021).

Pumiliopareia pricei: BP/1/81, alternative number BPI 6, holotype skull with occluded lower jaw, and a slab containing most of the vertebrae, osteoderms and ribs

("Luke", "brother"); GSP CM86/544: partial skull, left side only, missing braincase and lower jaw ("Leia", "sister"); SAM-PK-K10498: complete skull and occluded lower jaw, with articulated postcranium comprising most of the presacral axial skeleton of osteoderms, ribs and vertebrae ("Gordon").

Scutosaurus karpinskii: NHMUK PV R 4022, cast of skull and lower jaw, and several postcranial casted elements (NHMUK PV R 4024–NHMUK PV R 4034).

SYSTEMATIC PALEONTOLOGY

Class REPTILIA Laurenti, 1768
Order PARAREPTILIA Olson, 1947
Suborder PAREIASAURIA Seeley, 1888
Family PAREIASAURIDAE Cope, 1896
Pumiliopareiasauria Jalil & Janvier, 2005

Nanoparia Broom, 1936

Nanoparia luckhoffi Broom, 1936
(Figures 1–6)

Holotype. RC 109: skull missing paroccipital processes, lateral cheek flanges, and the lower jaw.

Referred material. None.

Brink (1955) described RC 784/310 as the second specimen of *Nanoparia luckhoffi* (paratype on the Rubidge Collection catalogue) based on similar cranial proportions to the holotype (*e.g*., short snout) but included little analysis or description of this skull. Lee (1994, 1997a) referred this skull to a juvenile *Pareiasuchus peringueyi*, which we could not confirm due to a lack of diagnostic features on the skull. We are unable to positively identify specimen RC 784, from the *Cistecephalus* AZ on the farm Bulberg, Richmond (Brink, 1955) and have excluded this poorly preserved skull, lacking teeth and lower jaw, from this study. This skull is severely dorsoventrally crushed, with the cheeks flattened and splayed out. The bony surface is not original and has been covered with a thick historic grey-purple glue, especially the palate and braincase. The snout is reconstructed in plaster.

Locality, stratigraphy, and age. Holotype RC 109 was found by a Mr R. Luckhoff from most probably rocks of the *Cistecephalus* AZ on the "Oudeberg Plateau", Graaff-Reinet district, Eastern Cape Province, South Africa (Broom, 1936). Smith (2020) notes the *Cistecephalus* AZ as late Permian (Lopingian), radiometrically dated to range from 256 to 255 MY, with the occurrence of *Nanoparia luckhoffi* in the upper *Cistecephalus* AZ.

Amended diagnosis. *Nanoparia luckhoffi* can be recognised by seven autapomorphies: (1) additional small bone on the posterior edge of the cheek, between the squamosal and supratemporal (see Element "B" and Discussion: Element "B" as a valid cranial element or an incorporated nuchal osteoderm); (2) parietal (flat in most pareiasaurs) swollen and thick and forms a pyramidal shape, the result of a large dome-shaped central boss, and 15–20 regular rugose radial ridges that are thick, wide and high near the central boss, narrowing and lowering in height dramatically as they extend radially outwards onto adjacent elements, producing an anteroventrally sloping oblique dorsal margin of the pineal foramen (see Parietal); (3) very short, square lacrimal (see Lacrimal); (4) paired prepalatal foramina positioned anterolaterally on the internal premaxillary palatal flange (not on the premaxilla-vomer contact), with two narrow posterior ridges extending to the midline (see Premaxilla); (5) presence of a notch on the anterior vomer, on the medial border of the choana (see Vomer); (6) presence of a ventrally extending flange along the lateral margin of the internal side of the tabulars (see Tabular); (7) posterior edge of the tabulars extends beyond the posterior edge of the supratemporals (see Tabular).

Remarks. Lee's (1994, 1997a) autapomorphy of a very pointed snout is invalid, as the appearance of a pointed snout is due to damage to the skull. On the right snout (and a little on the left), portions of the premaxilla and maxilla underneath and behind the external nares are cleanly sheared-off, creating an artificially slanted and sharply pointed snout (Figures 1A, 2A, 3).

We disagree with Lee's (1994, 1997a) and Brink's (1955) assertion of *Nanoparia* possessing very large external nares and have removed this character from the diagnosis. The external nares of other pareiasaur specimens and species are proportionally as large, or even larger, than those of *Nanoparia* (*e.g*., on the juvenile *Bradysaurus baini* specimen CGP/1/2269, and the large *Pareiasaurus serridens* specimen RC 28).

A very short face (Lee, 1994, 1997a) or considerably short snout (Brink, 1955) has been proposed as diagnostic in the past. The holotype of *Nanoparia* does have a very short snout (with a notably very short lacrimal), but proportional snout length increases with ontogenetic growth (Tsuji, 2013) and is difficult to quantify. We ascribe the short snout to the relatively early ontogenetic stage of the specimen (see Discussion: *Nanoparia* holotype as a juvenile), and not a true diagnostic feature. We thus replace the uncertain character of a short snout, with the definitive observation of a very short, square lacrimal (Autapomorphy number 3).

CRANIAL DESCRIPTION

The holotype of *Nanoparia luckhoffi* (RC 109) is a relatively complete small skull (152 mm long at the midline) comprising the snout, the dorsal central skull table, medial portions of the cheek flanges, the palate, and a partial basicranium. Most of the lateral quadratojugals and most of the paroccipital processes of the opisthotics are not preserved. The lower jaw is not preserved (characters 60:?, 61:?, 62?, 63:?, 64:?).

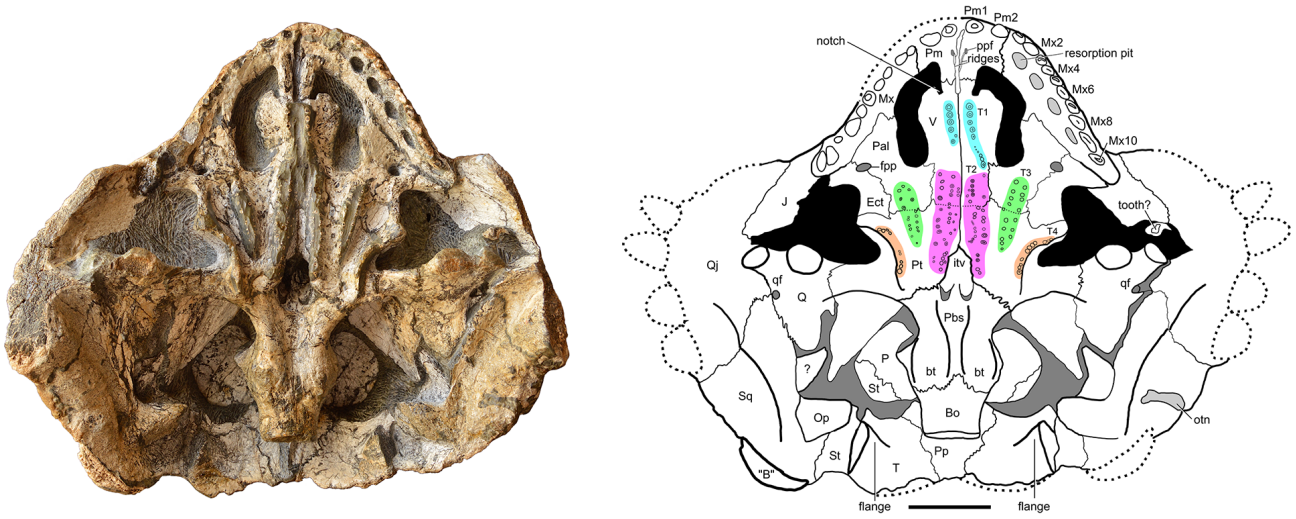

Figure 3. Photograph and interpretative drawing of the holotype skull of *Nanoparia luckhoffi* (RC 109) in ventral view. **Abbreviations: "B"**, Element B; **Bo**, basioccipital; **bt**, tubera basispheniodales (basal tubera); **Ect**, ectopterygoid; **fpp**, foramen palatinum posterius (suborbital vacuity); **itv**, interpterygoid vacuity; **J**, jugal; **Mx**, maxilla; **Mxn**, maxillary tooth numbers; **otn**, otic notch; **Pal**, palatine; **P**, parietal; **Pbs**, parabasisphenoid; **Pm**, premaxilla; **Pmn**, premaxillary tooth numbers; **ppf**, prepalatal foramina; **Pt**, pterygoid; **Q**, quadrate; **qf**, quadrate foramen; **Qj**, quadratojugal; **Sq**, squamosal; **St**, supratemporal; **T**, tabular; **T1–T4**, palatal denticle platforms; **V**, vomer. Scale bar = 20 mm.

Skull roof

General comments

The skull is slightly dorsoventrally crushed, producing somewhat flattened orbits that are posterodorsally elongated (nearly twice as long, 39 mm, as high, 22 mm, in lateral view). There is no posterior emargination or notch on the border of the orbit (character 36:0). The snout is wider (70 mm) than high (40 mm) (character 33:1), slightly exaggerated by the dorsoventral compression. The lateral cheeks are slightly "splayed out" due to dorsoventral compression, the right more than the left, and both cheeks are obliquely oriented (approximately 45°, or midway between a vertical and horizontal plane).

The skull is very heavily ornamented. A dominant protruding boss, high and dome-shaped is present near the centre of the lacrimal, prefrontal, postfrontal, parietal, supratemporal, tabular, and jugal. On the postorbital and the squamosal, this large boss is positioned more anterodorsally on each element. On the frontals, tabulars and median postparietal, the central boss is very low and wide, essentially just a swelling. The nasal has a central complex of three to four small bosses or tubercles or tab-like ridges. The premaxillae and maxillae lack central bosses.

The large rounded central bosses on most elements do not form long pointed horns (character 58:0) and are surrounded by regularly spaced, straight, rugose ridges that emanate in a radial pattern (character 21:1), as illustrated in Broom's original description (1936: 349: fig. 1). The radial ridges on *Nanoparia* are relatively long and straight, but they are not as distinct or thick or long as the radial ridges of *Scutosaurus*, *Bradysaurus*, *Embrithosaurus*, *Nochelesaurus* and *Provelosaurus*, and are often interrupted by cranial pits and irregular grooves. These radial ridges extend from the central bosses of most elements towards the central bosses of adjacent elements (*e.g.*, frontal to nasal, parietal to tabular, Figure 1A). A dense covering of hundreds of small circular to slightly oval pits, 1–2 mm wide (character 22:1) often filled with dark matrix are present on ridges and bosses, and in the grooves between ridges.

Nanoparia is the only Lopingian South African pareiasaur to possess relatively distinct, long and straight radial ridges surrounding central bosses of cranial elements. In comparison the cranial sculpturing of both *Pumiliopareia* skulls is very different and unique among pareiasaurs, as in addition to central bosses on the major elements, the entire skull is covered with hundreds of spherical to conical, dome-shaped, short protuberances, creating a bubbly rugose texture, and there are not long, straight, regular radial ridges. The cranial ornamentation of *Anthodon* is challenging to determine from the poorly preserved holotype. *Provelosaurus* shows distinct bosses at the centre of most cranial elements, with long straight radial ridges, similar to *Nanoparia*. All *Pareiasaurus serridens* specimens have unique and distinctive sculpturing comprising a very smooth overall ornamentation style. The relatively smooth and equal level of the cranial ornamentation forms a random, net-like arrangement pattern of light ornamentation, comprising small to medium sized deep pits, and irregularly shaped, short and deep grooves below the general skull level, described by Lee (1997a: 266) as a "reticulate network of very fine pits and grooves". There are no long straight, radial ridges and no distinct central bosses on cranial elements, but there is some indication of low central swellings on certain cranial elements. The cranial ornamentation styles of the two species of *Pareiasuchus* are challenging to identify from the holotypes, which are damaged, distorted and suffer from historic over preparation and plaster reconstructions.

Premaxilla

The paired premaxillae are small triradiate bones, unornamented and form the anterior tip of the snout. They contact the nasal dorsally, the maxilla laterally and the vomer posteriorly. The anteroventral edges of both premaxillae are damaged and eroded (especially on the right) and the crowns of the teeth are not preserved. Only partial tooth roots of two teeth are visible in each premaxilla, along with two large matrix-filled resorption pits behind the first and second left premaxillary teeth (Figure 4B). Since the midline is mostly intact and preserved, the eroded lateral sides create the appearance of a relatively sharply pointed snout in dorsal and ventral views, but the snout would be more rounded if it were fully preserved (Figures 1A, 3).

The medial internarial bar, formed by the dorsal ascending processes of the left and right premaxilla, is smooth and narrow and covered in a thin layer of matrix. It is convexly curved and oriented posterodorsally, exposing much of the ventral floor and internal anterolateral edges of the external nares in dorsal view. The external nares are anteroposteriorly elongated (character 29:1). The dorsal contacts of the premaxillae with the nasals are obscured by matrix. The premaxillae form the anteromedial floors of the external nares. Anteriorly, the lateral contacts with the maxilla are clear on the left and "drawn on" on the right.

Internally, the flat palatal flange of the premaxilla is present well above the level of the premaxillary tooth row and extends posteriorly to contact the vomer, where it forms the anteromedial border of the choana. Additional preparation has revealed a long and deep medial midline groove, extending the entire length of the palatal flange of the premaxilla and posteriorly onto the anterior vomer. This is flanked on either side by a narrow, longitudinal ridge which terminates anteriorly in two tiny prepalatal foramina, positioned about 5 mm lingual to the first left premaxillary matrix filled resorption pit (Figures 3, 4A) (character 23:1). The lateral and more anterior position of the prepalatal foramina, on the premaxilla (*i.e*., not on the premaxilla-vomer contact), and two instead of one foramen, is autapomorphic of *Nanoparia*. All well-known pareiasaurs (*Bradysaurus*, *Nochelesaurus*, *Embrithosaurus*, *Deltavjatia*, *Pareiasuchus nasicornis*, *Pareiasuchus peringueyi*, *Scutosaurus*, *Elginia mirabilis*, *Anthodon*, and *Bunostegos*) have a single, medial prepalatal foramen (see Supplementary material, Appendix 1: Data Matrix, and Appendix 2: Character List, character 23) on the premaxilla-vomer contact. Two small lateral (not medial) prepalatal foramina on the premaxilla-vomer contact are present in *Contritosaurus simus* (Ivakhnenko, 1979: fig. 8 "Fab") and *Tichvinskia vtyakensis* (Ivakhnenko, 1979: fig. 9 "Fab") and two small lateral (not medial) prepalatal foramina are present on the premaxilla, far anterior to the premaxilla-vomer contact, in *Captorhinus laticeps* (Heaton, 1977: fig. 7C. "prepal.f.").

Maxilla

The left maxilla is much better preserved than the right (which is eroded and has a light-coloured plaster infill) and forms the basis of this description. The maxilla is a large bone forming most of the lateral surface of the snout and has a vertical suture with the premaxilla anteriorly, and dorsal to this the bone forms the posteroventral and posterolateral border of the external nares, but no part of the posterodorsal margin (character 30:0). The maxilla is highest anteriorly and has a long oblique suture with the lacrimal and jugal dorsally (Figure 1B). The maxilla is smooth and relatively unornamented compared to the other more heavily ornamented dorsal cranial elements. The left maxilla has a slightly worn external surface, and anterodorsally shows a very low swelling or maxillary bulge (not a maxillary boss) (character 31:0) and a very poorly defined posterodorsally oriented maxillary-lacrimal ridge behind the external nares. All four members of Pumiliopareiasauria lack a maxillary boss.

The holotype of *Pareiasuchus nasicornis* (SAM-PK-3016) has a distinct and large maxillary boss on each maxilla, as does a smaller skull (SAM-PK-K6607) currently referred to *P. nasicornis*, and in our phylogenetic analysis we have updated the character from absence to presence of a distinct maxillary boss for *P. nasicornis* (character 31:1).

There are three small circular pits (matrix filled nutritive foramina) along a horizontal row above the upper left second to fourth maxillary marginal teeth (Figure 1B, Mx2-Mx4). One of these pits is the anterolateral maxillary foramen, described in most well-known pareiasaurs. The horizontal groove that probably accommodated an important blood vessel seen in several pareiasaurs, such as *Embrithosaurus* (Van den Brandt *et al*., 2020), *Nochelesaurus* (Van den Brandt *et al*., 2021b), and *Pareiasuchus nasicornis* (Lee *et al*., 1997) does not appear to be present, but this is probably the result of poor preservation, since there is a fourth small matrix filled circular nutritive foramina at the same horizontal level, positioned posteriorly, above the eighth upper left maxillary marginal tooth (Figure 1B, Mx8).

Posteriorly, the maxilla almost contacts the quadratojugal, at a level slightly posterior to the anterior border of the orbit, where these the two bones are separated by about 2–3 mm on the left, the gap is filled with matrix (Figure 3), is not well preserved and is obscured by plaster on the right.

Internally, the maxilla forms an oblique to flat medial palatal flange, that itself forms the anterolateral border of the internal naris or choana and posterior to this it has a long suture with the palatine and the ectopterygoid. The new preparation of RC 109 revealed evidence of tooth replacement in *Nanoparia luckhoffi*. The marginal dentition is better-preserved on the left side of the skull, where six resorption pits can be seen, two on the premaxilla still filled with matrix/glue and four on the maxilla that have been prepared (Figures 3, 4B). The first pit is located lingual to the first premaxillary tooth (Pm1), and is unprepared, but shows a slightly ovoid depression, matrix filled, that we interpret as a resorption cavity (Figure 4B). The second pit is lingual to the second marginal tooth (Pm2), also in the premaxilla and is also unprepared and partially covered by some glue, but it clearly shows an elliptical margin and is slightly larger than the first pit (Figure 4B). This second resorption pit is followed by four deep and fully prepared pits, all in the maxilla, located lingual to Mx2, Mx4, Mx6, and

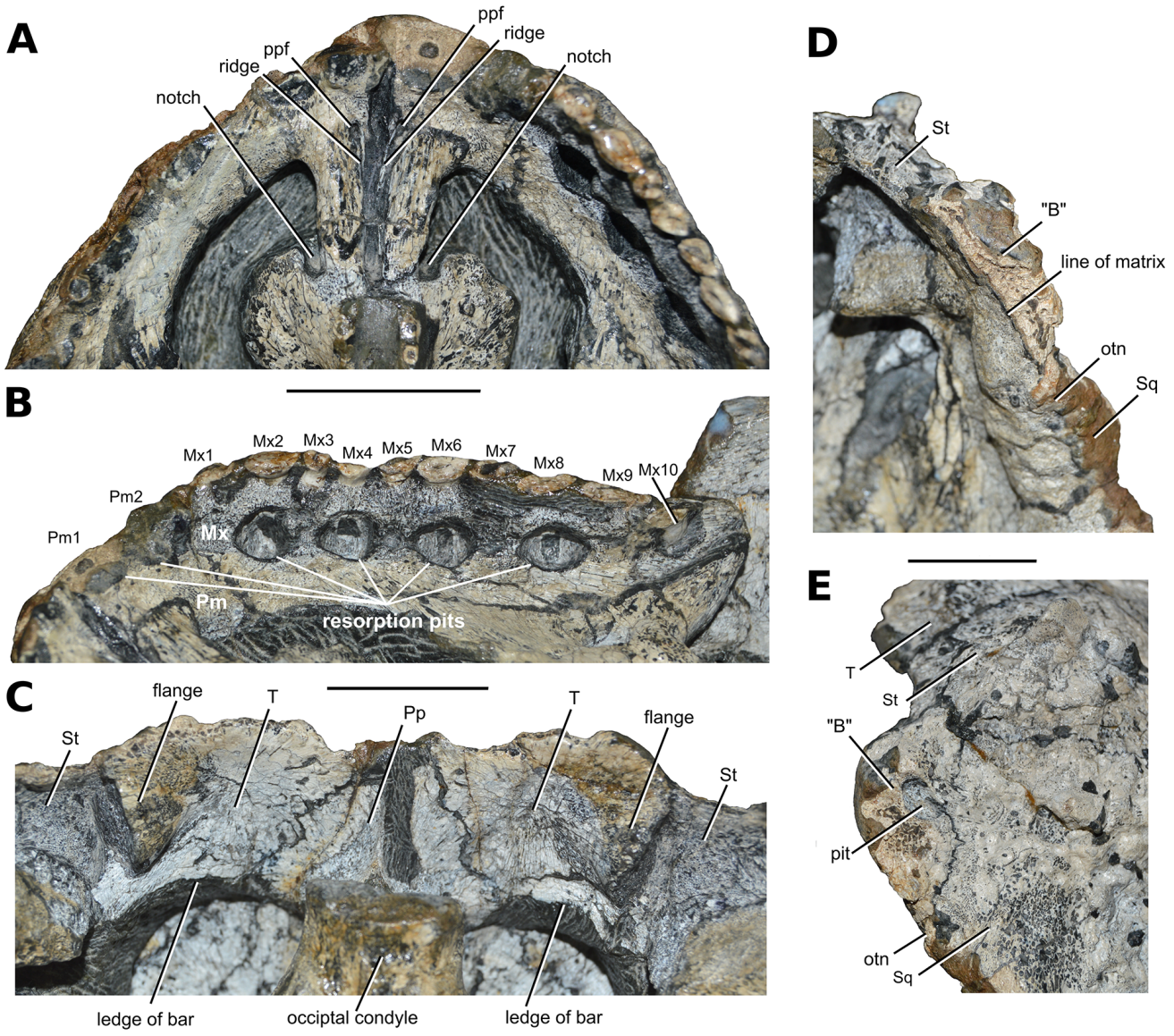

Figure 4. Close-up photographs of autapomorphies or interesting features of *Nanoparia luckhoffi* (RC 109): (**A**) ventral view of the anterior palate showing the two anterolateral prepalatal foramina, posterior ridges and the vomer notch; (**B**) ventrolateral view of the internal left palate showing six resorption pits, two matrix filled pits the premaxilla, and four prepared pits on the maxilla; (**C**) ventral view of the tabular flanges; (**D**) occipital view of Element "B"; (**E**) right lateral view of Element "B". **Abbreviations: "B"**, Element B; **Mx**, maxilla; **Mxn**, maxillary tooth numbers; **otn**, otic notch; **Pm**, premaxilla; **Pmn**, premaxillary tooth numbers; **Pp**, postparietal; **ppf**, prepalatal foramina; **Sq**, squamosal; **St**, supratemporal; **T**, tabular. Anterior to the top in (A), to the left in (B), to the bottom in (C), into the page in (D), and to the right in (E). Scale bars = 20 mm.

Mx8 tooth positions (Figure 3). These four deep pits on the maxilla are fully prepared. The placement and arrangement of the resorption pits is consistent with the alternate replacement model that is typical of many reptiles and was previously proposed for pareiasaurs by Edmund (1960) based on an indeterminate pareiasaur from South Africa (*Pareiasaurus* '*bombidens*' NHMUK PV R 1970, referred to *Bradysaurus baini* by Lee 1994, 1997a, and Van den Brandt *et al*., 2022). This model is now well documented in this group. Examples of additional pareiasaur taxa where tooth replacement events supporting an alternate model have been recorded include *Nochelesaurus alexanderi* (Van den Brandt *et al*., 2021b), *Embrithosaurus schwarzi* (Van den Brandt *et al*., 2020), *Provelosaurus americanus* (Cisneros *et al*., 2005, 2021), *Shihtienfenia permica*, *Sanchuansaurus pygmaeus* (Gao, 1983; Benton, 2016), *Pareiasuchus nasicornis* (Lee *et al*., 1997), *Pareiasuchus peringueyi* and *Bradysaurus seeleyi* (Cisneros *et al*., 2005).

Lacrimal

The left lacrimal of the holotype forms the basis of this description, as it is better preserved than the right. The lacrimal is anteroposteriorly very short, almost square, only very slightly obliquely elongated (Figures 1B, 2A). The bone is anteroposteriorly much shorter than the very elongated lacrimal of *Provelosaurus americanus* (Cisneros *et al*.,

2021: figs. 3A, 4D) and *Bunostegos akokanensis* (Tsuji *et al*., 2013: fig. 5C) and even *Pareiasuchus nasicornis* (Lee *et al*., 1997). The lacrimal is positioned between the anterodorsal nasal, posterodorsal prefrontal, anteroventral maxilla, and posteroventral jugal. Anteriorly, the lacrimal forms a very small portion of the posterolateral border of the external naris, and the posteriorly, a small portion of the anteroventral border of the orbit (character 32:0).

The internal wall of the left orbital rim was prepared to reveal the antorbital buttress. Here a horizontal matrix-filled line is present near the lacrimal-prefrontal contact. We interpret this horizontal line as a crack or buckling of the prefrontal in the orbital rim. Most of the antorbital buttress is formed by a wide, ventrally tapering descending flange of the prefrontal, as in most pareiasaurs (*e.g*., *Pareiasuchus nasicornis*, Lee *et al*., 1997; *Embrithosaurus schwarzi*, Van den Brandt *et al*., 2020*; Nochelesaurus alexanderi*, Van den Brandt *et al*., 2021b) and the lacrimal makes a very small contribution to the lateral edge of the orbital rims, and no contribution (ascending flange) to the internal orbital wall (Figures 1B, 2A). The right orbital rim is damaged and reconstructed with plaster, so we cannot confirm the lacrimal-prefrontal orbital rim contact.

The lacrimal surface is heavily ornamented and rugose. It has a distinct, pointed, high boss near the centre of the bone, in line with the posterodorsal maxillary-lacrimal ridge. *Provelosaurus americanus* also has a prominent boss, anteriorly (Cisneros *et al*., 2021: fig. 4D). Six to nine rugose radial ridges emanate from the central boss: two to three parallel ridges extend to each of the nasal, prefrontal and jugal (Figure 1B). The right lacrimal of *Pumiliopareia* (BP/1/81) is also rugose, with a central boss and several rugose tab-like ridges, as is the left lacrimal of *Anthodon* (RC 785). A prominent single central lacrimal boss or a complex of several small bosses or rugose tab-like processes, are common to most pareiasaurs (*e.g*., *Pareiasuchus nasicornis* and *Pareiasuchus peringueyi*, *Deltavjatia rossica*, Tsuji, 2013; *Embrithosaurus schwarzi*, Van den Brandt *et al*., 2020; *Nochelesaurus alexanderi*, Van den Brandt *et al*., 2021b; *Provelosaurus americanus*, Cisneros *et al*., 2021).

Prefrontal

The prefrontal is relatively small, curved and forms the anterodorsal rim of the orbit, contacting the lacrimal anteroventrally, and the postfrontal posteriorly. Medially the bone is flatter and contributes a small portion to the dorsal skull table, contacting the nasal anteromedially and the frontal medially. In dorsal view it is roughly triangular, widest anteriorly, and narrowing posteriorly to a transverse suture with the postfrontal, preventing the frontal from contributing to the margin of the orbit (character 55:1). Additional preparation has revealed the contribution of the left prefrontal to the inner orbital rim (antorbital buttress) and shows the bone forming a strong descending ventral process (Figure 1B) (see Lacrimal).

The prefrontal is heavily ornamented and rugose. The bone has one small round boss positioned posteriorly on the orbital rim (Figure 1B), as in *Pumiliopareia* and *Provelosaurus*. Other pareiasaurs possess two distinct bosses on the prefrontal (*e.g*., *Elginia wuyongae*, Liu & Bever, 2018; *Deltavjatia rossica*, Tsuji, 2013; *Pareiasuchus nasicornis*, Lee *et al*., 1997; *Embrithosaurus schwarzi*, Van den Brandt *et al*., 2020) but these differences do not appear to be taxonomically significant. Single large and dominant circumorbital tuberosities are also present on both the postfrontal and postorbital of *Nanoparia* (character 37:1). Pairs of two to three rugose, irregular, tab-like ridges extend medially onto the frontal, anteromedially onto the nasal and anterolaterally onto the lacrimal (Figure 1B).

Postfrontal

As in all pareiasaurs, the postfrontal forms part of the dorsal-most margin of the orbit and a portion of the dorsal skull table. Its contribution to the dorsal orbital margin is relatively large when compared to certain other pareiasaurs (*e.g*., Bradysauria).

The postfrontal of *Nanoparia* is a relatively small, roughly square to slightly rectangular (anteroposteriorly elongated) cranial element. This roughly square shape is shared with several pareiasaurs: *Provelosaurus americanus* (Cisneros *et al*., 2021: figs. 3B, 5B), *Bradysaurus baini* (CGP/1/2269)*, Nochelesaurus alexanderi* (SAM-PK-6239, SAM-PK-6238), *Elginia wuyongae* (Liu & Bever, 2018) and *Deltavjatia rossica* (Tsuji, 2013) (character 34:1). The bone sutures between the prefrontal anteriorly, the large frontal medially, the large parietal posteromedially and the postorbital posterolaterally.

The surface of the postfrontal is dominated by the second largest boss on the skull of *Nanoparia* (after the large central boss on each supratemporal) which forms a smooth convex, high dome. This large boss is however not elongated to form a postfrontal 'horn' as seen in *Bunostegos akokanensis* (Sidor *et al*., 2003: fig. 2; Tsuji *et al*., 2013: fig. 6), *Elginia mirabilis* (Spencer & Lee, 2000: fig. 1; and NHMUK PV R 2114) or *Arganaceras vacanti* (Jalil & Janvier, 2005) (character 35:0). Pairs of two to three rugose, irregular, tab-like ridges extend anteromedially onto the frontal, posteromedially onto the parietal and posterolaterally onto the postorbital.

Postorbital

The postorbital is a large and complex element which forms the posterodorsal margin of the orbit. The bone is pentagonal (similar to *Nochelesaurus*, *Embrithosaurus* and *Bradysaurus*), sharing five roughly equally long, straight to slightly curved, sutural contacts with the postfrontal anteromedially, the parietal medially, the supratemporal posteromedially, the squamosal posterolaterally, and the jugal ventrally.

The postorbital is curved and situated behind the orbit, at the junction of the dorsal skull table and the lateral cheek. The junction between the dorsal skull table and the lateral cheek region is curved as in most pareiasaurs and all known Lopingian South African pareiasaurs (character 49:1), unlike the sharp and distinct angle seen in *Provelosaurus*, three genera of Bradysauria, and reported for *Bunostegos* (Tsuji *et al*., 2013) and *Elginia wuyongae* (Liu & Bever, 2018).

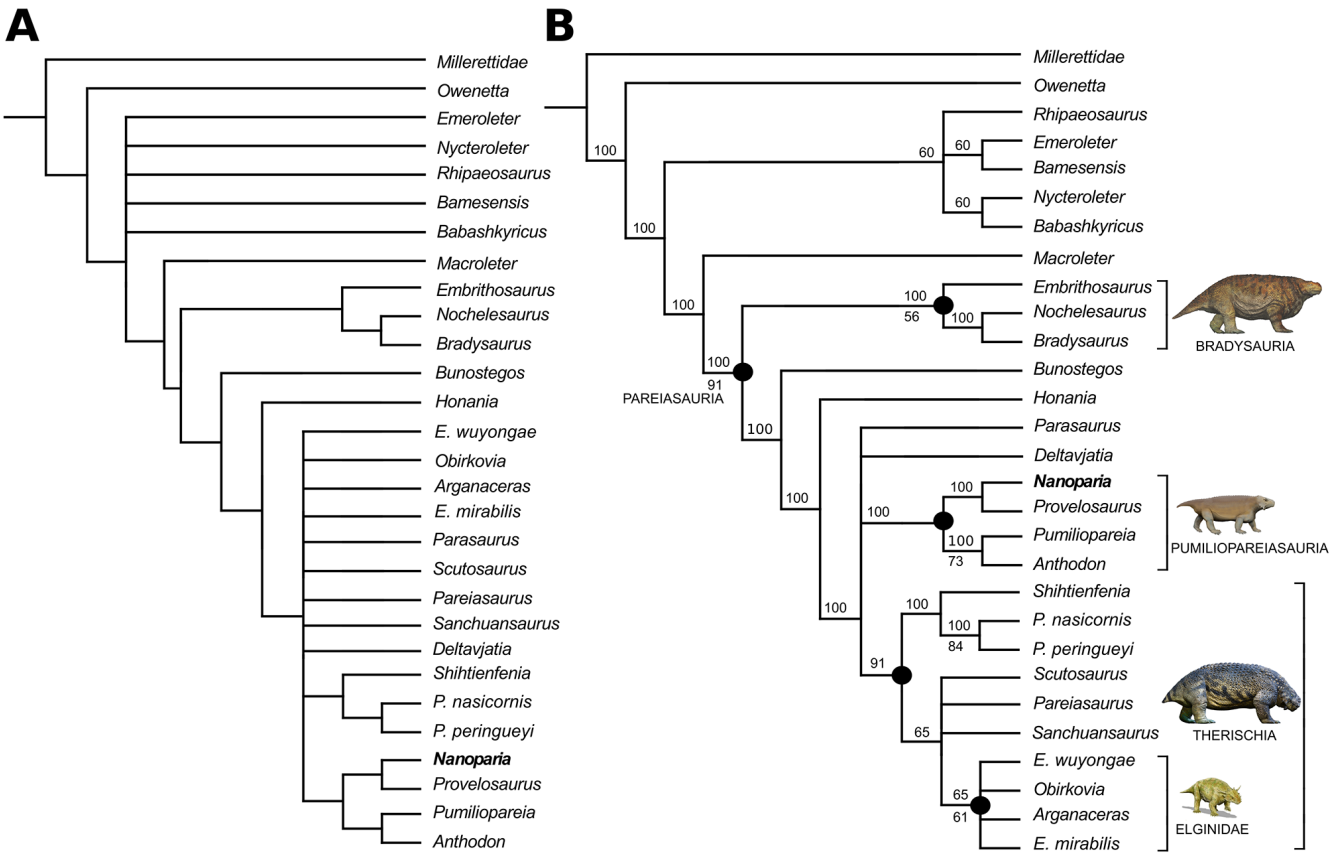

Figure 5. Cladistic relationships of *Nanoparia* within Pareiasauria, 705 most parsimonious trees (mpt) of length 284. (**A**) strict consensus tree, (**B**) 50% majority-rule consensus tree. Numbers above each node indicate the frequency of clades in the fundamental trees, numbers below each node indicate standard bootstrapping (100 replicates, cut = 50). Bradysauria: *sensu* Van den Brandt *et al.* (2020), representative specimen: FMNH UC 1533, *Bradysaurus baini*, reproduced with permission from Van den Brandt *et al.* (2023); Pumiliopareiasauria: based on several specimens of *Provelosaurus americanus*, reproduced with permission from Cisneros *et al.* (2021); Therischia: *sensu* Jalil & Janvier (2005), representative specimen: PIN 2005/1537, *Scutosaurus karpinskii*, reproduced with permission from Romano *et al.* (2021); Elginidae: *sensu* Liu & Bever (2018), representative specimen: holotype GSE 4780-4788, *Elginia mirabilis*, copyrighted to Nobu Tamura, nobu.tamura@yahoo.com, under Creative Commons 3.0 Unported (CC BY-NC-ND 3.0).

The postorbital carries one irregular and rugose large boss, positioned anterodorsally, on the orbital rim, near the suture with the postfrontal. It is surrounded by an irregular radial pattern of ridges, in which two vectors are prominent: (1) three very thick ridges extend from the postorbital boss posteromedially towards the central boss of the supratemporal; and (2) one to two thick rugose ridges extend posteriorly along the side of the cheek towards the central boss of the lateral squamosal (Figure 1A). These two prominent ridge complexes are found in all three genera of Bradysauria. In Bradysauria and *Provelosaurus*, the more dorsal ridge complex, that extends through the supratemporal, is very prominent and creates a distinct skull angle.

A few irregular and less prominent ridges extend medially and slightly posteriorly towards the centre of the parietals, and anteroventrally, along the orbital rim, towards the centre of the jugal. The postorbital region of the skull is at least 1.5 times the anteroposterior extent of the orbit (character 54:0).

Nasal

The nasal is a relatively small rectangular bone, slightly convex, with a narrow midline anteroventral process that forms part of the internarial bar. The nasal also forms the posterodorsal and dorsomedial border of the external naris and most of the anterior dorsal snout. As in all pareiasaurs, the nasal sutures with the lacrimal laterally, the prefrontal posterolaterally, and the frontal posteriorly.

The left nasal is heavily ornamented (damaged on the right). A large percentage of the dorsal bony surface is covered by a wide, central cluster of four to five thickened, tab-like tubercles (Figure 1A). There is no obvious single central boss, but the nasal tubercle complex of this juvenile specimen, would probably have enlarged and thickened with age, and may well mature into a single large central boss later in ontogeny, as seen in larger pareiasaur specimens of all species. Interestingly, this cluster of nasal tubercles of *Nanoparia* is positioned centrally on the dorsal nasal surface, and not anteriorly or directly above the external margin of the naris, where a single prominent nasal boss is located in most pareiasaurs, such as *Deltavjatia rossica* (Tsuji, 2013), *Bunostegos akokanensis* (Tsuji *et al*., 2013), *Pareiasuchus peringueyi* (SAM-PK-2337), and *Elginia mirabilis* (NHMUK PV R 2114). *Pareiasuchus nasicornis* has two small bosses, anteromedially obliquely positioned (Lee *et al*., 1997,

BP/1/3653) or one elongated boss on each nasal (SAM-PK-3016). The three genera of Bradysauria (Van den Brandt *et al*., 2022) all have one distinct anteromedially elongated boss, with two or three prominent rugose tab-like ridges. Finally, several narrow, thin, irregular radial ridges are present, with two to three ridges each extending posteriorly onto the frontal, posterolaterally onto the prefrontal, and laterally onto the lacrimal, above the margin of the external naris.

Frontal

The frontal is a large, flat, element and forms the flat medial anterodorsal skull table, between the anterior nasals, the lateral prefrontals and postfrontals, and the posterior parietals. As in all known pareiasaurs, the frontal is excluded from contributing to the orbital margin by the prefrontals and postfrontals (Figure 1A) (character 55:1). It is a rectangular elongated element, approximately twice as long as wide (character 56:1). In common with most other pareiasaurs, the posterior border with the parietal is transversely straight, unlike the condition in *Deltavjatia rossica* (Tsuji, 2013), where there is a narrow tapering posterolateral process.

A central boss dominates each frontal (character 57:1), as in most pareiasaurs, apart from *Bunostegos* (Tsuji *et al*., 2013)*, Arganaceras* (Jalil & Janvier, 2005), and *Pareiasaurus* (NHMUK PV R 4063, SAM-PK-K10036, RC 28). However, this central boss is notably low and wide, and is much lower than the high and distinct central bosses on the lacrimals, prefrontals, postfrontals, postorbitals, parietals and supratemporals of *Nanoparia*. Even though the frontal central bosses are slightly weathered, better preserved, they must still have been relatively low. Interestingly, *Nanoparia* and *Pumiliopareia* lack the swelling or strong ridge in the posterolateral corners of the frontals, which are seen in *Provelosaurus* (Cisneros *et al*., 2021: figs. 3B, 5B) and *Embrithosaurus* and *Nochelesaurus* (Van den Brandt *et al*., 2020, 2021b, 2022) that extend posterolaterally to connect with the largest boss on the postfrontal orbital rim.

Fifteen to twenty short and regularly spaced radial ridges extend from the low central frontal boss, anteriorly onto the nasals, anterolaterally and laterally onto the prefrontals, laterally and posterolaterally onto the postfrontals, posteriorly and posteromedially onto the parietals, and anteromedially, medially and posteromedially onto each contralateral element. This is the same pattern seen in all three members of Bradysauria.

Parietal

The parietal is one of the largest elements of the skull, forming a large portion of the medial posterodorsal skull table. This element is seven sided (Figure 1A) and is roughly diamond-shaped, anteroposteriorly longer than mediolaterally wide, with short, blunt, transverse anterior and posterior edges. It sutures with the frontal anteriorly, postfrontal anterolaterally, postorbital laterally, supratemporal posterolaterally, tabular posteriorly, and the median postparietal posteromedially. Posteriorly each parietal forms a tapering wedge between the supratemporal, and the postparietal, to a short blunt transverse suture with the tabulars.

The parietal is heavily ornamented and is not a flat bone. Instead it presents a low pyramidal or triangular shape (Figure 2B), the result of (1) a large, dome-shaped, central boss, comprising two lobes which are anterolaterally oriented and almost fused, and (2) 15–20 rugose radial ridges, swollen and thick near the central boss, dramatically decreasing in height radially away from the central boss and extending onto all adjacent elements, producing an anteroventrally sloping oblique dorsal pineal foramen margin. Interestingly, the parietal boss of the holotype of *Pumiliopareia pricei* (BP/1/81) also comprises a double-lobed central boss which is also anterolaterally oriented. These are a bit more separated and distinct from each other than in *Nanoparia*, probably the result of the very small size of the skull and its presumed early ontogenetic stage, whereby ornamentation had not yet fully developed. *Anthodon* (RC 785) also shows these two lobes.

Three radial vectors are prominent and swollen: the ridges that extend medially to the contralateral element, anterolaterally to the postfrontal boss, and posterolaterally to the supratemporal boss. This is in strong contrast to the flat parietals and very low, indistinct, central parietal boss, little more than a slight swelling, observed in Bradysauria.

The pineal foramen of *Nanoparia*, *Pumiliopareia* (BP/1/81), *Anthodon* (RC 785) and *Pareiasaurus* (RC 28, SAM-PK-K10036), is anteroposteriorly elongated and forms a tear-drop shape on the dorsal skull table (anteriorly pointed, posteriorly rounded or blunt), whereas in *Provelosaurus* the pineal foramen is oval and nearly twice as wide as long. In all other pareiasaurs, it is circular to oval (anteroposteriorly elongated). The borders of the pineal foramen of *Nanoparia* are formed by ridges that extend from the central parietal bosses, transversely to form the posterior border, and anteromedially to form the lateral borders, as in all pareiasaurs that possess strong radial ridges for cranial ornamentation.

The pineal foramen is situated entirely within the anterior half of each bone, close to the frontal-parietal suture (character 38:1) as in most pareiasaurs, which is different to the situation in *Bunostegos* (Tsuji *et al*., 2013) and *Deltavjatia rossica* (Tsuji, 2013) where it is situated close to the half-way or the midpoint of the anteroposterior length of the parietal.

Postparietal

The postparietal is a small, single, median element, that forms most of the median posterodorsal skull table (characters 42:1, 43:1) and a very small portion of the occiput or posterior edge of the skull. The bone is about the same size as each tabular, anteroposteriorly elongated, diamond-shaped, wider and blunter anteriorly and tapers posteriorly (Figure 1A). The postparietal shares long jagged or wavy, oblique sutures with the tabular posterolaterally, and with the parietals anterolaterally. These sutures are very clearly defined on the internal surface (Figure 3), confirming that the external cranial sutures pass perpendicularly directly through the bone. Compared to *Nanoparia*, *Provelosaurus* has a smaller postparietal, which is loosely pentagonal in dorsal view, with a much shorter and lateral contact with the tabular. The tabular prevents the postparietal of *Nanoparia* from contacting the large supratemporal laterally.

The dorsal surface of the postparietal is very rugose. The centre of this bone does not have a distinct boss, but it is slightly swollen and raised to create a very low irregular boss. Irregular and low radial ridges emanate from the swollen centre and extend anterolaterally onto the parietal and posterolaterally onto the tabular.

Posteriorly the postparietal narrows to a point only 2 mm wide, and therefore makes virtually no contribution to the posterior edge of the occiput, where it forms the midline point of the very thin (2 mm dorsoventral height) occipital flange. This is very different from *Provelosaurus*, where the posterior edge of the postparietal is much wider. The posterior edge of the postparietal of *Nanoparia* is anterior to the posterior edge of the tabulars (the posterior edge of the skull is embayed at the midline) as in all known pareiasaurs (Figure 1A). The dorsoventral height of the occipital flange (posterior portions of the postparietal, tabulars, supratemporals and squamosals) is very thin or low in *Nanoparia*, and horizontally very flat. In most other pareiasaurs the posterior portions of the elements that make up the occipital flange are thicker and are oriented obliquely posteroventrally. This is marked anterodorsally by a transverse ridge, which is not present in *Nanoparia*.

Ventrally, the newly prepared internal surface of the postparietal reveals, as in all known pareiasaurs, a short, robust and pillar-like, midline descending process which is triangular in cross-section (tapering posteriorly). This must connect with the supraoccipital ascending process of the braincase, as in all pareiasaurs, at a typically horizontal suture (as in *Embrithosaurus*, Van den Brandt *et al*., 2020) (character 28:1). The supraoccipital is not preserved in *Nanoparia*.

Tabular

The tabulars of *Nanoparia* are small, paired elements, which form the posterodorsal skull table on either side of the median postparietal. They are roughly triangular to trapezoid in dorsal view, narrow anteriorly and are wider posteriorly. The tabulars have a short transverse suture with the parietals anteriorly, a long oblique lateral suture with the supratemporals, and a long oblique medial suture with the postparietal. The presence of the tabular prevents the supratemporal from contacting the postparietal (Figure 1A) (character 39:0). The tabulars of *Provelosaurus americanus* are proportionally smaller than those of *Nanoparia* and are notably shaped differently (Cisneros *et al*., 2021).

There is a rugose, low boss on each tabular, similar to the low central boss on the frontal, that is essentially an irregular rugose thickening of the bone and is better preserved on the left. Irregular, short, tab-like radial ridges extend onto the adjacent elements: anterolaterally onto the supratemporal, anteriorly onto the parietal, and anteromedially and medially onto the postparietal.

The tabular is clearly strongly fused between the lateral supratemporal and the medial postparietal and integrated into the dorsal skull table (character 40:1). The two tabulars do not contact each other posteriorly (character 41:1) and contact the parietals anteriorly (character 142:1). The thin and delicate posterior edge of both tabulars is slightly eroded and we have reconstructed the actual edges (Figures 1A, 3).

Posteriorly the tabular thins in dorsoventral thickness to form a thin, flat occipital flange over the occiput. The posterior edge of the tabular is posteriorly bulged (also the condition in *Provelosaurus* and *Elginia mirabilis*). In all other pareiasaurs, the posterior edge of the tabular is straight to anteriorly concave, and the entire occipital flange between the postparietal and the laterally positioned supratemporals is anteriorly concave (medially embayed). It is important to note that we interpret the severe posteriorly convex or bulged tabulars as a new autapomorphy for *Nanoparia*, since the posterior border of these bones extend posteriorly well beyond the posterior border of the supratemporals, which is the reverse condition to the situation in all other pareiasaurs. In *Provelosaurus* and *Elginia mirabilis* the posteriorly bulged tabulars do not extend posteriorly further than the supratemporals.

An unexpected new autapomorphy of *Nanoparia* was revealed by preparation on the internal surface of the tabulars, where the lateral portions of each tabular forms a large, ventrally projecting, curved flange, such that the ventrolateral margins of the internal tabulars extend ventrally about 5 mm (Figures 3, 4C). Partially prepared at the time, Brink (1955:62) noted this feature as a "distinct ridge" on the lateral suture of the internal tabulars and figured it (Brink, 1955: fig. 18) but did not seem to have recognised this feature as autapomorphic. We have not observed this internal tabular flange in any other pareiasaur.

The freshly prepared internal surface of the skull shows the tabulars and postparietal forming a thick bar of bone extending parallel to the occipital flange, with a sharp ledge or step down to the level of the rest of the internal skull roof, when viewed ventrally (Figure 4C). This bar of bone is also present in the three genera of Bradysauria, and the holotype of *Pumiliopareia* and is probably standard in all pareiasaurian species, but it is seldom reported or described, possibly due to poor preparation. The unique wing-like, ventral flange of the tabulars of *Nanoparia*, is positioned on the ventral surface of this thickened bar of bone. This internal tabular ventral flange may be similar to the "very large supernumerary bones [tabulars] with a large ventral blade joining the supratemporal ventrally" of *Arganaceras vacanti* (Jalil & Janvier, 2005: 37), and the "internal crest of the supernumerary [tabulars] bone, which prolongs dorsally the internal crest of the squamosal and supratemporal and thus suggest a contribution of the supernumerary bone [tabular] to the contact with the paroccipital process of the opisthotic". In *Nanoparia*, this internal tabular flange, does not connect with the internal supratemporal/squamosal flange, nor the distal paroccipital process of the opisthotic, and we are comfortable to interpret this as a new autapomorphy.

Supratemporal

The supratemporal is large and robust and forms the posterolateral corner of the skull in all known pareiasaurs. Traditionally called the tabular by earlier researchers (*e.g*., Watson, 1914a; Boonstra, 1934), the supratemporal (Tsuji, 2013; Tsuji *et al*., 2013; Van den Brandt *et al*., 2020, 2021b; Cisneros *et al*., 2021) is a large bone that contacts

the squamosal laterally, postorbital anterolaterally, parietal anteromedially and the tabulars medially. In contrast to the condition in Bradysauria, the supratemporal of *Nanoparia* is prevented from contacting the median postparietal, through the presence of the tabulars. The supratemporal is curved and contributes to both the horizontal dorsal skull table and the laterally oriented cheeks (as the postorbital in front of it does).

As in most pareiasaurs, the central supratemporal boss of *Nanoparia* is the largest boss on the skull. It is consistent with the general ornamentation style of the skull, and is large and high, but not developed into a pointed "horn" (cf. *Elginia mirabilis*, Newton, 1893; Spencer & Lee, 2000: fig. 2; *Arganaceras*, Jalil & Janvier, 2005: fig. 9; *Bunostegos*, Sidor *et al*., 2003: fig. 2).

Slightly weathered on the left and severely damaged on the right, this complete boss appears to have been very similarly sized and shaped, but slightly higher and more pointed than the large central bosses on the prefrontal, postfrontal, postorbital, and the parietal. Posterior to the boss, the supratemporal is noticeably steep, dorsoventrally oriented, with an almost vertical posterior edge, which is slightly forward-leaning (as in *Deltavjatia rossica*, Tsuji, 2013), and still heavily ornamented and tapers posteriorly to a thin, dorsoventrally flat and sharp-edged occipital flange.

Regularly spaced radial, short tab-like, rugose ridges extend anterolaterally from the central boss, onto the postorbital as a group of two to three thick ridges. The prominence of this complex of ridges creates either a rounded angle between the horizontal dorsal skull roof and the lateral cheek when this ridge is less developed, or a distinct angle when the ridge is thick and well developed (see Postorbital). Although more prominent on the left, this ridge is weak on the right, creating a rounded junction, which we interpret as characteristic for the species (character 49:1). From the base of the large supratemporal boss, rugose ridges extend ventrolaterally onto the squamosal, anteromedially onto the parietal, and posteromedially onto the tabular.

The internal surface of the supratemporal has been cleared of most matrix, and as in all known pareiasaurs, the internal supratemporal (and internal squamosal) suture strongly with the distal end of the paroccipital process of the opisthotic, on a ventrally-directed flange (character 6:1).

Element "B"

Broom's (1936: 350) second "supernumerary dermal element", labelled as "B" (Broom, 1936: fig. 1) is a very small bone, positioned on the external surface of the lateral edge of the flat posterior occipital flange, on the lateral skull, between the right supratemporal and right squamosal (Figures 2A, 4D, 4E), and is not preserved on the left. As Broom (1936: 350) recorded about the supratemporal, tabular and Element B, "these three bones are not imaginary bones, but bones whose sutures are perfectly distinct, and which are as I have figured them".

This is a small, thin bone, oriented obliquely, roughly crescent-shaped (anteriorly vertical, posteriorly convex), vertically elongated and, with a short anterodorsal suture with the supratemporal and an interdigitating vertical, anterior suture with the squamosal (Figures 2A, 4E). The posterior edge is strongly convex to form a semi-circular posterior projection. The element is heavily ornamented externally, somewhat eroded or weathered, and has one very large and deep oval pit, irregular rugose ridges, and the remains of a damaged central boss or tubercle on the posterolateral surface below the large pit.

This bone overlies the posterodorsal corner of the right squamosal, as shown by: (1) a thin infilled line of dark matrix visible on the posterior edge of the skull, between the squamosal and this overlying element (Figure 4D); and (2) the internal surface of the skull does not show any indication of a suture of this element with the squamosals (Figure 3). The anterior (vertical) suture of this small element has strong interdigitating edges (Figures 2A, 4E), and is very strongly fused with the squamosal and integrated into the rest of the skull table. Broom (1936: 350) was uncertain whether this bone was an integral part of the cranium or a displaced, fused osteoderm. We interpret this unique bone as part of the cranium (see Discussion: Element "B" as a valid cranial element or an incorporated nuchal osteoderm).

Jugal

The right jugal is damaged and the ventral half is reconstructed in plaster whereas the left is well preserved (Figure 1B). The jugal is a plate-like, flat, crescent-shaped bone which is oriented ventrolaterally. It forms the anteroventral and ventral margins of the orbit, and the anterodorsal part of the lateral cheek. As in all pareiasaurs, the jugal sutures with five elements. It has a short oblique suture with the lacrimal anterodorsally, a longer oblique suture with the maxilla anteroventrally, a long convexly curved suture with the quadratojugal ventrally, and short straight sutures with the squamosal posteriorly and the postorbital dorsally (character 46:0). The internal surface of the left jugal was prepared anteriorly and confirms the external suture with the quadratojugal, perpendicular through the bone. The jugal forms a very large and significant portion of the cheek flange of *Nanoparia*, whereas in Bradysauria the jugal forms a very small part of the cheek (and the cheeks are far smaller).

In lateral view, the large jugals of *Nanoparia* extend ventrally just below the level of the alveoli of the maxillary tooth row (Figures 1B, 2A), as in the large cheeked *Pareiasuchus nasicornis* (Lee *et al*., 1997), *Scutosaurus* (Lee, 1994, 1997a) and *Provelosaurus* (Cisneros *et al*., 2021). In all three genera of the smaller cheeked Bradysauria, the smaller jugal does not extend ventrally below the maxillary tooth row.

The anterior process of the jugal, beneath the lacrimal, is relatively long and extends well beyond the anterior margin of the orbit, approximately 10 mm (character 45:1). The jugal forms an extremely small part of the anterior-most portion of the ventral margin of the cheek flange, where the ventrolaterally oriented jugal detaches from the vertically directed maxilla (best seen in ventral view, left side of skull, Figure 3). Here, the overhanging detached jugal prevents the quadratojugal from contacting the maxilla (the false contact shown in Figure 1B is create by the viewing angle).

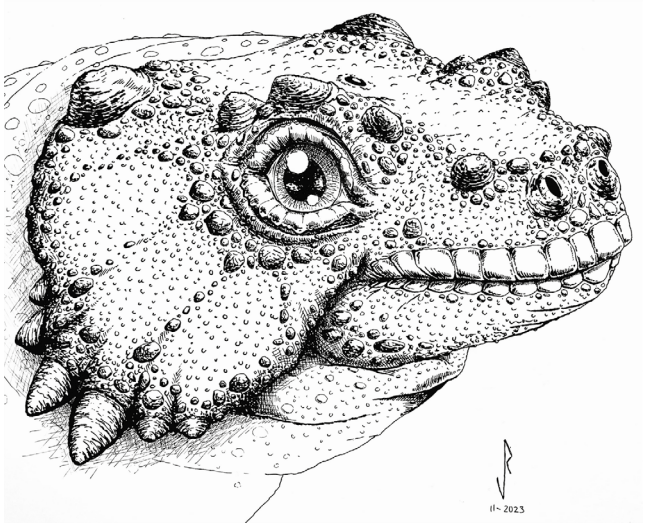

Figure. 6. Artistic reconstruction of *Nanoparia luckhoffi* (RC 109) by Viktor Radermacher.

Slightly anterior to the centre of the lateral surface of the jugal, beneath the orbital rim, the external surface of the jugal is swollen to form a low, irregular boss, which is very rugose and therefore has poorly defined borders. This low boss is in the same general position where other pareiasaurs have one boss (*Elginia mirabilis*, Newton, 1893; Spencer & Lee, 2000; *Bunostegos akokanensis*, Tsuji *et al*., 2013; *Elginia wuyongae*, Liu & Bever, 2018), two close, posterodorsally oriented bosses (*Bradysaurus*, *Embrithosaurus*, *Nochelesaurus*, and *Provelosaurus*) or a complex or cluster of small bosses or large tubercles (*Pareiasuchus nasicornis*, Lee *et al*., 1997; *Deltavjatia rossica*, Tsuji, 2013). Irregularly placed straight, pitted radial ridges extend posterodorsally from this swollen region along, and thickening the orbital rim onto the postorbital; posteriorly and slightly upwardly curving, reaching the squamosal's anterodorsal lateral boss or ridge; and posteroventrally onto the quadratojugal.

Squamosal

The squamosal is a large, flat element with a slightly curved dorsal portion, and forms the posterodorsal portion of the cheek flange. It is roughly square to slightly rectangular, 1.1 times dorsoventrally taller (49 mm right side) than anteroposteriorly long (45 mm right side), and in this way it is similar to most pareiasaurs which have roughly square squamosals. In contrast, the squamosal of *Provelosaurus* has a dorsoventral extent that exceeds the anteroposterior extent by nearly 1.5 times, being autapomorphic. *Arganaceras vacanti* (Jalil & Janvier, 2005: fig. 3B) and *Bunostegos akokanensis* (Tsuji *et al*., 2013: fig. 5C) also have dorsoventrally elongated squamosals. The squamosal of *Nanoparia* has a dorsal horizontal suture with the supratemporal, an oblique suture anterodorsally with the postorbital, and vertical suture anteroventrally with the jugal, and a horizontal suture ventrally with the quadratojugal.

Irregular rugose ridges extend radially from the lateral squamosal: long, curved ridges extend anteroventrally onto the jugal, and ventrally towards the large squamosal posterior cheek boss and the quadratojugal (Figure 1B). One to two large tubercles or small bosses are present in the dorsal portion of the lateral squamosal. These are formed by thickening of the rugose, straight ridges that extend posteriorly from the postorbital central boss onto the squamosal. These lateral squamosal bosses or tubercles are not found in members of Bradysauria (Van den Brandt *et al*., 2022), but are present in more derived pareiasaurs (*e.g*., *Pumiliopareia* BP/1/81, *Pareiasuchus nasicornis*, Lee *et al*., 1997; *Provelosaurus americanus*, Cisneros *et al*., 2021; *Deltavjatia rossica*, Tsuji, 2013).

As in all known pareiasaurs, the posterior edge of the squamosal carries one dominant boss near the posteroventral corner of the bone, beneath and separated from the thin occipital flange. In *Nanoparia*, this boss flares laterally and extends anteriorly on the lateral squamosal. It is oval (dorsoventrally elongated) (character 50:2). On the lateral surface of the squamosal, this large boss extends irregular ridges posterodorsally onto the supratemporal.

The posterior edge of the squamosal is thin dorsally where it forms the ventral-most end of the thin, sharp-edged, overhanging occipital flange, and the internal surface here is smooth. Ventrally, there is an abrupt change where the thin occipital flange ends and the posterior edge of the squamosal thickens and widens drastically, becoming swollen, rugose and ornamented, at the level of the large squamosal posterior cheek boss, and ventrally, the posterior cheek continues to widen on the quadratojugal. At the junction of the thin occipital flange and the rugose wider posterior squamosal, at the level of the large squamosal boss, there is a matrix-filled horizontal groove of the otic notch (left side) on the posterior side of the squamosal, that extends medially along the internal surface of the squamosal, but does not reach the internal flange of the squamosal (Figures 1B, 2A, 2C, 3, 4D) (characters 51:1, 52:0, 53:0).

On the internal surface, the squamosal forms a thin vertical flange over its entire dorsoventral height, which has a long vertical, medial contact with the quadrate dorsal ramus (Figure 2C). The long vertical contacts between these two flanges are displaced by a few millimetres and filled with matrix. Only the distal ends of both paroccipital processes of the opisthotics are preserved (better seen on the right, Figure 2C) and make a strong, blunt, sutural abutment with the top of the vertically directed flange of the squamosal. (character 6:1)**.** Ventrally, the internal squamosal flange ends as a sharp tapering point that overlies the quadratojugal (Figure 2C).

Quadratojugal

Only small medial parts of the quadratojugals of *Nanoparia* are preserved, the ventral part of the bone is broken at the same level on either side of the skull (Figures 1A–B, 2A). As in all pareiasaurs, the quadratojugal is a flat, plate-like bone forming the ventrolateral portion of the skull and

most of the cheek flange. It shares a concave suture with the jugal anterodorsally, and a straight suture with the squamosal posterodorsally (Figures 1B, 2A). At the anterior-most tip of the quadratojugal, the bone comes close to contacting the maxilla, but does not, unlike the condition in *Deltavjatia rossica* where these two bones meet (Tsuji, 2013).

The lateral surface of the quadratojugal is heavily ornamented. The anterodorsal portion preserves oblique ridges extending towards the central boss of the jugal, and posterodorsally vertical ridges extend medially onto the squamosal.

On its internal surface, anterior to the wide and rugose posterior cheek margin, the quadratojugal narrows mediolaterally and forms a small ventral portion of the vertical flange that comprises mostly the squamosal (Figure 2C). A large medially positioned quadrate foramen is present on the suture between the quadrate and the quadratojugal.

Anteroventrally, the quadratojugal extends forwards, reaching the anterior margin of the orbit (Figures 1B, 2A) (character 47:2). This condition is shared with *Pumiliopareia* (BP/1/81 and GSP CM86/544), specimens of *Provelosaurus*, and the holotype of *Pareiasuchus peringueyi*. To document this condition, we introduced a new character state (state 2) for character 47. In all other pareiasaurs, the anterior part of the quadratojugal reaches the level of the posterior border of the orbit (state 1) but does not extend anteriorly beyond the midpoint of the orbit.

We have reconstructed and scored a large cheek flange for *Nanoparia* (character 44:2) with relatively large, pointed bosses on the posterior cheek margin (character 50:2), small bosses on the ventral cheek margin (character 48:?), and an arc of small lateral cheek flange bosses (not a phylogenetic character) (Figures 1A–B, 2, 3) (See Discussion: Reconstructed cheeks).

Palate

General comments

The palate of the *Nanoparia* holotype has been extensively prepared for this project, revealing new autapomorphies and all sutural contacts for the first time. The bony elements of the palate are slightly displaced or shifted and so easily reveal the sutures between bones. The preserved rows of delicate palatal denticles were retained in protective matrix. The ventral surfaces of most of the bones of the anterior palate are slightly eroded as a result of historic overpreparation, and the internal structure of the bone is visible in places. As in all pareiasaurs, the palate of *Nanoparia* forms a flat horizontal plate, at a level well above the maxillary tooth row. The dorsal surfaces of the palatal elements are not accessible for this description.

Vomer

The vomer is a small, paired element, located anteriorly on the palatal flange, behind the premaxillae. The transverse, matrix-filled groove drawn by Brink (1955: fig. 18) separating the vomers from the premaxillae, is a misinterpretation resulting from a lack of complete preparation. The actual suture is positioned slightly further anteriorly (Figure 3).

The paired choanae form reniform lobes with concave medial borders. They are positioned medially, oriented parallel, and bordered medially by the vomer. The palatine forms about 50% of the lateral border, the maxilla most of the remaining 50% of the anterolateral border, and the premaxilla forms a small anteromedial border (character 18:2). New preparation has revealed the autapomorphic presence of a short notch on each vomer, on the anterolateral margin of the choana, and this feature does not occur in any other pareiasaur (Figures 3, 4A).

We have corrected Brink's (1955: fig. 18) interpretation of the anterior contacts of the vomer with the pterygoid (which was a misinterpretation of a thin crack on the bone) and we consider the sutures to be more posteriorly placed (Figure 3). The vomer of *Nanoparia* therefore extends well beyond the posterior border of the internal nares. This new interpretation of the posterior contact of the vomer with the pterygoid posteriorly and the palatine posterolaterally, resembles the condition in *Deltavjatia* (Tsuji, 2013) and *Bunostegos* (Tsuji *et al*., 2013).

The vomer is dorsoventrally thick and high anteromedially where it forms a raised ridge that bears a single longitudinal row of five to six large denticles either side of the midline (Figure 3, T1) (as in *Pareiasuchus nasicornis*, Lee *et al*., 1997; and *Bunostegos*, Tsuji *et al*., 2013). These rows of denticles are about 8 mm apart, and their crowns are broken off at the bases, which are 1-1.5 mm in diameter. Behind the posterior border of the internal choana, the midline ridge widens, and the single row is replaced by two parallel rows of much smaller denticles (Figure 3, T2), with a diameter of about 0.5 mm at the base of the crown. These two parallel rows of denticles extend posteriorly onto the pterygoid, as in all known pareiasaurs. In members of Bradysauria, the anteriorly positioned large vomer denticles are arranged irregularly and are randomly scattered.

Lateral to the large denticles, the vomer flattens-out to form the alar flanges (character 19:1) which are mediolaterally broad and partially damaged through historic overpreparation. The transition between the thick medial vomer and the thin lateral alar flange is oblique and smooth and not stepped. This transition is stepped in *Nochelesaurus* (SAM-PK-6238), but the smooth oblique transition in *Nanoparia* could be the result of over preparation.

Palatine

The palatine is small and forms the palatal flange between the maxilla, ectopterygoid, pterygoid and vomer. It has a long posterolateral contact with the maxilla and medially it forms the posterolateral border of the internal naris. Posterolaterally the suture with the ectopterygoid is short and passes through the large, circular, foramen palatinum posterius, with the palatine forming the anteromedial half of the border, and the ectopterygoid the posterolateral half (character 20:1).

The posterolateral corner of the palatine bears two oblique posteromedially directed rows of three to four small denticles

that extend onto the pterygoid (Figure 3, T3). These rows of denticles are parallel and equidistant from each other on the palatine, but on the pterygoid, they converge posteriorly (see Pterygoid).

Pterygoid

The pterygoid is a complex bone, forming most of the medial portion of the palate as a flat, horizontal palatal flange. It contacts the vomer anteriorly, palatine anterolaterally, ectopterygoid laterally, quadrate posterolaterally, and the parabasisphenoid posteromedially. New preparation has revealed that the anterior contacts with the palatine and ectopterygoid are more posteriorly positioned than shown by Brink (1955: fig. 18). Anteriorly, the pterygoid does not reach the posterior margin of the choanae (internal nares) (character 75:1)**.**

Either side of the midline the pterygoid has a paired parallel row of about 11 denticles that extend posteriorly from the vomer (Figure 3, T2). These rows do not converge anteriorly (character 77:0). Extending posteromedially from the palatine onto the pterygoid is another parallel pair of palatal denticles, obliquely directed as in all known pareiasaurs, and numbering about six denticles per row (Figure 3, T3). These two oblique rows of denticles are not parallel (as on the palatine) but instead gradually converge posteromedially (Figure 3, T3). Interestingly, on the holotype of *Pareiasuchus peringueyi* this double row of denticles is oriented longitudinally, and not obliquely.

Additional preparation of *Nanoparia* shows the posterior margin of the pterygoid at the midline forming an anteriorly narrowing, sharply pointed, V-shaped interpterygoid vacuity (also the condition in the holotype of *Pumiliopareia*), reaching a level in front of the posterior-most medial palatal denticles that flank the midline on the pterygoid (character 25:0).

The short transverse flange of the pterygoid is laterally directed, but oblique and not horizontal or flat, and extends less than half way to the cheek (jugal). Ten to eleven small denticles are arranged in a row on the posterior edge of each transverse flange (Figure 3, T4) (characters 26:1, 74:1). Laterally, the transverse flange curves and extends ventrally, with the margins of the posterolateral "wing" severely ventrally curved and extending downwards, but it does not reach the level of the maxillary tooth row or alveolar ridge (character 27:1).

Posteromedially, each pterygoid forms short cylindrical bars that have very strong oblique to transverse sutures with the basipterygoid process of the parabasisphenoid. Posterolaterally the quadrate ramus of the pterygoid extends laterally as a cylinder of bone to suture strongly with the quadrate (Figure 3). The quadrate ramus of the pterygoid has a deep excavation on its dorsal posterolateral surface, above which the pterygoid forms a large, flat, vertical flange of bone, sharing a long vertical, uneven suture with the quadrate flange (character 76:1) (Figures 2C, 3). The dorsal lamella of the pterygoid, dorsal to the quadrate ramus of the pterygoid, is similar to the condition in procolophonids (Figures 2C, 3). New preparation revealed an unidentified triangular wedge of bone, lateral to the dorsal lamella of the pterygoid, dorsal to the quadrate, which may be quadrate, squamosal or pterygoid, and which sutures with the squamosal (Figures 2C, 3, labelled as ?).

Ectopterygoid

The crescent-shaped ectopterygoid is the smallest bone of the horizontal palatal flange, and is wedged between the maxilla laterally, the palatine anteromedially and the pterygoid posteromedially. An oblique anteromedial suture with the palatine, passes through the foramen palatinum posterius. The ectopterygoid is generally flat and has a transverse lateral process that narrows to a pointed tip along the contact with the maxilla, behind the last maxillary tooth. The ectopterygoid reaches neither the quadratojugal nor jugal.

Quadrate

The quadrate is a wall-like, vertical flange of flat bone. It wedges between the lateral squamosal and quadratojugal flanges (with which is shares a long vertical suture) and the medial pterygoid (with which it shares a shorter, curved suture). The large quadrate foramen has now been exposed through preparation, and is positioned at the junction of the quadrate, squamosal and quadratojugal (Figure 3, qf), as in all known pareiasaurs, although it appears to be positioned higher on the quadratojugal than in most pareiasaurs (Figure 2C, qf)

Ventrally the jaw articulation of the quadrate comprises two transversely expanded condyles, better preserved on the left (Figures 2C, 3). Each medial condyle is larger (transversely more expanded) rounder and more convex than each lateral condyle (Figure 3). This articulation for the lower jaw is positioned far anterior of the occipital plane (character 59:0).

Braincase and occiput

General comments

The braincase and occiput of *Nanoparia* have been extensively prepared and much to our chagrin, revealed that only ventral portions of the braincase are preserved: parts of the parabasisphenoid and basioccipital (occipital condyle), a very small wedge of the right anterior prootic, and the distal-most extremes of both paroccipital processes of the opisthotics sutured to the internal skull roof. The exoccipitals, supraoccipital and almost the entirety of the prootics and opisthotics are not preserved (characters 4:?, 5:?). We surmise that the dorsal half of the braincase was probably cartilaginous and has therefore not been preserved in this juvenile individual. The region below the pineal foramen, and the ventral surfaces of the frontals and parietals remain obscured by matrix as it is inaccessible for further preparation. It remains unknown whether the sphenethmoid (pleurosphenoid) is preserved (character 2:?).

Parabasisphenoid

Most of the parabasisphenoid is preserved, but dorsally, the floor of the braincase (cavum cranii) is not exposed (character 9:?). Anteriorly, the two basipterygoid processes of the parabasisphenoid form the posterior border of the interpterygoid vacuity, where they have very robust and

immobile, transverse to oblique, interdigitating sutures with the pterygoids (character 1:1). Posteriorly, the sutures with the basioccipital are present as matrix-filled interdigitating lines that ring the posterior edge of the ventral and lateral surfaces of each basal tubera (Figure 3). Dorsally, the right parabasisphenoid shows a long horizontal suture, anteriorly with a small section of the prootic (not figured).

Despite being obscured in matrix prior to this project, the cultriform process of the holotype of *Nanoparia* was coded as present, short and with a blunt anterior tip (characters 10, 11 and 12 respectively). We have now exposed the midline cultriform process for the first time in *Nanoparia*, as a result of preparation into the interpterygoid vacuity (character 10:1), which shows it is short (character 11:1). The anterior tip of the cultriform process, however, remains obscured with matrix and is inaccessible for preparation, and we could not confirm its shape (character 12:?), which we have updated to unknown (?).

Two elongated, slightly eroded, basal tubera are present on the posteroventral extremity of the parabasisphenoid, immediately anterior to the jagged contacts with the basioccipital (character 16:1). As in *Pumiliopareia*, these tubera are very slightly mediolaterally wider than the narrowest part (the "waist") of the parabasisphenoid or basipterygoid processes, the "waist" itself being relatively wide compared to other pareiasaurs and not strongly laterally constricted (Figure 3) (character 13:1). The ventral surface of the parabasisphenoid at the midline between the basal tubera, has a deep midline depression or groove that widens as it extends anteriorly into the interpterygoid vacuity. The ventral surface of each of the basipterygoid processes, anterior to the basal tubera, is smooth and lacks tubercles (character 14:0).

The basal tubera are positioned approximately midway, between the occipital condyle and the narrowest part or "waist" of the basipterygoid process (character 17:1) as in the holotype of *Pumiliopareia* (BP/1/81) and in contrast to the more primitive condition of the three genera of middle Permian pareiasaurs, where the tubera are positioned more posteriorly (Van den Brandt *et al*., 2020, 2021b, 2022) and *Bunostegos* (Tsuji *et al*., 2013). The midline interpterygoid vacuity between the pterygoid and the parabasisphenoid is narrow and anteroposteriorly relatively long (17 mm) but is less than 15% of the length of the skull, which is 152 mm long (character 24:1).

Basioccipital

Most of the basioccipital is preserved and is strongly fused with the parabasisphenoid anteriorly. Posteriorly, the basioccipital forms most (ventral portion) of the occipital condyle, and the dorsal portion of the condyle (presumably the exoccipital) is not preserved. A central median tubercle or boss is absent from the ventral surface of the basioccipital (character 15:0).

Prootic

A very small section of the right anterior prootic is preserved, dorsal to the horizontal suture with the basioccipital, but we cannot confirm the presence of the fenestra ovalis (character 3:?).

Opisthotic

Only very small portions of the extreme distal ends of the paroccipital processes of the opisthotics are preserved (ossified) where they suture strongly against the internal cranial surfaces of the supratemporals and squamosals (characters 6:1, 7:?, 8:?).

Dentition

Upper marginal dentition

There are two teeth on each premaxilla of the holotype of *Nanoparia* (Figure 3, Pm1, Pm2), in agreement with the ventral cranial figure of Brink (1955: fig. 18) (character 141:2). Two premaxillary teeth are also present in *Provelosaurus* (Cisneros *et al*., 2021), *Anthodon* (RC 785), *Pumiliopareia* (BP/1/81), *Deltavjatia* (Tsuji, 2010, 2013), *Pareiasuchus peringueyi* and *Pareiasuchus nasicornis* and possibly also in *Bunostegos* (see Supplementary material, Appendix 1, Data Matrix) whereas three or more premaxillary teeth are present in *Bradysaurus*, *Embrithosaurus*, *Nochelesaurus*, *Scutosaurus*, and possibly in *Elginia mirabilis* and *Bunostegos* (see Supplementary material, Appendix 1, Data Matrix).

Broom (1936: 351) reported 10–11 maxillary teeth with "numerous" cusps, and briefly described several rows of palatal teeth on the prevomer (vomer), palatine and pterygoid of *Nanoparia*. The upper right marginal teeth are all sheared-off at the base of their crown, but the left maxilla preserves 10 teeth (Mx1-Mx10). Therefore, there are 12 upper marginal teeth in total on the left (Figure 3) (character 68:1). The preserved bases of the crowns of the last few distal-most positioned marginal teeth of *Nanoparia* appear to flare out rapidly mesiodistally (Figures 3, 4B, Mx7-Mx10), so these distal-most maxillary teeth were possibly similar to the very wide crowns of *Anthodon*, but most teeth of *Nanoparia* are moderately labio-lingually flattened (Figures 3, 4B, Pm1-Mx7) (character 65:1), varying from oval in cross section to thinner and flatter, but not as labio-lingually flattened or highly compressed as the extreme condition in *Anthodon* and *Pumiliopareia* (character 65:2).

The height (length) of the tooth crowns cannot be assessed (character 140:?). The maxillary teeth are vertically oriented (character 67:0). Tooth crowns are not preserved and therefore the cusp arrangement pattern on the margins of the crowns and whether they were regularly positioned or not relative to each other (character 66:?) and the numbers of cusps per tooth (character 69:?) cannot be determined. New preparation of the lingual surfaces shows that there are no cingula present on the preserved crowns (characters 72:0, 73:?). There is no caniniform region on the skull (character 78:1). The broken bases of the maxillary teeth show the teeth at an oblique angle to the tooth row, suggesting overlapping tooth crowns if preserved.

Provelosaurus (Cisneros *et al*., 2021) bears two premaxillary and 13 maxillary teeth (total of 15 marginal teeth), and relatively few (7–9) marginal cusps. The numbers

and morphology of the upper and lower marginal teeth of *Pumiliopareia* are not accurately determinable from the holotype due to a tightly occluded lower and upper jaws and will be the subject of a future study. The severely damaged holotype of *Anthodon* preserves only five partial upper left teeth and three upper right, but a specimen of *Anthodon* (RC 785), bears 13 upper right teeth, (*i.e*., 10 upper left teeth preserved and three large gaps between teeth suggesting that 13 were probably present in life). The *Pareiasaurus serridens* holotype skull cast preserves teeth and space for 15 estimated teeth on the upper right and 12 estimated teeth on the upper left, and specimen RC 28 has space for 14 upper teeth on each side (with 13 right and 12 left actually preserved). The holotype of *Pareiasuchus nasicornis* bears at least 12 upper teeth per side, and for the holotype of *Pareiasuchus peringueyi* we estimate 14 per side. The number of upper marginal teeth per side (12–15) in these Lopingian South African pareiasaurs is significantly fewer than that of Bradysauria (*Bradysaurus*: 20 teeth, *Embrithosaurus* 18 teeth, and *Nochelesaurus* 18 teeth, character 68).

Lower marginal dentition

The lower jaw and lower teeth are not preserved (characters 70:?,71:?). However, there appears to be partial mandibular tooth crown preserved ex situ in matrix, at the inner left jugal-quadratojugal suture (Figure 3).

Palatal dentition

As mentioned in the description of the palate, the remnants of small palatal teeth (denticles) are present on the vomers, palatines, and pterygoids (Figure 3, T1–T4). These denticles are mapped into four regions or pavements, which are labelled T1–T4. The denticles of T1 form the rostral-most pavement, with elements arranged in a single row. The left contains ~11 denticles, with the first five decreasing in diameter caudally, whereas the six distal elements increase in diameter caudally. The right T1 preserves ~six denticles, which correspond to the five larger elements of the left T1. The smaller denticles of the right T1 were likely destroyed during previous preparation of the specimen or are still preserved but obscured by matrix. The largest pavements (T2) each consist of more than 30 elements, roughly arranged in three parallel rows extending from the vomer to the pterygoid. Pavement T3 extends from the palatine onto the pterygoid and contains two well-defined parallel rows of denticles that converge posteriorly and each T3 contains ~17 denticles. Finally, the 9–11 denticles situated along the margin of the transverse processes of the pterygoids are identified as T4.

DISCUSSION

Phylogenetic results

We conducted one phylogenetic analysis using TNT with all 142 characters unweighted (equally weighted). TNT found 705 most parsimonious trees (mpt) of length 284 (Retention Index RI = 0.764, Consistency Index CI = 0.588). The strict consensus (Figure 5A) in this analysis is better resolved than the strict consensus of Van den Brandt *et al*. (2022: fig. 4A) and is similar to the higher resolution of the majority consensus of Van den Brandt *et al*. (2022: fig. 4B). In our majority consensus (Figure 5B), Elginidae form a polytomy with *Sanchaunsaurus, Pareiasaurus* and *Scutosaurus*. *Parasaurus*, *Deltavjatia* and Pumiliopareiasauria and Therischia form another polytomy.

Synapomorphies

The clade formed by *Pumiliopareia* and *Anthodon* is united by four synapomorphies: character 62, angular, boss, form: low and rounded (also the condition in *Shihtienfenia*); character 65, teeth, labiolingual compression (anteroposteriorly expanded), labio-lingual compression very pronounced, giving the marginal teeth a fan shape (unambiguous); character 69, maxillary teeth, cusp number, more than 11 cusps (unambiguous); and character 138, osteoderm, position, osteoderms overlapping, articulated or sutured, forming a continuous layer on the dorsal surface of the body (unambiguous).

The clade formed by *Nanoparia* and *Provelosaurus* is united by one synapomorphy: character 21, skull roof, radiating ridges, dermal sculpturing in the form of relatively straight, regularly placed ridges radiating from the centre of dermal skull roof bones present (also the condition in *Scutosaurus*, *Bradysaurus*, *Embrithosaurus* and *Nochelesaurus*). Based on our cranial description, we rescored the condition in *Nanoparia* from radial ridges absent, to present.

The clade formed by all four members of Pumiliopareiasauria (*Nanoparia*, *Provelosaurus*, *Pumiliopareia* and *Anthodon*) are united by three synapomorphies: character 25, interpterygoid vacuity, anterior shape, V-shaped (unambiguous, unknown in *Provelosaurus*); character 72, marginal teeth, lingual surface, horizontal cingulum: absent (also the condition in *Pareiasuchus peringueyi*, *Pareiasuchus nasicornis*, *Bradysaurus* and *Embrithosaurus*, unknown in *Pumiliopareia)*; and character 110, ilium, blade, expansion, not or only slightly anteriorly (unambiguous, unknown in *Pumiliopareia* and *Nanoparia*).

Nanoparia holotype as a juvenile

The most extensive works on pareiasaur ontogeny were undertaken by Tsuji (2010, 2013) in her description of several *Deltavjatia* specimens of multiple size classes (inferred ontogenetic stages), and Spencer and Lee (2000) in their description of a very small partial skull and skeleton of *Elginia mirabilis*.

Qualitatively, Tsuji (2013) found dramatic ontogenetic size and shape changes in the angular boss of the lower jaw (changing from a low lump to a long horn), dermal sculpturing becoming more ornate/rugose/developed in larger/older individuals, including larger and more prominent bosses on the dorsal skull roof elements and posterior and ventral cheek flange surfaces (this positive allometry was also demonstrated in *Elginia mirabilis* (Spencer & Lee, 2000) and asserted by Brink (1955) for pareiasaurs in general). Increased ossification of cranial elements (especially the connection of the braincase to the palate and individual braincase elements to each other), and increased ossification between neighbouring skull roof

cranial elements was also qualitatively observed by Tsuji (2013). Quantitative cranial geometric morphometrics by Tsuji (2013) found with size increases, increases in the length of the snout, the length of the postorbital region of the skull, and the length of the anterior embayment of the posterior skull table; and decreases in the posterior extent (size) of the orbit, and the width of the posterior skull (*i.e*., tabular), the length (size) of the parietal foramen, and the size of the median postparietal.

On the holotype skull of *Nanoparia* we note the following seven factors that support our interpretation of a juvenile ontogenetic state for the individual:

1) Small size of the cranium (length of 152 mm), smaller than all South African pareiasaur skulls, apart from two specimens of *Pumiliopareia* (BP/1/81, GSP CM86/544).

2) Cranial sutures are unossified, open and easily identifiable, and appear as wide interdigitating, matrix-filled cavities.

3) Short snout.

4) Very shallow (undeveloped) medial embayment of the posterior skull table.

5) Unpreserved (unossified) dorsal braincase elements (supraoccipital, prootics, exoccipitals, and most of the opisthotics), indicating they were probably cartilaginous in life. Only the ventral braincase elements are preserved and are ossified (parabasisphenoid, basioccipital). The smaller holotype skull of *Pumiliopareia* (BP/1/81, length of 100 mm) also has an unossified dorsal braincase, resembling the condition in *Nanoparia*, but with even less of the braincase ossified, likely indicating an earlier ontogenetic state than *Nanoparia*. These unossified braincases alone indicate that the holotypic skulls of *Nanoparia* and *Pumiliopareia* are almost certainly juvenile specimens.

6) The irregular complex of small and distinct globular (separate) nasal tubercles of *Nanoparia* supports our interpretation of the juvenile state of the skull, and we expect these numerous tubercles to likely have grown allometrically and merged to form a single larger nasal boss during ontogenetic development. Tsuji (2013: 29) noted increased positive allometry of the nasal bosses on *Deltavjatia* and Spencer & Lee (2000:1194) marked positive allometry in *Elginia* and many other taxa.

7) The relatively few upper marginal teeth (12) compared to the larger number of teeth in co-occurring, larger pareiasaur species (approximately 14 in *Pareiasuchus nasicornis* and *Pareiasuchus peringueyi*, and 15 in *Pareiasaurus serridens* (Lee 1994, 1997a)).

Based on cranial features alone, Tsuji (2013) speculated that the South African "dwarf" pareiasaurs (*Nanoparia*, *Pumiliopareia* and *Anthodon*) might be based on juvenile specimens. Based on preliminary new data using features of osteoderms for species-level systematics, Boyarinova *et al*. (2023) have identified large specimens of *Pumiliopareia* (unpublished SAM-PK-K10498 "Gordon", and possibly BP/1/548) and *Anthodon* (SAM-PK-10074), suggesting that the holotypes of these two taxa, which are small individuals, may represent juveniles. *Pumiliopareia* and *Anthodon* will be the subject of future studies. Applying the size classes defined by Van den Brandt *et al*. (2023), SAM-PK-K10498 and SAM-PK-10074 are classified as moderately sized pareiasaurs, 1–2 m long, and not as small pareiasaurs, <1 m long.

We consider that there is strong evidence for the juvenile status of the holotype of *Nanoparia*, however, its species validity must be retained based on several identified autapomorphies.

Element "B" as a valid cranial element or an incorporated nuchal osteoderm

Focusing his description on the posterodorsal cranial elements, Broom (1936) found two unexpected additional paired elements which had not been described on any pareiasaur up to that time. He labelled "A" a roughly triangular supernumerary wedge of bone between the median postparietal and the large central boss dominated supratemporals (tabular) (Broom, 1936: fig.1), and "B" a small bone between the squamosal and the supratemporal (tabular) (Broom, 1936: fig.1). Broom speculated that these bones might not be cranial elements, but rather "supernumerary dermal ossifications" (Broom, 1936: 350) similar to the row of numerous ossifications found on the posterior margins of skulls of the dinosaur *Triceratops* and the placodont *Placochelys.* Broom (1936) also speculated that *Nanoparia* was probably covered in a well-developed carapace of osteoderms as in the closely allied *Anthodon*, and that the two additional cranial bones may be fused nuchal (neck shield) osteoderms and not integral cranial elements.

The small, paired triangular bones between the median postparietal and the posterolateral supratemporals (Broom's element "A") were later also found to be present in other pareiasaurs as well, and termed "supernumerary bone" (*e.g*., *Pareiasuchus nasicornis*, Lee *et al*., 1997; *Elginia mirabilis* Spencer & Lee, 2000; *Bunostegos akokanensis*, Sidor *et al*., 2003; *Arganaceras vacanti*, Jalil & Janvier, 2005). However, Tsuji (2006) showed this element to be homologous to the tabulars of parareptiles. We therefore adopt the interpretations of Tsuji (2006, 2010, 2013), Tsuji *et al*. (2013), Liu & Bever (2018), and Cisneros *et al*. (2021) for this supernumerary element as the tabular. This element is not present in the three genera of Bradysauria.

Lee (1994, 1997a) and Tsuji (2013: appendix 3, Autapomorphies per species) retained Broom's additional element "B", between the squamosal and supratemporal as an autapomorphy of *Nanoparia*. We have not positively identified a bone of this size and shape in this position on any other pareiasaur skull. Anteriorly, it is deeply and strongly integrated into the skull roof, but posteriorly (in occipital view, Figures 2C, 4D), it is clearly lying "on top" of the lateral surface of the right squamosal, indicated by a thin layer of dark matrix between the two bones. The bone is missing or not preserved on the left, which if present would confirm its validity as a contralateral element.

Due to the presence of the robust anterior suture with the squamosal, we interpret this element as a valid separate cranial dermal ossification, not as a displaced osteoderm from the

neck region. The shape of this element is not consistent with an osteoderm. Neck shield osteoderms (*e.g.*, *Pareiasaurus serridens*, SAM-PK-K10036) are round, square, rectangular, pentagonal, or hexagonal in shape, and symmetrical, whereas "Element B" is crescent shaped (posteriorly convex) and irregular (non-symmetrical). It is important to note that this element, which appears as an extra boss on the posterior skull, must not be confused with the large boss on the posterior squamosal (cheek flange) which is present in all known pareiasaurs. The boss on the posterior squamosal is always positioned low on the posterior margin of the squamosal, below the thin occipital flange, immediately above the suture with the quadratojugal. Element "B" is, in contrast, positioned high on the posterior squamosal margin, on the thin occipital flange, at the horizontal level of the prominent lateral squamosal ridges.

Reconstructed cheeks

We have reconstructed (Figures 1A–B, 2, 3) and scored a large cheek flange for *Nanoparia* (character 44:2), distinct pointed and large posterior cheek bosses on the quadratojugal (character 50:2), small ventral marginal cheek bosses (character 48:?), and an arc of small lateral cheek flange bosses (not a phylogentic character).

Cheek flange size

Despite most of the quadratojugals not being preserved, factors taken together strongly suggest a large cheek (> 41°, Figure 1B) was almost certainly present in *Nanoparia*.

1) All known pareiasaurs have large cheeks (character 44:2) defined as the bone sweeping out 41° or more below the maxillary tooth row, apart from *Bradysaurus*, *Nochelesaurus*, *Elginia mirabilis* and *Elginia wuyongae* which all have smaller cheek flanges extending 40° or less (character 44:1). *Pareiasaurus serridens* (holotype NHMUK PV R 4063, skull cast R1710a) has the largest cheek flanges we have observed in any pareiasaur, extending approximately 70° on the right and 80° on the left side, below the maxillary tooth row. *Pareiasaurus* specimen (SAM-PK-K10036) also has very large cheek flanges of approximately 70° on either side. Small cheeks are always the result of small jugals and small quadratojugals. Small jugals, defined as those that do not extend below the level of the maxillary tooth row, are found only in the three members of Bradysauria, and in the two species of *Elginia*, which correspondingly all have small cheeks (apart from some specimens of *Embrithosaurus*). Large jugals that extend well below the level of the maxillary tooth row are found in at least *Bunostegos*, *Provelosaurus*, *Scutosaurus*, *Pareiasuchus nasicornis*, *Pareiasuchus peringueyi*, and *Pareiasaurus serridens*, and are always present with corresponding large quadratojugals, together creating large cheek flanges. The jugals of *Nanoparia* are very large, extending well below the level of the maxillary tooth row, as in the large cheeked *Bunostegos* (Tsuji *et al*., 2013), *Pareiasuchus nasicornis* (Lee *et al*., 1997), and *Provelosaurus* (Cisneros *et al*., 2021), which strongly suggests that the quadratojugals of *Nanoparia* were also large.

2) The anterior-most portion of the ventral edge of the quadratojugal is always shallow (horizontal) when small cheeks are present and steeper (vertical) when large cheeks are present. The small preserved anterior section of the ventral quadratojugal margin of *Nanoparia* is oriented very steeply, almost vertically, suggesting a very large cheek flange was present (Figure 1B).

3) The large jugal, tall squamosal, and small dorsal portion of the quadratojugal that is preserved, alone form a relatively sizable cheek flange, extending approximately 10° degrees below the maxillary tooth row, despite that fact that most of the quadratojugals are not preserved. This strongly suggests that the complete quadratojugal and cheek flange must have been very large.

4) All known pareiasaurs possess three to four bosses on the posterior or posteroventral margin of the quadratojugal. Since only a part of the dorsal-most posterior marginal boss of the quadratojugal of *Nanoparia* is preserved, the complete quadratojugal including all three to four bosses must necessarily have been very large, certainly extending the cheek flange more than 41° (character 44:2) below the level of the maxillary tooth row. We accordingly feel comfortable to phylogenetically score and to reconstruct a large cheek for *Nanoparia*.

Cheek flange bosses, posterior margin

The three to four bosses on the posterior or posteroventral quadratojugal of pareiasaurs generally follows one of two arrangement patterns (Van den Brandt *et al*., 2020), as is evident in *Bradysaurus, Embrithosaurus, Nochelesaurus*, *Pumiliopareia*, *Provelosaurus, Pareiasuchus nasicornis, Pareiasuchus peringueyi,* and *Obirkovia*. A large dorsal-most posterolaterally directed boss is present (and may comprise two smaller, almost coalesced bosses), followed by either one (1st arrangement type) or two (2nd arrangement type) smaller bosses ventrally and more posteriorly directed, and these are followed by a large corner boss which is posterolaterally directed. Usually, one of these two patterns are symmetrically present on an individual skull, however, one specimen of *Bradysaurus baini* (SAM-PK-5624) manifests both arrangement patterns, that is, a different arrangement pattern on each cheek! We have reconstructed the posterior boss arrangement pattern on the quadratojugal of *Nanoparia* (Figure 1B), as being similar to the pattern of two of its closest phylogenetic cousins: *Pumiliopareia* and *Provelosaurus* (Figure 1C–D). These have two dorsal-most posterior cheek bosses close together, almost coalesced, and followed ventrally by two long, pointed bosses of roughly the same size at the cheek corner. We have also reconstructed an arc of three small bosses or tubercles on the lower portion of the lateral quadratojugal, as is typical of most pareiasaur species.

The preserved posterior cheek flange boss on the squamosal of *Nanoparia* is large and distinct, and the morphology of this boss is usually similar to the posterior quadratojugal of the same individual in other pareiasaur species. This strongly suggests that a similar morphology of distinct bosses was present on the unpreserved posterior quadratojugal of *Nanoparia*.

The large posterior cheek boss on the squamosal (character 50:2), large and distinct orbital rim bosses (character 37:1), presence of a frontal central boss (character 57:1) and the general cranial ornamentation style of large and distinct central bosses on most cranial elements, indicate a relatively heavy ornamentation style for the skull and suggest that the posterior cheek bosses of *Nanoparia* were large and distinct.

Interestingly, the posterior cheek flange boss arrangement pattern and sizes in *Pareiasaurus serridens* may be autapomorphic, and this requires further research to confirm as the posteroventral corner boss is not the largest (which is the case in most pareiasaurs) and the largest boss is on the ventral surface of the cheek, anterior to the posteroventral corner boss (*e.g*., NHMUK PV R 4063, SAM-PK-K10036, RC 28).

Cheek flange bosses, ventral margin

The ventral margin of the cheek flange (quadratojugal) is not preserved and so we cannot confirm the presence of ventral cheek bosses in *Nanoparia* (character 48:?). But *Nanoparia* most likely did possess ventral cheek bosses as in all known pareiasaurs apart from the three members of Bradysauria, *Provelosaurus*, and the enigmatic *Parasaurus*. Accordingly, we have reconstructed *Nanoparia* (Figures 1B, 2A) with the most commonly observed Pareiasaurian arrangement of two small ventral cheek bosses immediately anterior to the corner boss (present in *Pumiliopareia* but not in *Provelosaurus*).

Our reconstructed large cheek, posterior cheek boss sizes and arrangement pattern, ventral marginal cheek bosses, and even the arc of lateral cheek bosses, will hopefully be confirmed or corrected when additional specimens of *Nanoparia* are discovered as a result of future studies of existing collections or new collecting efforts.

CONCLUSION

We present the first detailed cranial description and analysis of *Nanoparia luckhoffi*, enabled through new preparation of the holotype skull, and we find this taxon to be valid based on seven autapomorphies: (1) additional bone on the posterior margin of the cheek flange between the squamosal and quadratojugal; (2) pyramidal-shaped parietal; 3) very short, square lacrimal; (4) paired prepalatal foramina positioned anterolaterally on the internal premaxillary palatal flange; (5) notch on anteromedial border of the choana; (6) ventral flange along the lateral margin of the internal tabulars; and (7) tabulars that extend posteriorly further than the supratemporals.

We provide evidence that strongly supports a juvenile ontogenetic state of development for the single specimen of *Nanoparia*, most notably the small size of the skull, the easily identifiable open cranial sutures, unossified dorsal braincase, short snout, and fewer marginal teeth than most pareiasaurs. We do not believe that this individual represents the juvenile state of a larger pareiasaur species from the same stratigraphic interval (*e.g*., *Pareiasaurus serridens, Pareiasuchus nasicornis,* or *Pareiasuchus peringueyi*) and we consider *Nanoparia* valid due to the described autapomorphies that allow clear distinction of the species.

We combined and consolidated the two latest pareiasaurian phylogenetic data matrices and character lists (Cisneros *et al*., 2021, 142 characters; and Van den Brandt *et al*., 2022, 139 characters), which confirmed *Nanoparia luckhoffi* as the sister taxon of *Provelosaurus americanus* from Brazil. We reconstructed the skull and the missing cheek flanges of *Nanoparia luckhoffi* with a large cheek flange, with bosses on the posterior and ventral margins, and justified our reconstruction based on features known in all pareiasaurs and alignment with the closest pareiasaur sister taxa to *Nanoparia luckhoffi* (*Pumiliopareia pricei* and *Provelosaurus americanus*).

Provelosaurus americanus was recently extensively researched (Cisneros *et al*., 2021) and we here provide new information for *Nanoparia luckhoffi*. Further study is needed to update our knowledge of the remaining members of Pumiliopareiasauria: *Anthodon serrarius* and *Pumiliopareia pricei*, and other South African late Permian pareiasaurs, especially the historically significant and bio-stratigraphically long-lived and abundant *Pareiasaurus serridens* for which modern detailed descriptions do not exist. Preliminary new research on the use of osteodermal morphology for systematics suggest that relatively large specimens of the "dwarf" species *Anthodon serrarius* and *Pumiliopareia pricei* exist, and this is the subject of future research. New analyses of historic holotypes, newly discovered currently unpublished specimens, and the use of computed micro-tomography (CT) scans of skulls and osteoderms, are being employed to enhance our understanding of this group of pareiasaurs.

ACKNOWLEDGEMENTS

For additional preparation over several months of the holotype skull of *Nanoparia*, we are indebted to J. Arnols. For access to collections, we thank the Rubidge family, Rubidge Collection, Wellwood; M. Day, Natural History Museum, London; C. Browning and Z. Skosan, Iziko South African Museum, Cape Town; and B. Zipfel and S. Jirah, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg. We thank the editor of the journal and two anonymous reviewers for their diligent feedback on the text and for very useful recommendations which have improved the layout of the figures.

The support of GENUS (DSI-NRF Centre of Excellence in Palaeosciences, UID 86073) and the Millenium Trust towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the authors and are not necessarily to be attributed to the funders. F. Abdala's research is financed by the NRF of South Africa and CONICET from Argentina. The work of E.I. Boyarinova and V.K. Golubev was funded by the subsidy allocated to Kazan Federal University for the state assignment project № FZSM-2023-0023 in the sphere of scientific activities.

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Supplementary material

S1 – Data Matrix used in the phylogenetic analysis.

S2 – Character List used in the phylogenetic analysis.

Received in 08 July, 2023; accepted in 27 November, 2023.