



UNIVERSITY OF THE
WITWATERSRAND,
JOHANNESBURG

**THE TAXONOMY AND PHYLOGENY OF VARANOPIDAE FROM THE MIDDLE
PERMIAN OF SOUTH AFRICA.**

By

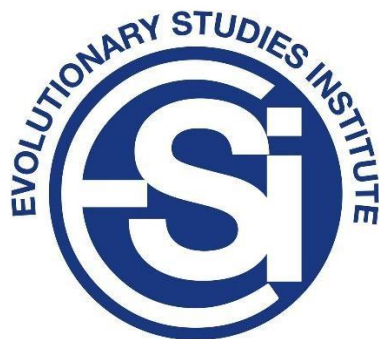
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Abstract

Varanopidae are the only pelycosaur-grade tetrapods from the Abrahamskraal Formation of the Beaufort Group. Although four varanopid species are described from the middle Permian of South Africa (SA), their validity has been questionable. Moreover, Ford and Benson recently proposed that varanopids belong to the Diapsida rather than Synapsida. Given this taxonomic and phylogenetic turmoil, this study i) describes two newly discovered and well-preserved varanopid specimens from the middle Permian of SA using CT scanning and ii) re-assesses the validity of the four species from the Karoo Basin in the light of new data from these specimens. The phylogeny of the group is addressed by updating two pre-existing cladistics matrices. The two new specimens exhibit a mosaic of features that overlap the diagnoses of several species of SA varanopids. In addition, some diagnostic traits of the four SA varanopid genera and species are found to be variable across ontogeny. For instance, dorsal osteoderms and the extent of ornamentation on the angular bone co-vary with size. It is therefore proposed that all varanopid specimens currently described from the middle Permian of South Africa belong to a single valid species, *Heleosaurus scholtzi*, with differences between specimens being accounted for by ontogenetic changes. The phylogenetic analysis supports Ford and Benson's hypothesis but contra the prediction of this hypothesis, no differences in cranial fenestration during ontogeny are observed. Morphological characters preserved in the manus of the newly discovered specimen BP/1/8499 suggest that *Heleosaurus* was arboreal.

1. INTRODUCTION

1.1 General Introduction

The South African fossil record of non-mammalian synapsids extends over a period of more than 70 million years from the middle Permian to the Early Jurassic (Botha-Brink & Modesto, 2009; Romer & Parsons, 1985). Synapsida are divided into three paraphyletic grades, the Pelycosauria, Therapsida and Cynodontia (Modesto et al, 2011; Carroll, 1988). The “Pelycosauria” is a paraphyletic grouping of basal synapsids which existed from the Late Carboniferous to the middle Permian (Modesto et al, 2011; Carroll, 1988; Romer & Price, 1940) and include the Varanopidae, Ophiacodontidae, Edaphosauridae, Sphenacodontidae, and Caseasauria (Modesto et al, 2011). The Varanopidae were among the earliest basal synapsid

clades to diverge from basal amniotes and are also the clade to have survived the longest from the Late Carboniferous to the middle Permian. In addition, they were also the most widely dispersed geographically, with localities spanning North America, Europe, Asia, and Africa (Bazzana et al, 2021; Campione & Reisz, 2010; Reisz & Dilkes, 2003; Reisz & Modesto, 2007).

Only four pelycosaur-grade species have been described from the South African Karoo Basin, all of them are currently considered to be varanopids (Spindler et al, 2018); *Heleosaurus scholtzi*, *Elliotsmithia longiceps*, *Microvaranops parentis* and *Anningia megalops* (Spindler et al, 2018; Reisz & Modesto, 2007; Botha-Brink & Modesto, 2009). Spindler et al. (2018) considers all South African species to belong to the Mesenosaurinae and form a subclade, the Afrothyra.

1.2 Taxonomic history

The first described species, *Heleosaurus scholtzi*, was introduced by Broom (1907) (**Table 1**), who provided a brief description and considered it to be an early diapsid reptile. Subsequently, Carroll (1976) described it as a younginid. Reisz and Modesto (2007) reassessed the holotype and only specimen of *Heleosaurus scholtzi* and considered it a varanopid synapsid. However, prior to this recent classification, *Heleosaurus* was thought to belong to stem diapsids by Benton (1985) and Currie (1982) who classified it as a younginid. *Elliotsmithia longiceps* was named by Broom (1937) and is considered similar to *Mycterosaurus*, a varanopid from the early Permian of America (Reisz et al, 1998). *Anningia* was initially described as a therapsid by Broom (1927) until Romer and Price (1940) noted the proportions of the cranium to resemble those of varanopids. The most recently named species is *Microvaranops parentis*, which was introduced by Spindler et al. (2018) based on specimen SAM-PK-K8305, which was initially described as *Heleosaurus scholtzi* by Botha-Brink & Modesto (2009).

Reisz and Modesto (2007) suggested that *Heleosaurus scholtzi* and *Elliotsmithia longiceps* are synonymous. Both genera share the presence of a concave and posteroventrally inclined occipital shelf of the occipital margin, as well as the presence of osteoderms along the vertebral column (Reisz & Modesto, 2007; Dilkes & Reisz, 1996). Botha-Brink & Modesto (2009) argued against the synonymy of *Heleosaurus scholtzi* and *Elliotsmithia longiceps*, as *Heleosaurus scholtzi*

possesses features that are not shared with *Elliotsmithia longiceps*. These include an opisthotic that is not fused to the braincase, the maxilla not reaching the quadratojugal and a tall neural spine axis (Botha-Brink & Modesto, 2009; Spindler et al, 2018). *Anningia megalops* was later considered a *nomen vanum* because of the poor state of preservation of the holotype and only the specimen which comprises an occiput that has been serially sectioned (Dilkes & Reisz, 1996; Spindler et al, 2018). From the above, it is evident that the taxonomy of the South African varanopids is uncertain. There may be up to four species of middle Permian varanopids from the South African Karoo, or only one. This can possibly be ascribed to ontogeny, as suggested in recent work done on basal therapsids (Duhamel et al, 2021).

Table 1. Species of South African varanopids.

Holotype	Genus	Species	Original Identification
SAM-PK-1070	Heleosaurus	<i>Heleosaurus scholtzi</i>	Broom, 1907
TM-1483	Elliotsmithia	<i>Elliotsmithia longiceps</i>	Broom, 1937
Transvaal Museum N. 4024	Anningia	<i>Anningia megalops</i>	Broom, 1927
SAM-PK-K8305	Microvaranops	<i>Microvaranops parentis</i>	Spindler et al, 2018

Recently, there has been discussion as to whether varanopids do indeed belong in Synapsida with Ford and Benson (2018 & 2020) hypothesising that they are actually diapsids. This hypothesis is supported by the shared presence of osteoderms, a long, narrow posterolateral process of the frontal, a narrow ventral temporal bar, an edentulous ectopterygoid, the absence of a supraglenoid foramen, a poorly developed trochlea and capitulum of the humerus, holocephalous ribs, and a low cnemial crest of the tibia (Ford & Benson, 2018 & 2020). Ford and Benson (2020) suggest an independent origin of the synapsid-like temporal fenestration in the Synapsida and Varanopidae.

There has been resistance to this hypothesis, as it completely changes the classification of amniotes based on cranial fenestration (Sues, 2019; Benoit et al, 2021, Bazzana et al, 2021). Benoit et al. (2021) studied the condition of the maxillary canal for the maxillary branch of the

trigeminal nerve in varanopids and noted its similarity to the synapsid condition. Bazzana et al. (2021) mentioned the significance of palaeoneurological information when discussing the placement of varanopids within amniotes. Synapsida has a highly ossified inner ear, which varanopids also possess, in contrast to the lack of ossification seen in sauropsid (Bazzan et al, 2021; Gardener et al. 2010). The most recent phylogenetic results by Simões et al. (2022), support the traditional hypothesis of varanopids belonging to Synapsida. It is thus apparent that the hypothesis that varanopids are diapsids requires scrutiny.

1.3 Importance of studying varanopids

Varanopids further provide the earliest evidence of parental care for amniotes (Botha-Brink & Modesto, 2009) based on a specimen from South Africa which comprises both adult and juvenile individuals. If varanopids are indeed diapsids, this would extend the evolution of parental care in reptiles by more than 200 million years as the earliest evidence of parental care in diapsids is currently from some Cretaceous non-avian dinosaurs (Maddin et al, 2020; Meng et al, 2004). Furthermore, removal of varanopids from Synapsida means the earliest evidence of parental care in the Synapsida would be much younger, from the Early Triassic (Jasinoski & Abdala, 2017). If varanopids are synapsids, they provide the earliest evidence of integumentary elements, demonstrating the presence of scales and osteoderms in synapsids (Spindler et al, 2018). Conversely, if varanopids are indeed diapsid, the presence of scales would be less remarkable.

Varanopids are of biogeographic significance as they are among the only pelycosaur-grade synapsids that lived alongside therapsids in the middle Permian of South Africa, along with Russian caseids (Dilkes & Reisz, 1996). Should it be determined that varanopids are no longer synapsids, it means that there are no known “pelycosaurs” that lived alongside therapsids in Africa (Ford & Benson, 2020; Modesto et al, 2011).

1.4 Scientific Questions

- What is the position of varanopids within the phylogeny of amniotes, Synapsida or Diapsida?

- Are the four South African varanopid genera (*Heleosaurus*, *Elliotsmithia*, *Anningia* & *Microvaranops*) and species valid?
- Could the inflated number of South African varanopid genera be ascribed to ontogenetic differences?

To answer these questions, a re-study of all holotypes as well as the best-preserved specimens of *Heleosaurus*, *Elliotsmithia*, *Anningia* and *Microvaranops* from South Africa is here conducted. As most of the previously described specimens are not well preserved, it is important to describe newly discovered specimens from the Abrahamskraal Formation of the Beaufort Group which have recently been collected by staff and students at the University of the Witwatersrand. In addition, the application of computed tomography makes it possible to explore anatomical regions of these specimens that were previously inaccessible.

1.5 Aims and Objectives

Describing and comparing the anatomy of new varanopid fossils from the Karoo Supergroup will shed light on the taxonomy and phylogeny of the taxon. This will further provide information on how many varanopid species are present in middle Permian rocks of South Africa.

Objective 1: Describe the two new specimens (BP/1/8499 & CG-RMS353) of Varanopidae.

Objective 2: Rerun the updated phylogenetic analyses of Spindler et al (2018) and Ford & Benson (2020) for internal varanopid relationships, as well as the relationship of varanopids among amniotes.

Objective 3: Reassess the validity of the four described varanopid species from the Karoo Supergroup given the observations of the holotype and referred material.

Objective 4: Discuss the position of varanopids among amniotes.

2. METHODS AND MATERIAL

2.1 Material

The material used for this study (**Table 2** & **Table 3**) is curated in the collections of the Evolutionary Studies Institute, Ditsong Museum, Iziko South African Museum of Natural History and the Council for Geoscience. These specimens are all from the *Tapinocephalus* Assemblage Zone of the Abrahamskraal Formation of the Beaufort Group. Four recently discovered varanopid specimens from the Karoo (BP/1/8535, BP/1/6881, BP/1/7395 and BP/1/5678) were not included as they did not produce good contrast of CT-scans and were thus not useful for this study. Specimen BP/1/5678 was described as *Elliotsmithia* by Modesto et al. (2001).

Table 2. List of specimens in South African museums which were used for morphological comparison with the newly discovered specimens.

Specimen	Type	Species	Institution
TM-1483	Holotype	<i>Elliotsmithia longiceps</i>	Ditsong Museum
Transvaal Museum N. 4024	Holotype	<i>Anningia megalops</i>	Ditsong Museum
SAM -PK-1070	Holotype	<i>Heleosaurus scholtzi</i>	Iziko Museum
SAM-PK-K8305	Holotype	<i>Microvaranops parentis</i>	Iziko Museum
SAM-PK-10407	-	? <i>Elliotsmithia</i>	Iziko Museum

Table 3. List of recently discovered specimens which were CT scanned and used in this study.

Specimens	Institution
CG-RMS353	Council for Geoscience
BP/1/8499	Evolutionary Studies Institute

2.2 Methods

2.2.1 Holotype visitation

Visits were undertaken to the Ditsong Museum in Pretoria to study the holotypes of *Elliotsmithia longiceps* (TM-1483) and *Anningia megalops* (TM. 4024), and Iziko South African Museum of Natural History in Cape Town to study the holotypes of *Heleosaurus scholtzi* (SAM -PK-1070) and *Microvaranops parentis* (SAM-PK-K8305). This was undertaken to compare previously described material with the new material to enable their taxonomic identification and assist when discussing the taxonomic validity of these genera and species.

2.2.2 Two newly described varanopid specimens:

Specimen CG-RMS353 - A skull that preserves the left lateral side with a partially preserved premaxilla, a maxilla, mandibular bones, articulated dentition, a fragment of a nasal, a lacrimal, prefrontal, sclerotic rings, a postorbital bone, a jugal, a quadratojugal and a fragment of a squamosal. The palate preserves a vomer with alveoli, an ectopterygoid, a pterygoid with a transverse process that bears teeth and parabasisphenoid.

Locality and Horizon - A locality on Botmasbad farm 288, Beaufort West District, Western Cape Province, South Africa. *Tapinocephalus* Assemblage Zone, Abrahamskraal Formation, Beaufort Group, Karoo Basin, Middle Permian.

Specimen BP/1/8499 - An almost complete skeleton with articulated left limbs, a vertebral column and a poorly preserved skull.

Locality and Horizon - A locality on the Stellenboschvlei (Diepleegte 146) farm, Murraysburg area, Central Karoo District Municipality, Western Cape, South Africa. Upper Abrahamskraal Formation, Beaufort Group, Karoo Basin, Middle Permian.

2.2.3 3D reconstruction

To enable descriptions of CG-RMS353 and BP/1/8499, mechanical preparation of specimens was undertaken at the Evolutionary Studies Institute (ESI) using air scribe equipment fitted

with tungsten-carbide tips. Specimens listed in **Table 3** were micro-CT scanned and 3D models were reconstructed using Avizo 9 (FEI VSG, Hillsborough, US).

2.2.4 CT Scan Parameters

Specimen BP/1/8499:

- Voxel size: 0.072mm
- Voltage: 110Kv
- Intensity: 180uA
- Exposure time: NA
- Average: NA
- Filter: NA

Specimen CG-RMS353:

- Voxel size: 0.0378mm
- Voltage: 70 kV
- Intensity: 80uA
- Exposure time: 1 fps
- Average: 2fa
- Filter: NA

2.2.5 Phylogenetic analyses

The phylogeny of varanopids was reconstructed using Paup* v4.0a and the application of maximum parsimony. The matrix was built using Mesquite version 3.81 (build 955). Two phylogenetic analyses are reconstructed: one to address the internal systematics of varanopids and another to address the phylogenetic position of varanopids across amniotes. They are based on updated scoring of the character matrices of Spindler et al. (2018) and Ford and Benson (2020) respectively. The character scoring was updated with new observations made during this project.

A Bayesian analysis was conducted using the Ford and Benson (2020) matrix. The analysis utilised the MKv model and included 294 morphological characters and 71 operational taxonomic units. *Microvaranops parentis* was added to the analysis, with *Gephyrostegus* and *Seymouria* used as the outgroups. The morphological data was analysed using a standard approach, focusing on variable characteristics and assuming a gamma distribution for the rates of evolution ($\alpha = 1$). Similar to Ford and Benson (2020), the MKv model was run twice with a temperature of 0.10. Each run sampled 50001 trees. The average effective sample size was 35040.61 for tree length and 35157.88 for the gamma distribution. The potential scale reduction factor was 1. The phylogenetic results are available in the appendix.

2.3 Abbreviations

2.3.1 Anatomical abbreviations-- **a**, angular; **af**, articular facet; **as**, astragalus; **ca**, calcaneum; **cau**, caudate; **ce**, centrum; **cl**, clavicle; **cv**, cervical vertebra; **eth**, cleithrum; **d**, dentary; **dv**, dorsal vertebra; **fe**, femur; **fi**, fibula; **h**, humerus; **il**, ilium; **is**, ischium; **j**, jugal; **qj**, quadratojugal; **m**, mandible; **ma**, manus; **mc**, medial centrale; **mx**, maxilla; **n**, nasal; **ns**, neural spine; **ne**, neural excavation; **l**, lacrimal; **lc**, lateral centrale; **pe**, pes; **pl**, palatine; **pmx**, premaxilla; **prf**, prefrontal; **pro**, prootic; **po**, postorbital; **poz**, postzygapophyses; **prz**, prezygapophyses; **pt**, pterygoid; **ptb**, pterygoid boss; **pbs**, parabasisphenoid; **pu**, pubis; **r**, radius; **rd**, radiale; **ri**, rib; **s**, skull; **sc**, scapula; **scl**, sclerotic rings; **sur**, surangular; **sq**, squamosal; **t**, tibia; **tp**, transverse process; **q**, quadrate; **v**, vomer.

2.3.2 Institutional abbreviations— **BP**, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg; **CG**, Council for Geosciences, Pretoria; **SAM**, Iziko South African Museum; **TM**, Ditsong Museum, Pretoria.

3. RESULTS

Two specimens, consisting of both cranial and postcranial elements, were discovered in the Abrahamskraal Formation. These specimens were previously undescribed and were subjected to micro-CT scanning for this study. The resulting scans were used to segment the individual bones, which are here described in detail.

3.1 SYSTEMATIC PALAEOLOGY

AMNIOTA

(unranked) SYNAPSIDA Osborn, 1903

Family VARANOPIDAE Romer & Price, 1940

Subfamily MYCTEROSAURINAE Reisz & Berman, 2001

Type species *HELEOSAURUS SCHOLTZI* Broom, 1907

3.2 Description and Comparison

3.2.1 Description of specimen CG-RMS-353.

Specimen CG-RMS353 is curated at the Council for Geoscience, Pretoria, and consists of a laterally compressed skull and lower jaw. When viewed from the left lateral side, most of the preserved bones including premaxilla, maxilla, jugal, quadratojugal, lacrimal, postorbital, and a portion of the squamosal and mandibular bones, can be seen. The length of the skull from the anterior part of the premaxilla to the most posterior part of the quadratojugal measures 52 mm. The skull roof preserves only the postorbital bone, while palatal bones such as the vomer, palatine, pterygoid, ectopterygoid, and parabasisphenoid are visible in both dorsal and ventral views. Most teeth on the left side are preserved, and they appear strongly recurved and oval to circular in transverse section (**Figure 1**). The teeth do not appear serrated, which is unexpected for a varanopid (Reisz & Modesto, 2007), but this may be due to weathering or damage during mechanical preparation. The orbit is significantly larger than the temporal fenestra, accounting for most of the posterior portion of the skull. The temporal fenestra, which is oblong and curves anteroventrally and is quite large, making up almost $\frac{3}{4}$ of the postorbital skull height as is in other varanopids (Reisz et al, 1998).

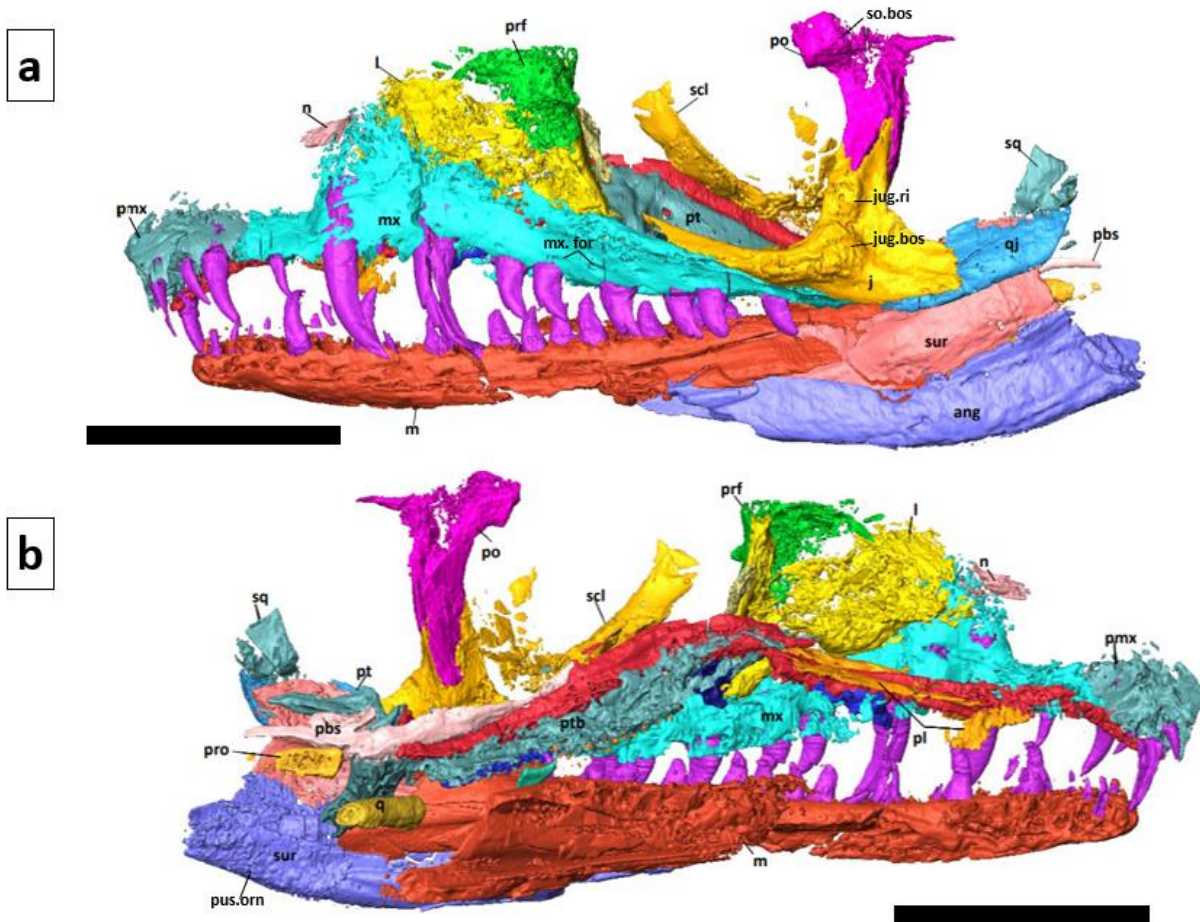


Figure 1. (a) Left and (b) right medial view of CG-RMS-353. **Abbreviations:** **jug.ri**, jugal ridge; **jug.bos**, jugal boss; **mx.for**, maxilla foramen; **so.bos**, supraorbital boss. Scale bar=15 mm.

Snout

The snout of CG-RMS353 is about 30 mm long from the most anterior surface of the orbit. The snout tip comprises the slender premaxillae at the anterior end of the skull which are 8 mm long and are separated from each other by a midline suture. The dorsal internarial process of the premaxilla is broken. Posteriorly, the premaxillary and maxillary suture slopes anteroventrally in lateral view (**Figure 1**). In contrast to the situation in *Mesenosaurus*, the premaxilla is rounded rather than rectangular at its anterior end in lateral view (Reisz and Berman, 2001). Three conical teeth are preserved on the left premaxilla and two poorly developed teeth are present on the right (**Figure 2**). The periodontal space of premaxillary teeth 1 and 2 is larger than the teeth, which suggests an early stage of tooth eruption (**Figure 2**).

The naris is present as an indentation on the anterodorsal side of the skull, but no septomaxilla is visible. In lateral view, the maxillary bone is broadly triangular, with the apex pointing

posteroventrally. Eight small foramina for the maxillary canal are aligned along its ventrolateral margin (**Figure 1a**). The maxilla makes a small contribution to the antero-ventral rim of the orbit, between the jugal and lacrimal. The tapering posterior ramus of the maxilla has a long dorsal sutural contact with the jugal and forms the ventral border of the skull (**Figure 1a**). As in *Elliotsmithia longiceps* (TM-1483), the maxilla has a short contact with the quadratojugal posteriorly, excluding the jugal from the ventral margin of the skull (**Figure 1**) (Reisz et al, 1998). The dorsal part of the maxilla on the skull roof is eroded such that it is not possible to determine its extent and sutural contacts. In ventral view, the maxilla makes up the lateral portion of the palate (**Figure 3**). It has a short contact with the anterolateral end of the vomer, posterior to the premaxilla (**Figure 3**). Medially, the maxilla has sutural contact with the palatine and further posteriorly meets the ectopterygoid.

The maxilla bears ten marginal teeth, with six empty alveoli a-b, e-f and f-g in alternating positions. The teeth are strongly recurved and do not have serrations. All the teeth are thecodont and subequal in height, apart from the two caniniforms on either side of the skull, which are slightly longer (**Figure 2a**). Three precaniniforms (1-3) are present on the premaxilla and one on the maxilla (4). They differ in size such that the most developed caniniform is the longest (**Figure 2a**). The postcaniniform teeth are relatively small and are only 1 mm long, similar to those of *Microvaranops* (Botha-Brink & Modesto, 2009). Although tooth replacement is seldom seen in varanopids, this specimen shows signs of it in different degrees (Norton, pers comm, February 14, 2024). Caniniform 5 is the longest and most developed based on the lack of space in the periodontal area of the tooth (**Figure 2b**). Tooth 6 is the least developed tooth with most periodontal space (**Figure 2b**). The empty sockets do not preserve any replacement teeth, thus suggesting that the teeth had not erupted (Edmund, 1960). Socket f (**Figure 2b**) shows a pattern

seen in most pelycosaurs where the old tooth leaves a remnant on the base of the alveoli (Edmund, 1960).

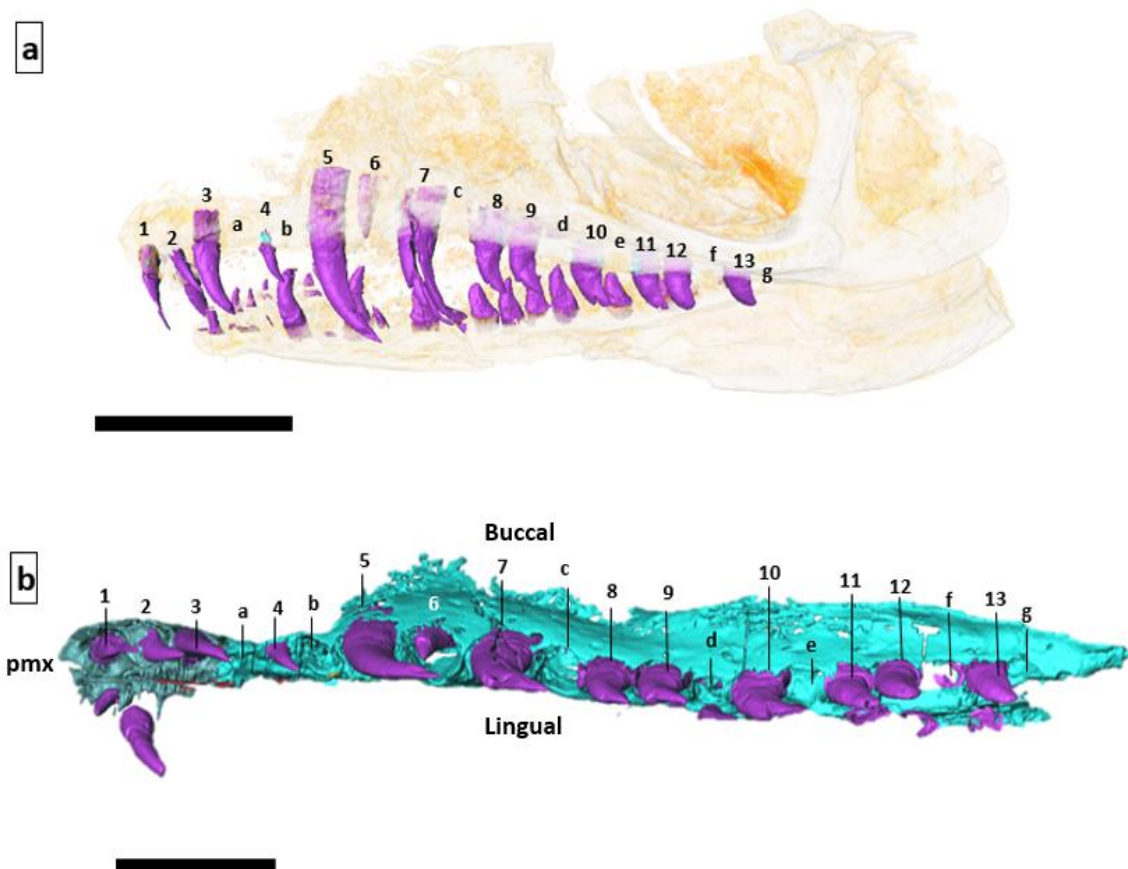


Figure 2. (a) Lateral view of the skull and lower jaw of CG-RMS353 and (b) ventral view of the maxilla of CG-RMS353 showing teeth development with caniniform 5 being the most developed and post-caniniform 6 being the least developed. **Abbreviations:** 1-13; present teeth, a-g; alveoli. (a) Scale bar = 15 mm and (b) scale bar = 10 mm.

Skull roof

The lacrimal is a relatively small bone, approximately a third the size of the maxilla but it appears larger than that described for *Elliotsmithia longiceps* (Figure 1a) (Reisz, 1998). In lateral view, the lacrimal is a thin anteroposteriorly elongated bone positioned between the prefrontal and maxilla. This prevents the maxilla from contacting the prefrontal, which is a primitive condition for pelycosaurs (Reisz et al, 1998; Modesto et al, 2001). The lacrimal contacts the prefrontal dorsally and maxilla ventrally and makes up the anteroventral margin of the orbit, similar to the condition in *Mesenosaurus* (Botha-Brink & Modesto, 2009; Reisz &

Berman, 2001). The lacrimal and nasal contact is not visible on this specimen as it is difficult to segment due to poor preservation. The suture between the lacrimal and prefrontal extends dorsolaterally. The lacrimal has a pinched process extending posteroventrally to contact the palatine. This posteroventral angle of the lacrimal is a shared character with *Elliotsmithia* (Modesto et al, 2001). The degree of anterior extension of the lacrimal is indeterminate, because it is very poorly preserved. The lacrimal and jugal contact is not visible. Ventrolaterally, the lacrimal bears a lamina with a conspicuous lacrimal foramen positioned within the orbit.

The skull roof preserves only a small remnant of the fragmentary prefrontal (**Figure 1a**) as the rest is weathered away. In both medial and lateral view, the prefrontal is positioned, dorsal to the lacrimal (**Figure 1**). It has a relatively long sloping ventral contact with the lacrimal and contributes to the antero-dorsal margin of the orbit (**Figure 1a**). The orbit contains some articulated fragments of the sclerotic ring that form an upturned crescent similar to that preserved in the *Elliotsmithia longiceps* (TM-1483) (Botha-Brink & Modesto, 2009) (**Figure 1**). As these sclerotic plates are very fragmentary, it is not possible to count them.

The postorbital makes up the dorsal half of the postorbital bar. It bears a prominent supraorbital boss on the posterodorsal aspect of the orbit, a typical feature of the Varanopidae (Reisz et al, 1998) (**Figure 1a**). The dorsal portion of the postorbital lacks the curvature observed in the lower Permian *Orovenator mayorum*, which has a free dorsal postorbital (Ford & Benson, 2018). This could imply absence of an upper temporal fenestra, as seen in other pelycosaur (Ford & Benson, 2020). In lateral view, the ventral ramus of the postorbital meets the dorsal extension of the jugal, two thirds up the postorbital bar, as in the holotype of *Microvaranops* and *Elliotsmithia* (Botha-Brink & Modesto, 2009; Reisz et al, 1998). In medial view, the ventral ramus of the postorbital extends over the entire postorbital bar. Posterodorsally, a short projection of the postorbital, separated from the rest of the postorbital by a crack, contributes to the dorsal margin of the temporal fenestra. This condition is unlike that of *Elliotsmithia* described by Reisz et al. (1998) where the postorbital is excluded by the anterior projection of the squamosal from the lateral temporal fenestra. It is similar to the situation in *Microvaranops* described by Botha-Brink and Modesto (2009) where the postorbital contributes to the whole dorsal part of the temporal fenestra. In the absence of an anterior ramus of the squamosal it is difficult to tell whether the

squamosal excludes the postorbital from the dorsal margin of the temporal fenestra because it may be present beneath the postorbital.

The jugal is shaped as an upturned T beneath the orbit and makes up the anteroventral margin of the temporal fenestra and ventral half of the postorbital bar. The suborbital ramus of the jugal is elongated anteroventrally, but it does not contact the lacrimal, possibly due to distortion. The postorbital ramus of the jugal extends further dorsally, thus contributing to half the anteroventral margin of the lateral temporal fenestra, as is present in other pelycosaurs (Reisz et al, 1998). In medial view, the jugal separates the maxilla and quadratojugal dorsally on the jugal arch. In lateral view, the jugal bears an anteroposterior ridge extending from the contact with the maxilla towards the mid-point of the postorbital ramus, as observed in *Heleosaurus* and *Microvaranops* (Carroll, 1976; Botha-Brink & Modesto, 2009). This ridge has a rugose texture also reported in *Heleosaurus* (Carroll, 1976). At the point where the ridge terminates, posteroventral to the orbit, the jugal bears a tuber-like boss as in other mycterosaurines, including *Heleosaurus scholtzi* (Reisz & Modesto, 2007). The postorbital ramus of the jugal also displays a ridge that extends ventrally from the dorsal suture of the jugal with the postorbital to the intersection of the three jugal rami as in *Microvaranops* and SAM-PK-10407 (?*Elliotsmithia*) (Carroll, 1976; Botha-Brink & Modesto, 2009; Modesto et al, 2011). Posteriorly, the postorbital ramus of the jugal is shortened and extends to the middle margin of the temporal fenestra. The posterior ramus partially covers the anterior portion of the quadratojugal.

The quadratojugal is a thin elongated bone extending anteriorly beneath the jugal. It does not contact maxilla. This is consistent with the situation *Elliotsmithia* (Reisz et al, 1998), and it is dorsoventrally longer than the infratemporal ramus of the jugal. The anteroventral side of the squamosal is poorly preserved, but presumably did not exclude the quadratojugal from the lateral temporal fenestra as is the situation in SAM-PK-8305 and the holotype of *Heleosaurus* (Modesto et al, 2001; Botha-Brink & Modesto, 2009). Most of the squamosal is eroded away and only its anteroventral portion is preserved and forms the posterior margin of the lateral temporal fenestra. The squamosal does not exclude the quadratojugal from the temporal fenestra i.e., it does not contact the posterior ramus of the jugal.

Palate

In ventral view the palate is masked by the tightly occluding lower jaw, however because of segmentation of the CT scans it has been possible to virtually remove the lower jaws and thus expose and fully describe the palate. The vomer appears as an unpaired bone and has a thin medial ridge in the ventral view. It is a long and slender bone, extending posteriorly from the premaxilla to meet the pterygoid below the orbit (**Figure 3**) and bearing an anteroposteriorly extending single row of teeth. Posteriorly, it extends up to the level of the anterior surface of the orbit. The vomer is long and covers almost three-quarters of the anterior part of the maxilla (**Figure 3**). It bifurcates in the middle of the skull below the anterior margin of the orbit where it also terminates (**Figure 3b**).

In dorsal view, a midline ridge extends from the premaxilla to the posterior region of the vomer. Anterolaterally, the vomer bears flat rami that have irregularly arranged alveoli (**Figure 3a**). They become mediolaterally broader and more prominent posteriorly, along the lateral margins of the palate. Posterolaterally, the vomer contacts the anterior ramus of the pterygoid (**Figure 3**). In dorsal view, the dorsal surface of the posterior ramus of the palatine bears a thin longitudinal ridge which is laterally concave (**Figure 3b**).

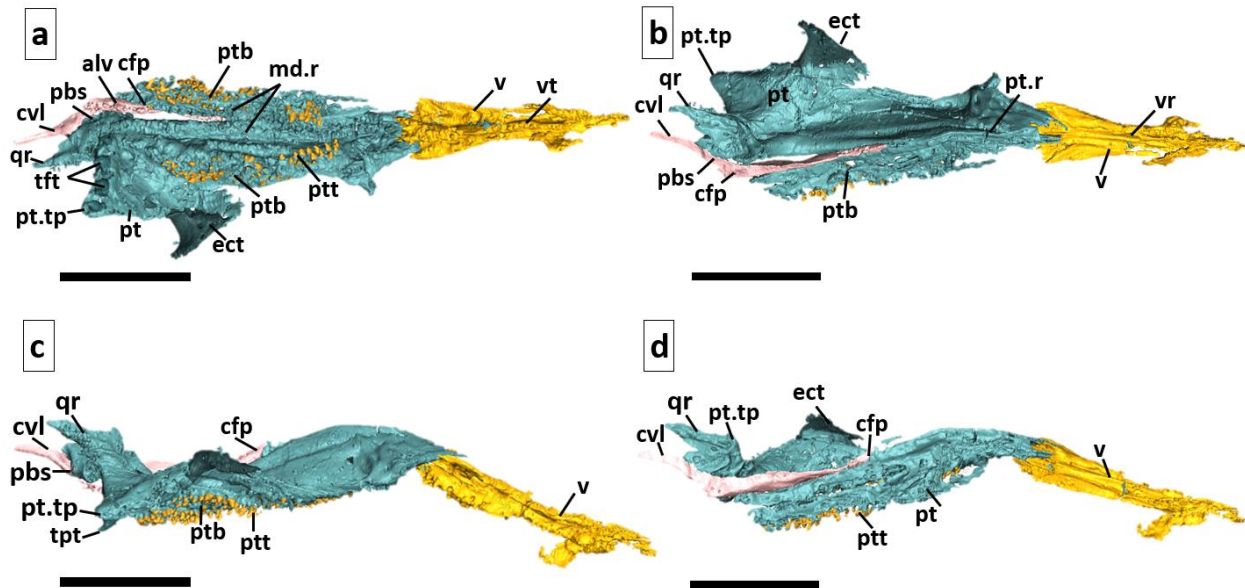


Figure 3. Specimen CG-RMS353 (a) ventral, (b) dorsal, (c) right lateral and (d) medial view of the palate of CG-RMS-353. **Abbreviations;** alv, alveoli; cfp, cultriform process of the parabasisphenoid; cvl, crista

ventrolaterales; **ect**, ectopterygoid; **md.r**, medial ridge of the pterygoid; **pl**, palatine; **ptb**, pterygoid boss; **ptt**, pterygoid teeth; **pt.r**, pterygoid dorsal ridge; **pt.tp**, pterygoid transverse process; **tpt**, pterygoid transverse process teeth; **qr**, quadrate ramus of the pterygoid. Scale bar=15mm.

The pterygoid is positioned posterior to the vomer. It is narrow anteriorly and expands in a posterior direction where it bears a convex boss, in ventral view (**Figure 3a**). A narrow medial ridge of the pterygoid that is positioned anteroventrally, forms a deep groove on the ventral aspect of the palate (**Figure 3c**) which accounts for the concave shape of the palate (**Figure 3c**). Laterally, the anterior ramus of the pterygoid has a short sutural contact with the ectopterygoid and slightly antero-laterally to that, it contacts the maxilla.

Medial to the palatal ramus of the pterygoid, is a large pterygoid boss with multiple rows of teeth aligned along the curve of the boss (**Figure 3a**). The teeth on the pterygoid boss are large and comparable in size to those on the anterior ramus of the pterygoid (**Figure 3a**). Medial to the pterygoid boss, the pterygoid bears double rows of dentition on each side. The medial ridges of the pterygoid meet anterior to the cultriform process of the parabasisphenoid and on the anterior side meet the vomer in the midline of the skull. The quadrate ramus of the pterygoid is positioned further posteriorly (**Figure 3**) and tapers postero-laterally. In ventral view, the pterygoid has a posteromedial sutural contact with the parabasisphenoid. Lateral to the quadrate ramus, the pterygoid has a dentigerous transverse process which is prominent in ventral view (**Figure 3b**). This process has a single row of large teeth, only four are preserved but there are seven sockets on either side. The teeth are strongly recurved in a posteroventral direction (**Figure 3a & c**). There are no teeth immediately anterior to the transverse process, as in *Elliotsmithia* (Reisz et al, 1998). The dorsal surface of the pterygoid is conspicuously smooth compared to the ventral surface, which is rugose.

The ectopterygoid is a small, flat triangular bone positioned anterolaterally to the palatal ramus of the pterygoid (**Figure 3**). The posterior margin of the ectopterygoid is concave and has a ramus meeting the maxilla anteriorly. The ectopterygoid does not contact the palatine, contrary to the situation in *E. longiceps* described by Reisz et al. (1998). The edentulous nature of the ectopterygoid is shared with diapsids (Reisz et al, 1998).

Braincase

Only the left anterior process of the parabasisphenoid is visible and has a slender cultriform process (**Figure 3b**), which extends anteriorly between the two pterygoids. In dorsal view, it bears a narrow ridge for the ethmoid cartilage (Gardner et al., 2011) (**Figure 3b**). In ventral view, the cultriform process bears small alveoli organised in two rows (**Figure 3a**). The left basiptyergoid process of the basisphenoid is positioned further posteriorly. There is a fragment of bone ventral to the crista ventrolaterales that might be the prootic bone, however it is too damaged for identification.

Mandible

The mandible is a long, slender element comprising several bones (**Figure 4 & Figure 5**) including the dentary, splenial, coronoid, prearticular, angular, surangular and the articular. The left mandible is well preserved. The dentary is the longest bone of the mandible extending from the anterior tip of the mandible to the level of the temporal fenestra posteriorly (**Figure 1a**). The anterior narrowing of the dentary is similar to the mycterosaurine condition described by Modesto et al. (2001). Nineteen tooth sockets are present on the right lower jaw but only 12 teeth are preserved (**Figure 4b**). Most of the empty alveoli resemble the condition visible in the maxilla, with no remnants of old teeth suggesting that the teeth had not yet erupted (**Figure 2a**). The tooth adjacent to tooth 6 of the maxilla is a replacement tooth and is the least developed out of all the teeth of the lower jaw (**Figure 2b**). Medially, the dentary symphysis resembles that of *Elliotsmithia longiceps*, which is antero-posteriorly long (Modesto et al, 2011). Antero-ventrally, the dentary bears three foramina on each side (**Figure 4a**). Multiple anteroposteriorly elongated foramina are present along the lateral surface of the dental margin, possibly for the mandibular canal. As in *Elliotsmithia*, the dentary meets the surangular towards the middle of the mandible, which is positioned medially beneath the temporal fenestra where the jaws are occluded (Botha-Brink & Modesto, 2009).

The splenial is a flat bone which is only partially preserved in the mandible and is positioned on the medial side of the dentary. In ventral view, the dentary-splenial suture is visible and tapers to a point anteriorly on the ventral surface of the dentary (**Figure 4a**) and, as is the situation in other varanopids, it does not contribute to the dentary symphysis (Ford & Benson 2020).

Posteriorly, the splenial widens dorsoventrally to make up most of the medial surface of the mandible.

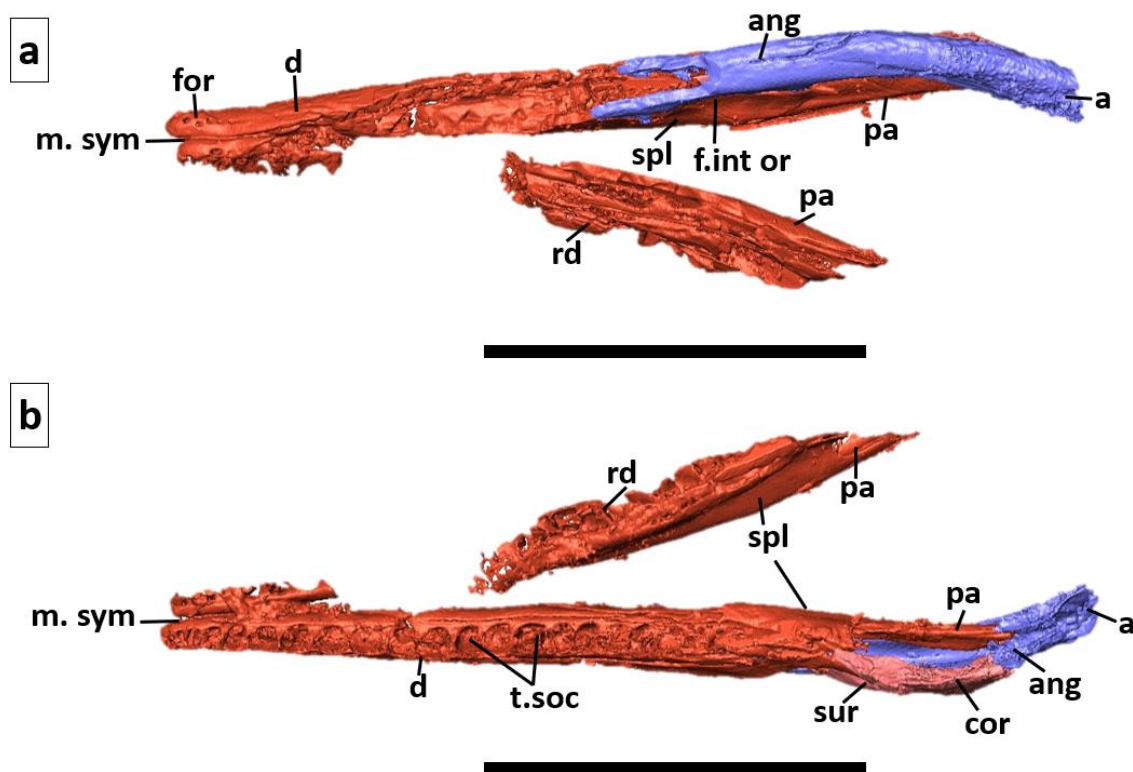


Figure 4. Specimen CG-RMS353, mandible in (a) ventral and (b) dorsal views. **Abbreviations;** a, articular; cor, coronoid; for, foramina; m. sym, mandibular symphysis; pa, prearticular; rd, right dentary; t.soc, tooth socket; spl, splenial. Scale bar = 35 mm.

Two foramina are present on the medial surface of the mandible, one in the angular and another in the dentary (**Figure 5b**). Both foramina are anteroposteriorly elongated and are subequal, contrary to the condition described in a South African mycterosaurine by Modesto et al. (2011), where the foramen intermandibularis caudalis is twice as large as the anteromedial opening (**Figure 5b**). The anteromedial foramen is the intermandibularis oralis of the trigeminal nerve, which has been described by Modesto et al. (2011), for an unidentified varanopid (SAM-PK-K10407). The intermandibularis oralis is the smaller of the two foramina and is positioned more anteriorly on the angular. The anteriormost part of the foramen is at the level of the 18th tooth and extends even more posteriorly up to the level of the posterior border of the orbit. Posterior to the foramen intermandibularis oralis, is the foramen intermandibularis caudalis (**Figure 5b**) which is on the labial surface of the mandible (**Figure 5b**), at the intersection of the splenial,

angular and prearticular. Is it 3mm long and more dorsoventrally expanded in comparison of the foramen intermandibularis oralis. The foramen is found at the level of the anterior border of the lateral temporal fenestra. The presence of both foramina in the lower jaw of a single specimen has only been described in early reptiles and some mycterosaurines (MacDougall et al, 2019; Modesto et al, 2011) but not in any other pelycosaur (Modesto et al, 2011).

The prearticular is a medially positioned thin element on the lower jaw. Is it located on the posterior termination of the dentary where it contacts the articular. It tapers anteriorly as it contacts the inner wall of the angular (**Figure 5b**). It ends half-way along the lateral temporal fenestra, almost equidistant with the coronoid region. The prearticular forms a sutural contact with the splenial anteriorly in a sigmoidal pattern as has been described for *Elliotsmithia* (Modesto et al, 2011). Similar to *E. longiceps*, the prearticular forms a ventral scarf joint with the angular (Modesto et al, 2011).

The surangular is a short but prominent bone in the mandible (**Figure 5**) forming the posterodorsal region of the lower jaw. It forms the coronoid eminence (**Figure 5**), as observed in *Heleosaurus* and *Elliotsmithia* (Spindler et al, 2018). Ventrally and anteriorly, it contacts the angular and dentary, respectively. The anterior contact is visible in lateral view (**Figure 5b**), where the dentary overlaps the anterior portion of the surangular. The surangular is broader postero-dorsally and extends towards the quadratojugal without contacting it. The lateral surface texture of the surangular is smooth, contrary to that of *Heleosaurus scholtzi* in which it is ornamented (Botha-Brink & Modesto, 2009). It is possible that the smooth surface of the surangular was caused by overpreparation.

The specimen preserves only a single coronoid, a character usually ascribed to diapsids (Laurin & Reisz, 1995). The coronoid is a convex bone located on the posterodorsal region of the surangular (**Figure 5**). It bears small teeth on the inner surface, giving it a granulated texture (**Figure 5b**). The presence of teeth in the coronoid region is a common character in early amniotes (Haridy et al, 2017; Ford & Benson, 2020) and is also present in most pelycosaurs (Williston, 1914; Romer and Price, 1940). This is a plesiomorphic character for synapsids, also seen in *Vaughnictis smithae*, a Caseasaurian, which was initially classified as a varanopid

(Brocklehurst et al, 2016). The coronoid and dentary contact in the dorsal region on this specimen.

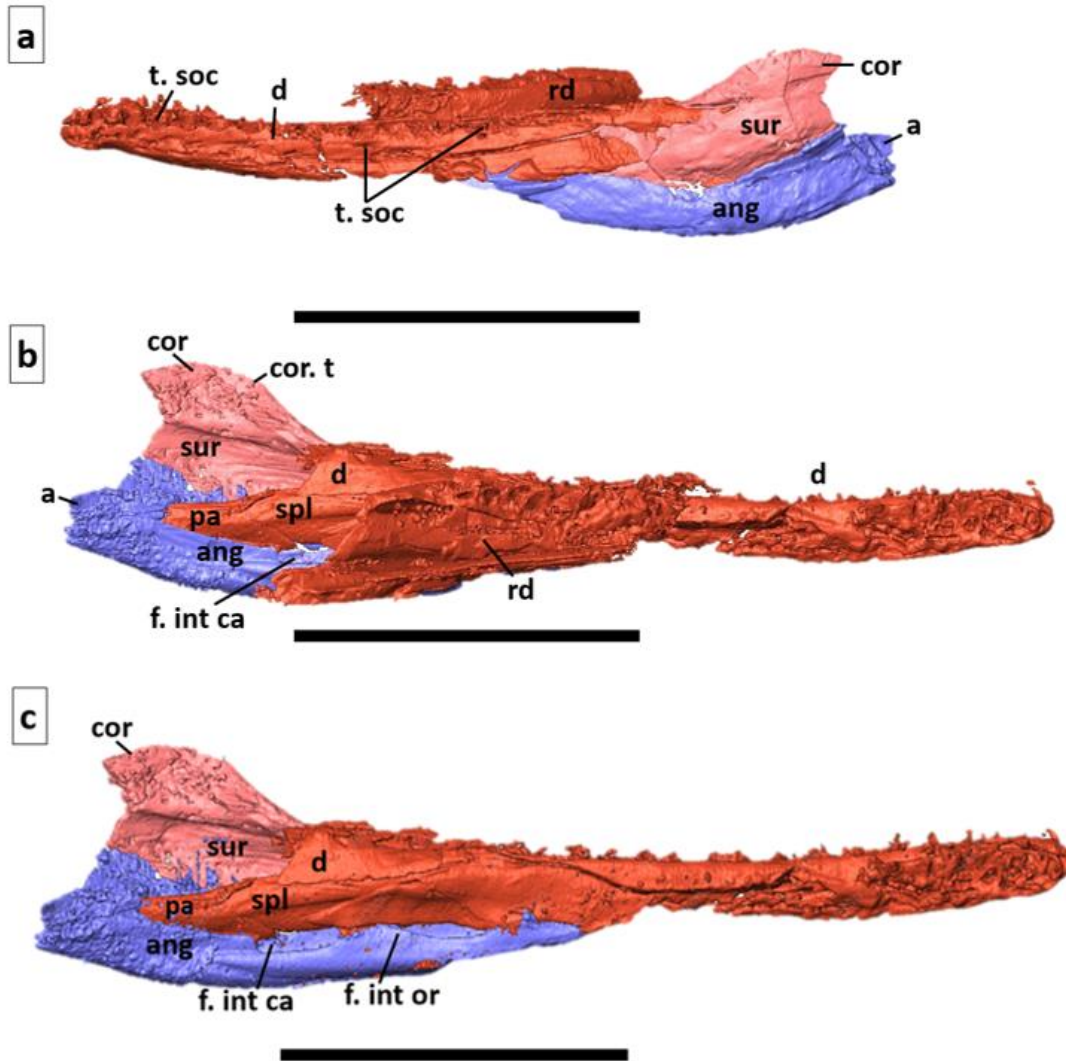


Figure 5. Specimen CG-RMS353, left (a) lateral and (b) right lateral and (c) medial view of the mandible. **Abbreviations;** **a**, articular; **cor**, coronoid; **cor.t**, coronoid teeth; **d**, dentary; **f. int ca**, foramen intermandibularis caudalis; **f.int.or**, foramen intermandibularis oralis; **m. sym**, mandibular symphysis; **pa**, prearticular; **rd**, right dentary; **t.soc**, tooth socket; **spl**, splenial. Scale bar = 35 mm.

The angular is a large bone positioned posteroventrally on the lower jaw (**Figure 5a**). Similar to the surangular, the angular lacks lateral ornamentation. It curves ventral to the surangular forming a banana-shaped bone as in other basal pelycosaurs (**Figure 5**) (Reisz, 1998; Olroyd & Sidor, 2022). It extends anteriorly to the dentary, overlapping the surangular medially and

posteriorly (**Figure 5b**). In medial view, it has two grooves that form the ventral walls of the intermandibularis openings mentioned above (**Figure 5b**). Posteromedially and posteroventrally, the surface of the angular is pustulous, resembling the situation in *Heleosaurus scholtzi* and is one of the synapomorphies of this species (**Figure 5a**) (Reisz & Modesto, 2007). The smooth texture on the lateral surface of the angular can possibly be ascribed to overpreparation as the rough texture extends all the way up to the medial wall of the articular (**Figure 5b**). The articular is the posterior most bone of the mandible. It is not sufficiently well preserved to determine whether a retroarticular process that is supported by the angular is present, as is in *Elliotsmithia longiceps* (Reisz et al, 1998). As mentioned above, the labial surface of the articular is granulated (**Figure 5b**).

3.2.2 Description of specimen BP/1/8499.

Specimen BP/1/8499 comprises an almost complete skeleton in articulation in a curled-up position and with a poorly preserved skull. The axial skeleton includes a long articulated vertebral column and ribs, with separate portions preserving caudal vertebrae. The left shoulder girdle includes the scapula, clavicle and cleithrum and the left forelimb comprises an articulated humerus, ulna, radius and an almost complete manus, all articulated. The pelvic girdle is incomplete, with only the left ilium clearly visible.

Similarly, the left hindlimb includes an articulated femur, tibia, fibula, and an almost complete foot. The skeleton is preserved ventral up and as such the dorsal aspect of the skeleton is the best preserved.

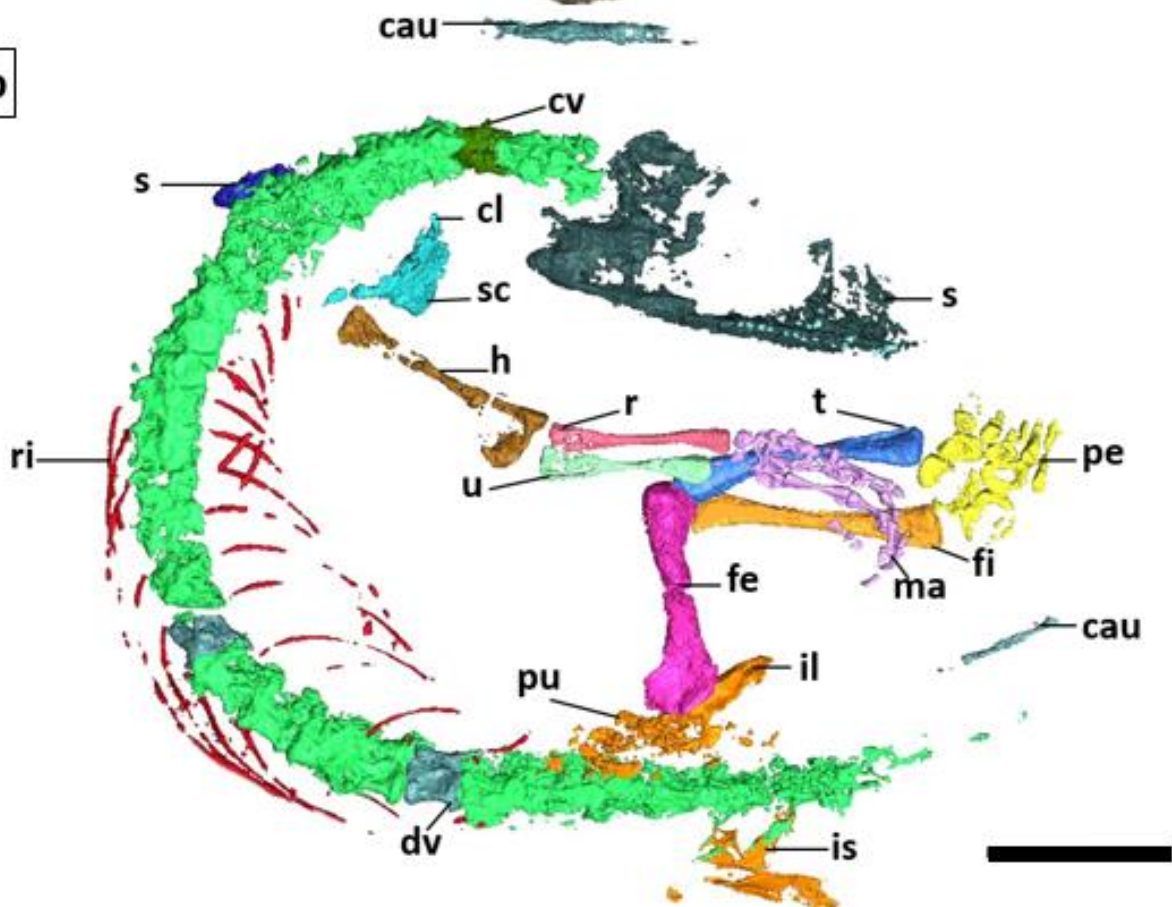
a**b**

Figure 6. Specimen BP/1/8499 in (a) photograph and (b) segmentation in ventral views. Scale bar = 25mm.

Skull

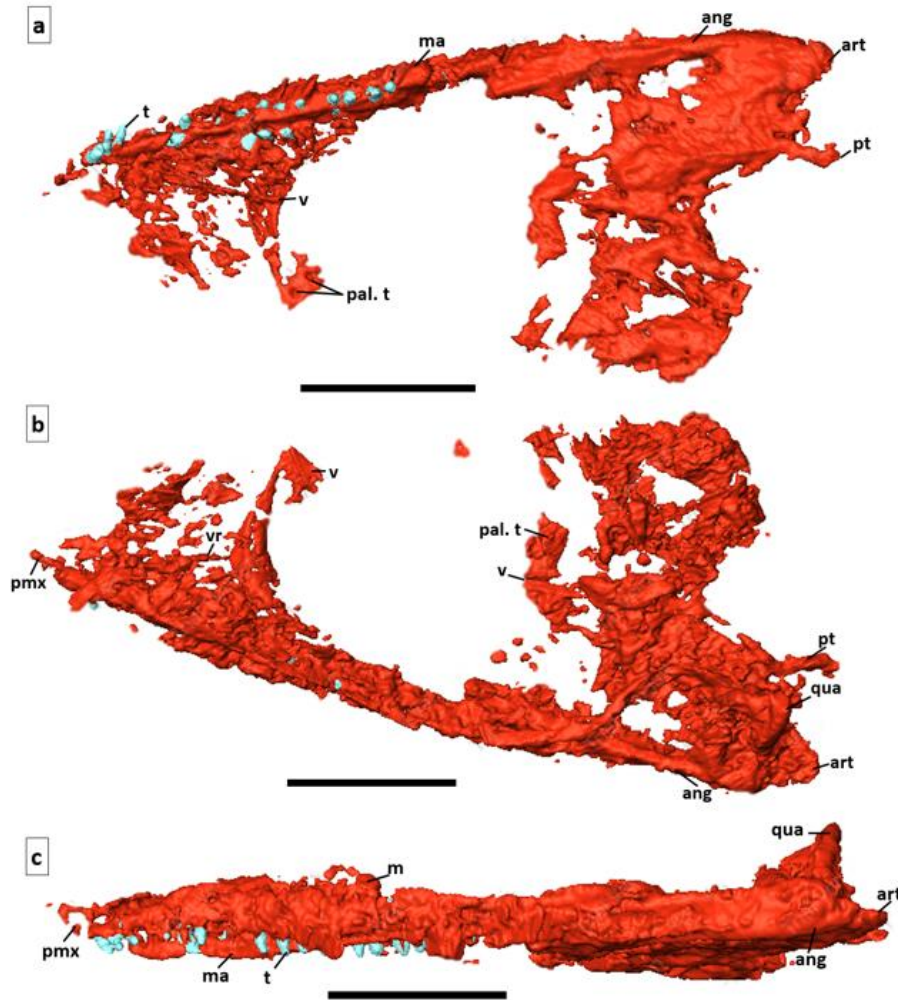


Figure 7. BP/1/8499 skull in (a) dorsal, (b) ventral and (c) lateral views. **Abbreviations;** art; articular, p; parietal, pal.t; palatal teeth, qua; quadrate. Scale bar = 7.5 mm.

Because of poor contrast of the CT images combined with poor bone preservation, many cranial characters are not visible in the segmented diagrams. The skull is about 30 mm long, and has the triangular shape seen in most pelycosaurs (Romer & Price, 1940). It is dorsoventrally compressed and missing most of the skull roof (**Figure 7**). It preserves the posterior portion of the mandible, some bones of the palatine and some of the alveoli of the maxilla. In ventral view, the vomer is preserved as a mold on the skull midline (**Figure 7b**). The vomer bears a thin ridge which has alveoli for denticles, as is in CG-RMS353 (**Figure 7b**). Twelve thecodont teeth are et

al present on the maxilla (**Figure 7b**) and in lateral view, they are strongly recurved, as in other varanopids (**Figure 7c**) (Reisz et al, 1998). No caniniform is preserved, and all the teeth appear to be proportionally smaller than those seen in other varanopids as reported by Botha-Brink & Modesto (2009).

Axial skeleton

Vertebrae

The vertebral column preserves cervical, dorsal and caudal vertebrae. The specimen has 29 dorsal vertebrae, which is close to the standard count of 27 for "pelycosaurs" (Pelletier, 2013; Reisz & Dilkes, 2003). There are seven preserved cervicals, approximately eighteen dorsal and six sacral vertebrae. The tail is not completely preserved but was likely exceptionally long as it appears to have curled around half the skeleton. Only 5 caudal vertebrae are preserved and are disarticulated from the rest of the specimen, it appears that more than 2/3 of the caudal vertebrae are missing.

The vertebrae are best preserved on the dorsal side which preserves the neural spine, a prominent neural excavation, pre-zygopophyses and post zygapophyses, transverse processes and for most of them, only the dorsal half of the centrum (**Figure 8**). None of the seven preserved cervical vertebrae have ribs articulating with them and they do not bear articulation facets. Contrary to the situation in *Heleosaurus* (Modesto et al, 2001), *Microvaranops* (Botha-Brink & Modesto, 2009) and *Elliotsmithia* (Reisz et al, 1998), no cervical osteoderms are preserved in specimen BP/1/8499. This may be a feature of young individuals as the juvenile *Microvaranops* specimens (SAM-PK-K8305) also lack dermal ornamentation (Botha-Brink & Modesto, 2009).

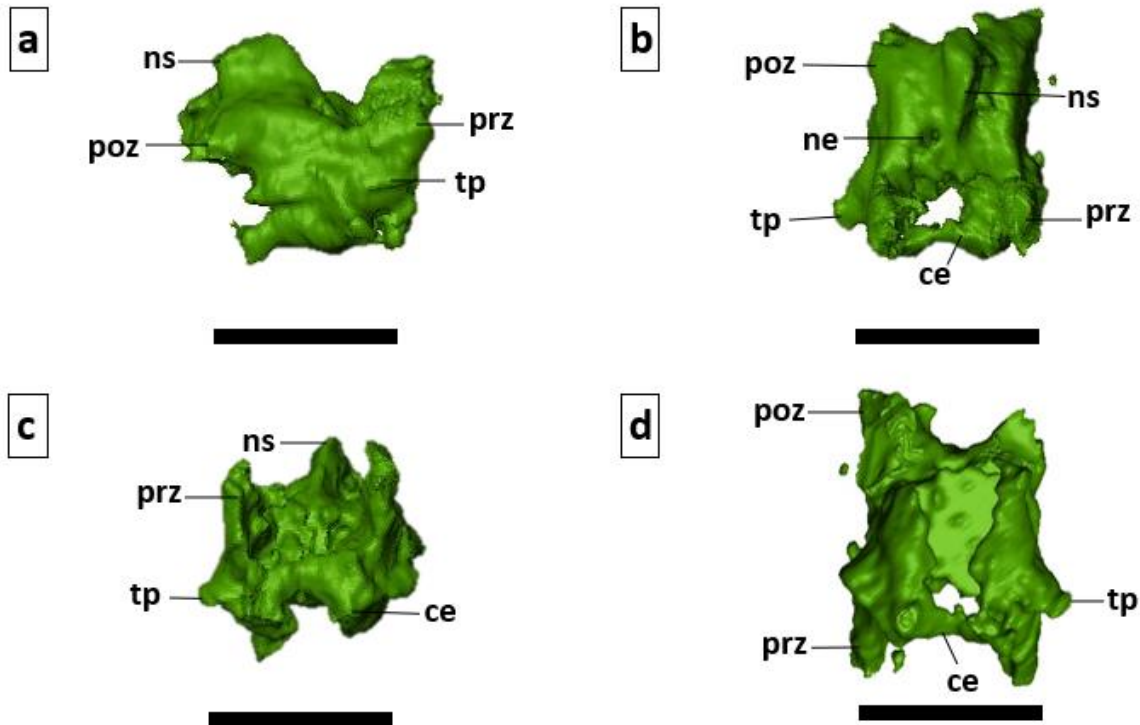


Figure 8. Cervical vertebra five of specimen BP/1/8499 in (a) right lateral, (b) dorsal, (c) anterior and (d) ventral views. Scale bar = 4 mm.

The outline of the cervical vertebrae is generally rectangular in lateral view and conforms to the standard shape of cervical vertebrae in all varanopid species (Botha-Brink & Modesto, 2009). Individual cervical vertebrae are almost 4 mm long and extend anterodorsally for approximately 1.5 mm from the centrum. The height of the neural spines of the cervical vertebrae of specimen BP/1/8499 is half the length of those of the dorsals (**Figure 8**) and the neural spines are laterally compressed (**Figure 8b**) and point posteroventrally (**Figure 8a**). The presence of a median ventral keel observed in other varanopids (Reisz & Modesto, 2007) cannot be determined on the cervical centrum of this specimen as the ventral surface is weathered away.

Only the dorsal half of the centrum is preserved in all the cervical vertebrae, this is 4 mm wide and a prominent notochordal foramen is present which is visible in anterior view. In dorsal view, a prominent excavation is present posterolateral to the neural spine in all cervicals (**Figure 8b**) as in *Heleosaurus* (Reisz & Modesto, 2007). A concave notch is present between the neural spine and prezygapophyses (**Figure 8a**). The zygapophyses overhang the lateral surfaces of the centrum in dorsal view, as in *Mycterosaurus* and *Heleosaurus* (Both-Brink & Modesto, 2009;

Pelletier, 2013), however, they are not noticeable horizontally. The postzygapophyses extend dorsomedially whereas prezygapophyses protrude ventrolaterally, contrary to the condition seen the varanopid *Aerosaurus* from New Mexico in which the extensions are in the opposite directions (Pelletier, 2013) (**Figure 8c**). In lateral view, a transverse ridge extends between the postzygapophyses and the transverse process (**Figure 8a**). The transverse process extends ventrolaterally below the centrum and extends approximately 1 mm laterally (**Figure 8**).

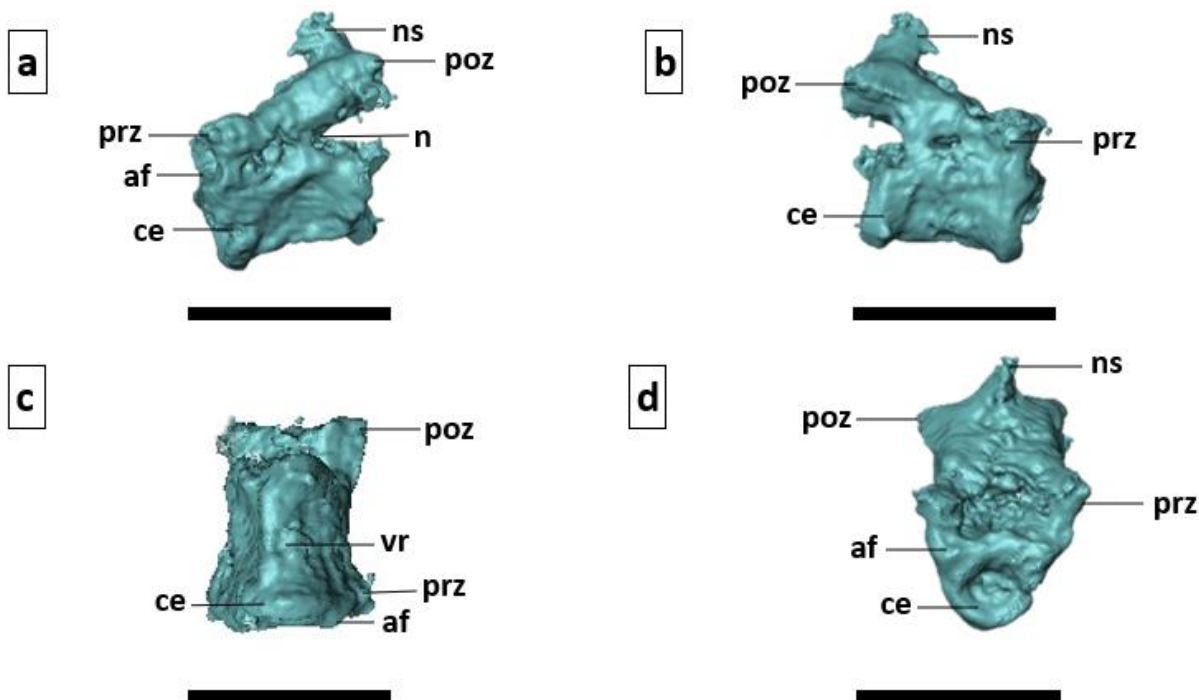


Figure 9. Dorsal vertebra 23 of specimen BP/1/8499 in (a) left lateral, (b) right lateral, (c) ventral and (d) anterior views. Scale bar = 7 mm.

About 18 dorsal vertebrae are present. The best-preserved dorsal vertebra is 15 mm long (maximum length) with a 13 mm long centrum which is longer than it is wide, with a maximum width of approximately 7 mm (**Figure 9**). In ventral view, the centrum exhibits a midventral groove that is parallel to the ventral ridges, which is an autapomorphy for *Heleosaurus* (**Figure 9c**) (Pelletier, 2013; Reisz & Modesto, 2007; Spindler et al, 2020). In diapsid reptiles from the Permian this feature is not present (Reisz, 2019). As in other pelycosaurs, the dorsal centrae are amphicoelous (Romer & Price, 1940) (**Figure 9b**) and bear a conspicuous notochordal foramen, visible in anterior and posterior views (**Figure 9d**). In lateral view, the neurocentral suture that joins the neural spine and centrum is unfused in the dorsal vertebra (**Figure 9a & b**) which is

common in non-adult varanopid specimens (Botha-Brink & Modesto, 2009). Dorsal vertebrae have a conspicuous sub-rectangular neural spine, as in the cervicals except that the neural spine on the dorsals extend 2 mm higher above the centrum than in the cervical vertebrae and is positioned slightly further postero-dorsally. Unlike the cervicals, the dorsal vertebrae do not have any neural excavations, as is the situation in *Heleosaurus* (Pelletier, 2013; Reisz & Modesto, 2007). The caudal vertebrae after the pelvis have long transverse processes (**Figure 10**).

The dorsal zygapophyses of the vertebrae are much smaller than those of the cervicals (**Figure 8** & **Figure 9**) and in posterior view, the postzygapophyses face ventromedially, with the prezygapophyses extending dorsolaterally (**Figure 9d**). The dorsal vertebrae do not preserve prominent transverse processes, but this is a result of weathering. The articulation facets for the presacral ribs are posterodorsal to the centrum (**Figure 9d**) and are preserved in articulation. This region of the skeleton does not have any osteoderms.

The morphology of the sacral vertebrae appears distorted due to poor contrast in the pelvic area. The caudals are all incomplete. They are slender with a rod-like appearance and do not articulate with any ribs. The morphology of the caudals is similar to that of *Microvaranops* (Botha-Brink & Modesto, 2009). On average, they measure 9 mm in length.

Ribs

Specimen BP/1/8499 possesses about fourteen pairs of slender ribs with a width of approximately 0.61 mm and the length of the longest rib being approximately 16 mm. The ribs are absent on the cervical area, they reach their greatest length on the 18th dorsal vertebra and shorten towards the sacrum. As in *Heleosaurus* (Botha-Brink & Modesto, 2009), *Mycterosaurus* (Berman & Reisz, 1982) and *Archaeovenator* (Reisz & Dilkes, 2003), the ribs have holocephalous heads. The gastralia cannot be observed from the CT images but they are evident on the specimen (see **Figure 11**). The presence of gastralia is consistent with the condition in *Microvaranops parentis* (Botha-Brink & Modesto, 2009).



Figure 10. Close-up photograph of the ventral view of BP/1/8499, showing the posterior dorsal view of the vertebrae and the pelvis at the posterior end. **Abbreviations:** **c. ver**, caudal vertebra; **gas**, gastralia; **r**, rib. Scale bar = 3cm.

Appendicular skeleton

Forelimb

The entire forelimb is preserved in articulation and includes the pectoral girdle, humerus, radius, ulna, as well as the manus and is 55.80 mm long from the proximal end of the humerus to the distal phalanges. The pectoral girdle is poorly preserved (**Figure 11**) with only the clavicle, cleithrum and coracoid portion of the scapula preserved. The clavicle is 9 mm long. In dorsal view, the clavicle is posteriorly curved as in the condition on *Aerosaurus* (Pelletier, 2013) (**Figure 11a**). The ventrally expanded plate of the clavicle, observed in other varanopids (Pelletier, 2013) is faintly visible in dorsal view (**Figure 11a**). The plate has a width of 3 mm and meets the scapula in the coracoid region.

A narrow fragment of bone that tapers anterior to the scapula (**Figure 8a**) is considered to be the cleithrum. In dorsal view, the bone is triangular and tapers anteriorly, as seen in *Heleosaurus* (Botha-Brink & Modesto, 2009) (**Figure 8a**). The coracoid and ventral portion of the cleithrum is poorly preserved (**Figure 8**). Similar to *Aerosaurus*, the anterior scapulocoracoid suture is not

visible, and is possibly the result of preservation. No foramina are visible on the scapula. This means that the supraglenoid foramen which is present in the holotype of *Heleosaurus* (Botha-Brink & Modesto, 2009), is not visible or present in BP/1/8499. The scapulocoracoid conforms to the curved and rounded shape observed in basal amniotes and pelycosaurs (Sumida et al, 2013) (**Figure 8b**).

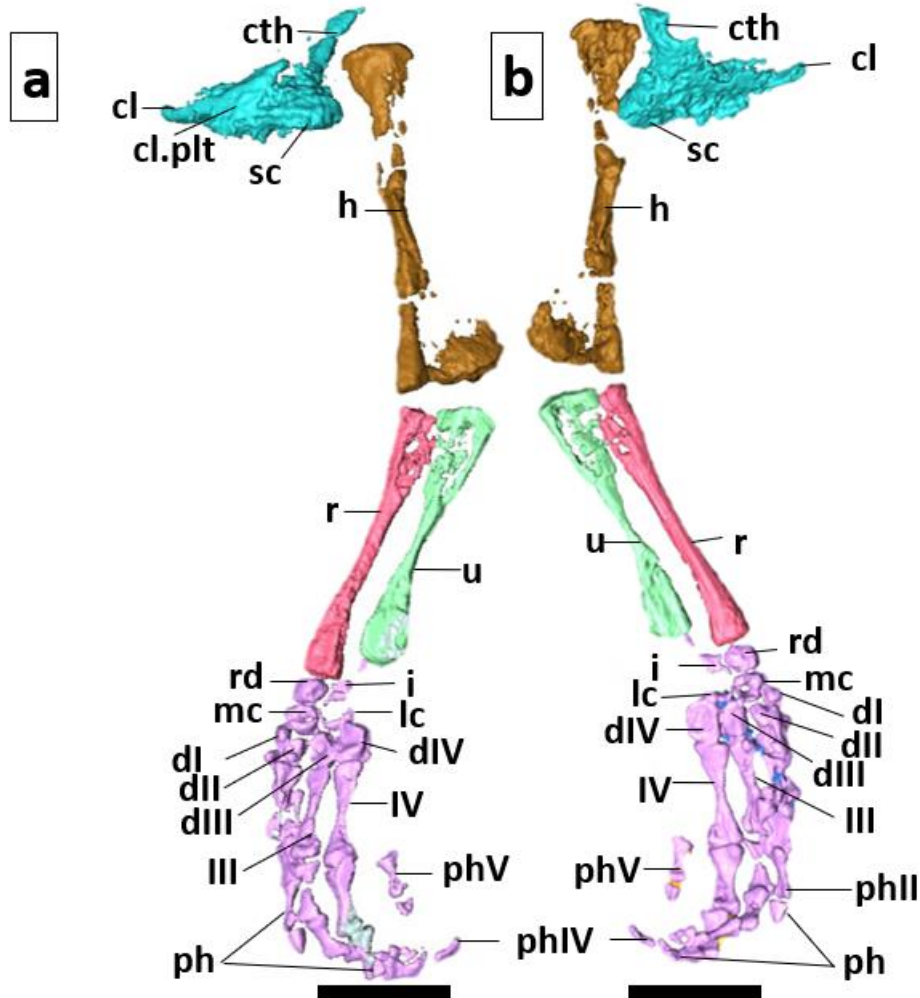


Figure 11. Forelimb of specimen BP/1/8499 in (a) dorsal (b) ventral view. **Abbreviations:** **cl.plt**; plate of the clavicle **dI-dIV**, distal carpals; **i**, intermedium; **I-IV**, metacarpals; **lc**, lateral centrale; **mc**, medial centrale; **ph**, phalanges; **rd**, radiale. Scale bar = 15 mm.

The humerus retains the tetrahedral shape common in most early tetrapods (Romer & Price, 1940) and is best preserved on the distal and dorsal surfaces (**Figure 12a & d**). It measures about 20 mm in length with a proximal and distal width of 7 mm. The humeral shaft is slender, with a width of 1 mm. It is smaller and shorter than the adult humerus of specimen

Microvaranops and is similar in size and proportions to those of the juveniles (Botha-Brink & Modesto, 2009) (**Figure 12**). Unlike the condition in *Archaeovenator* (Reisz and Dilkes, 2003), *Mycterosaurus* (Berman and Reisz, 1982), and *Heleosaurus* (Botha-Brink and Modesto, 2009) where the distal and proximal heads of the humerus are not broadly expanded, the distal head of the humerus in this specimen is relatively broad and resembles that of *Varanops* (Pelletier, 2013; Williston, 1911; Maddin et al, 2006; Campione & Reisz, 2010) and *Watongia* (Pelletier, 2013; Reisz and Laurin, 2004).

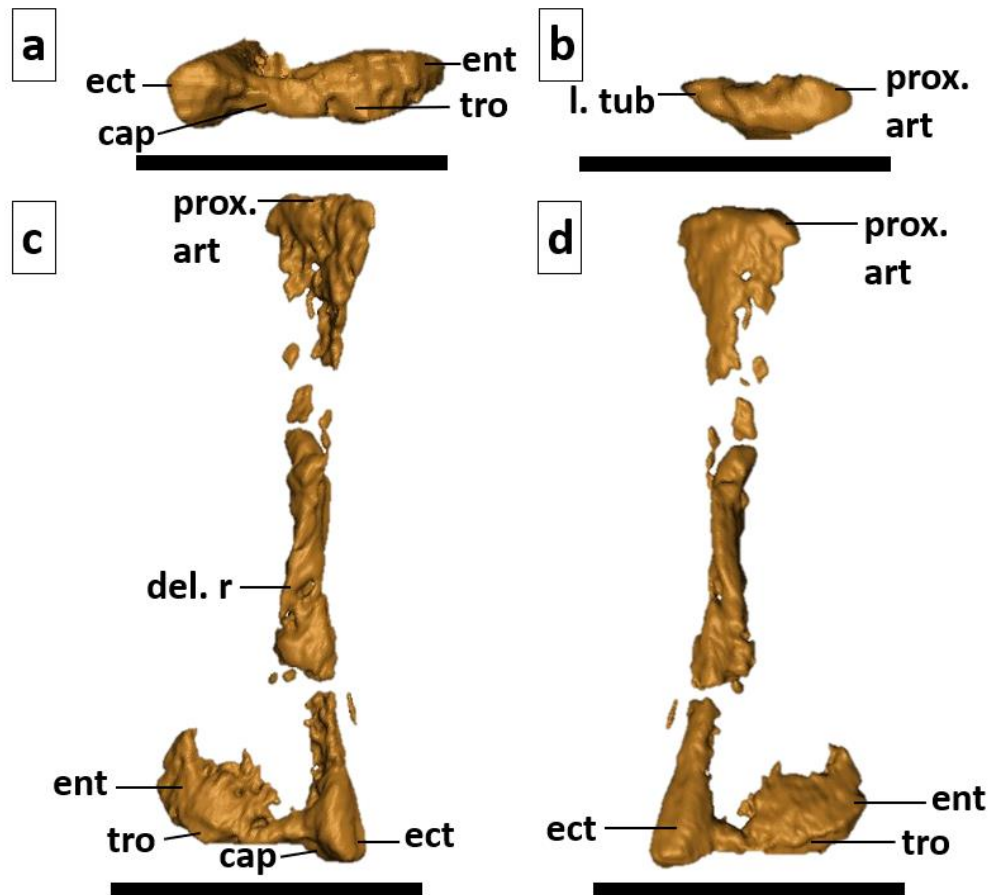


Figure 12. Humerus of specimen BP/1/8499 in (a) distal, (b) proximal, (c) ventral and (d) dorsal views. **Abbreviation;** **cap**, capitulum; **del.r**, deltoid ridge; **ect**, ectepicondyle process; **ent**, entepicondyle process; **l.tub**, lesser tubercle; **prox.art**, proximal articulation; **tro**, trochlea. Scale = 7.5 mm.

The proximal end of the humerus is poorly ossified; however, the proximal articulation is preserved (**Figure 12b**). The smooth articular surface with the shoulder runs down the dorsal margin of the bone in a slightly curved manner. The curve forms a concave recess, like that seen in pelycosaurs (**Figure 12b**) (Bishop et al, 2022). With the absence of the complete proximal

head, it is impossible to determine the degree of twisting between the proximal and distal end of the bone. Nonetheless, the oblique nature of the ectepicondyle provides a slight idea of the angle between the distal and proximal heads. Presumably, the angle would be acute, as in other varanopids (Pelletier, 2013). Part of the lesser tubercle is preserved but not much information can be deduced from it (**Figure 12b**).

Distally, distinct ectepicondyle and entepicondyle processes are visible (**Figure 12**). The ectepicondylar process extends towards the middle of the shaft (**Figure 12d**). An ectepicondylar foramen is absent in this specimen, this contrasts with the condition in the adult of *Microvaranops* (Botha-Brink & Modesto, 2009) where the ectepicondyle and supinator process join to form the ectepicondylar foramen (Botha-Brink & Modesto, 2009). This anomaly could be due to the absence of the supinator process caused by poor preservation. In this specimen, the ectepicondyle is thin and terminates towards the middle of the humeral shaft. In dorsal view, a ridge is present as a continuation of the ectepicondyle and terminates further proximally (**Figure 12d**). In ventral view, the humeral shaft retains a ridge that appears as part of the deltopectoral crest (**Figure 12c**). The articulation surface of the distal humerus is slightly preserved (**Figure 12a**). The capitulum for the radius has a deep groove that is also visible in ventral and dorsal view (**Figure 12c & d**). Proximally, a thin ridge extends from the ectepicondyle (**Figure 12a**). The trochlea for the articulation of the ulna is slightly preserved and is also visible in dorsal and ventral views (**Figure 12b & c**).

The radius and ulna have the bowed structure observed in *Microvaranops* (Botha-Brink & Modesto, 2009). The radius is more bowed distally, this extent of curvature resembles the one of the juvenile *Microvaranops* specimens (Botha-Brink & Modesto, 2009; **Figure 6b**). Similar to *Microvaranops*, the length of the radius and ulna is subequal (**Figure 11a**) (Botha-Brink & Modesto, 2009) with both the radius and ulna being 16 mm long (**Table 4**). Both elements are thin and long but the ulna is more robust than the radius, with a wider proximal and distal end. In *Heleosaurus*, the length of the radius and ulna are greater than 83% the humeral length, which is similar to the condition observed on this specimen BP/1/8499 (Pelletier, 2013; Botha-Brink & Modesto, 2009). The widths of the proximal and distal ends of the ulna are about 3 mm and 2.6 mm, respectively. The shaft of the ulna is relatively thin, with a width less than 80% of the

epiphyses (**Figure 11**). Thus, the ends of the ulna are more expanded, especially the proximal ends, as seen in *Aerosaurus* (Pelletier, 2013).

Both the radius and ulna are slightly curved, more so in the case of the ulna, as in *Microvaranops* (**Figure 11a**). In lateral view, the ulna is dorsoventrally flat, resembling that in *Aerosaurus* (Pelletier, 2013). The ulna has a concave proximal end in anterior view as in *Microvaranops* (Botha-Brink & Modesto, 2009). In posterior view, the proximal end of the ulna is not as ovoid as the proximal end of the radius. The distal lateral margin of the radius is not visible; thus, the posterior shape of the distal radius cannot be determined. A narrow ridge is present on the distal lateral surface of the bone (**Figure 11**). This condition is shared with *Mesenosaurus*, *Varanodon*, *Watongia* and *Varanops* (Maddin et al, 2006; Botha-Brink & Modesto, 2009). The articular surface of the ulna is not well ossified.

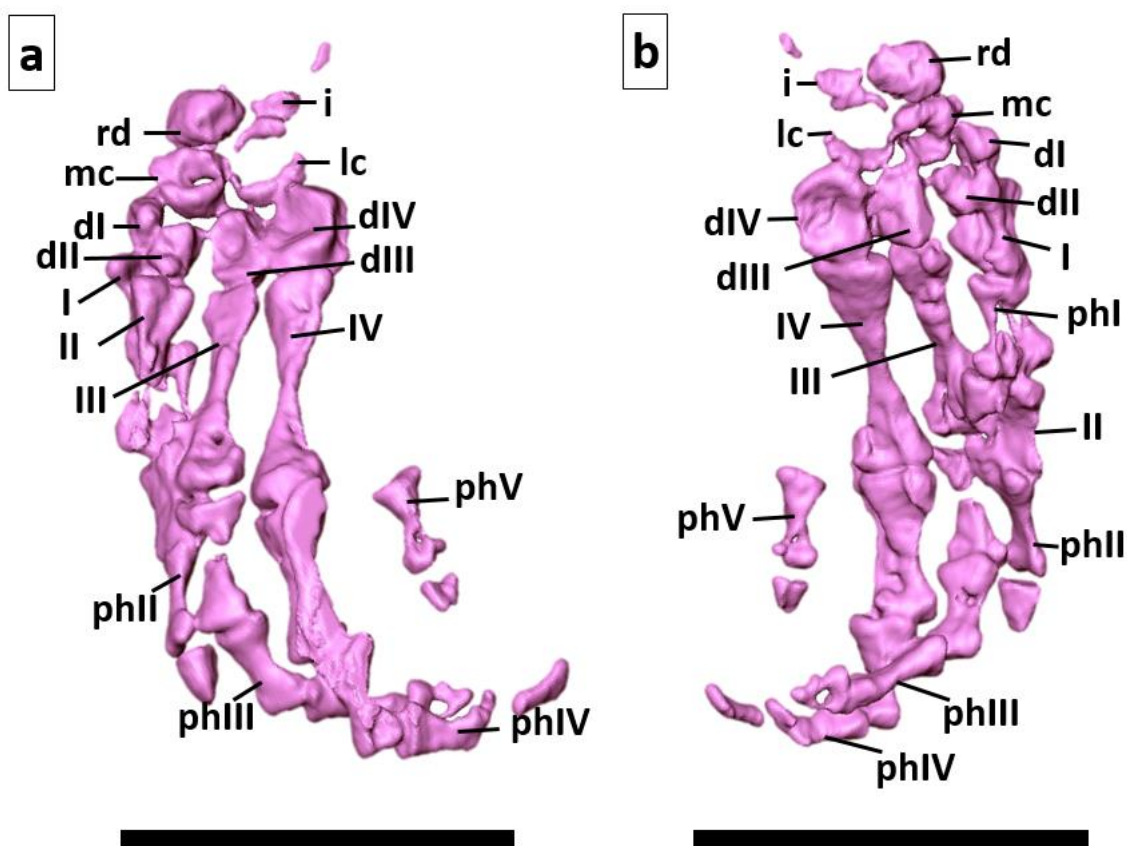


Figure 13. Specimen BP/1/8499, left manus in (a) dorsal and (b) ventral views. Scale bar = 10 mm.

Abbreviations: dI-dIV, distal carpals; i, intermedium; I-IV, metacarpals; lc, lateral centrale; mc, medial centrale; phI-phV, phalanges; rd, radiale. Scale bar= 10 mm.

The manus preserves almost all its constituent elements, with only the ulnare, pisiform and fifth metacarpal missing. The digits are tightly packed together. The radiale is fairly robust and, almost the same size as the medial centrale. It bears a slightly pointed tubercle dorsally (**Figure 13**), giving it a pyramidal shape, which is visible in posterior view. Posterolateral to the radiale, there is an element that appears to be the anterior remnant of the intermedium (**Figure 13**). In dorsal view, the fragment is concave at its anterior end (**Figure 13**). Most of the lateral centrale is missing, and only the outline of the bone is preserved. In dorsal view, it is triangular and points distally. The medial centrale is slightly smaller than the lateral centrale. It is convex in lateral view as in basal synapsid *Aerosaurus*, but it is not triangular (Pelletier, 2013). The lateral centrale bears a small tubercle that extends medially, in ventral view (**Figure 13b**). The dorsal

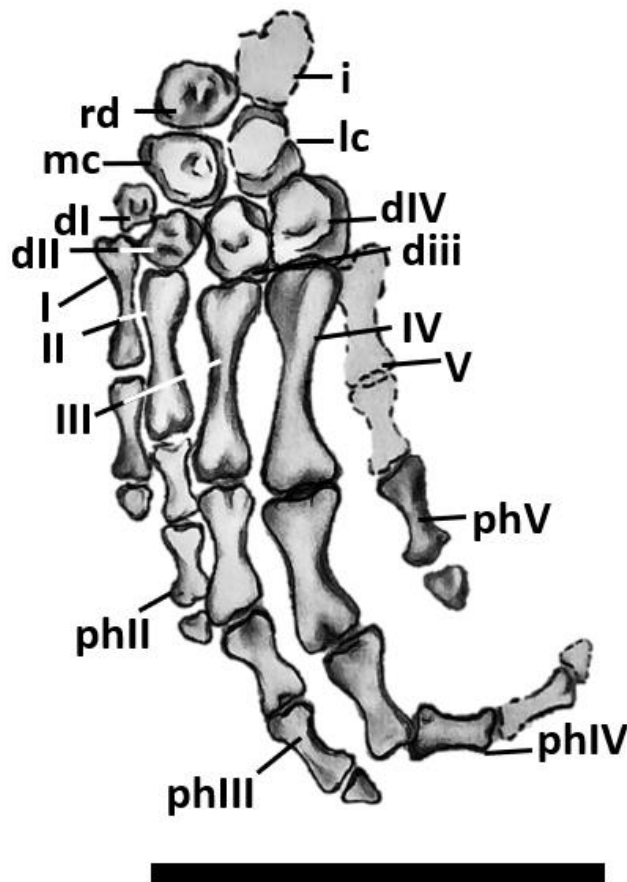


Figure 14. Illustration of manus of specimen BP/1/8499 in dorsal view. Scale bar = 10 mm.

and ventral surfaces of the centrale are concave and thus poorly ossified.

Only four distal carpals and metacarpals are preserved. The distal carpals are all sub-rectangular. Similar to *Microvaranops*, all the metacarpals are elongate and slender (Botha-Brink & Modesto, 2009). The penultimate digit has five phalanges and the third retains four, similar to *Microvaranops* (Botha-Brink & Modesto, 2009). The metacarpals and phalanges decrease in length, from the fourth to the first (**Figure 13**). Dorsoventrally, the phalanges are flattened and have expanded proximal and distal ends, with the proximal end being more expanded (**Figure 13**). This condition conforms to the situation described by Pelletier (2013) in *Aerosaurus wellesi*. In ventral and dorsal views, the unguals are triangular (**Figure 13b**).

Distal carpal one is subrectangular and is smaller than all the preserved distal phalanges. In ventral view, it bears a distal tubercle (**Figure 13b**). The first metacarpal is partially preserved and retains a long and slender appearance, similar to all the other metacarpals. The second distal carpal has two distal and proximal tubercles in dorsal view (**Figure 13a**). Between the tubercles, there is an indent. The second metacarpal is approximately 4 mm in length and possesses a furrow on the lateral margin of the bone, which is visible in dorsal view (**Figure 13a**).

The third distal carpal is slightly larger than the second and has a shallow notch in dorsal view (**Figure 13a**). Distodorsally, the fourth distal carpal is slightly wider than the proximal portion. The third metacarpal is also elongate and measures about 5 mm. Digit three has three phalanges and a triangular ungual. Distal carpal four is thinner in the middle, with a concave surface on the ventral and dorsal margin (**Figure 13**). The medial border of the carpal is more elongated anteroposteriorly, than the lateral margin (**Figure 13a**). This digit has four phalanges and no ungula preserved. The phalanges have a similar shape which is elongated with broad ends. While the phalangeal formula cannot be determined with certainty, the preserved manus of this specimen resembles the primitive formula observed in non-mammalian amniotes of 2-3-4-5-3 (**Figure 14**) (Hopson, 1995; Fröbisch & Reisz, 2009).

Hindlimb

The hindlimb preserves a femur, fibula, tibia and a partially preserved pes. The femur's position is similar to that of pelycosaurs and primitive tetrapods, projecting horizontally from the body (Romer & Price, 1940). The specimen does preserve the ischium and most of the ilium (**Figure 10**), and they could not be reconstructed in 3D because of poor contrast on the CT images.

(**Figure 10**). The pelvis exhibits a broad and plate-like shape that bears similarity to other pelycosaurs (Sumida et al, 2004). The anteroposterior elongate morphology of the ischium is shared with *Heleosaurus* (Reisz & Modesto, 2007). According to Reisz & Modesto (2007), this morphology is more similar to that of synapsids than sauropsids. In dorsal view, the ischium tapers slightly in the posterolateral direction (**Figure 10**). As in *Heleosaurus*, the ilium is elongated anteroposteriorly (Botha-Brink & Modesto, 2009) (**Figure 10** & **Figure 16b**). The length of the iliac blade is 12.11mm and it extends postero-ventrally from the anterior part of the

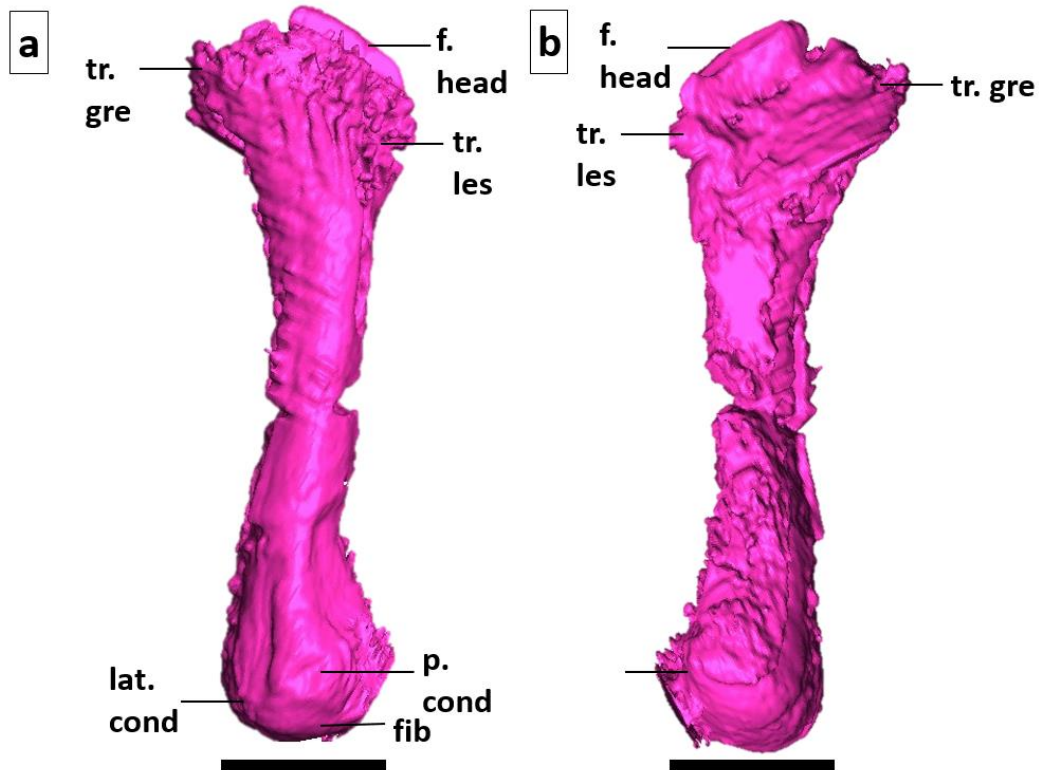


Figure 15. Specimen BP/1/8499 femur in (a) dorsal and (b) ventral views. Scale bar= 5 mm.

Abbreviations; **f.head**, femoral head; **fib**, fibula articulation surface; **lat.cond**, lateral condyle; **p.cond**, proximal condyle; **tr.gre**, greater trochanter; **tr.les**, lesser trochanter. Scale bar= 5 mm.

acetabulum. This condition resembles that of *Heleosaurus*, in which the blade tapers posteriorly too (Botha-Brink & Modesto, 2009) (**Figure 16b**).

The anterior process of the ilium is narrow and extends anteriorly above the midpoint of the acetabulum as in *Microvaranops* (Botha-Brink & Modesto, 2009). The contact between the pubis and ilium is not preserved. The acetabulum is also not visible, but its position can be inferred

from the position of the femur. In lateral view, dorsal to the acetabulum, the iliac blade bears a narrow ridge that tapers to the posterior point of the bone. This ridge appears to be the gluteal line, that serves for muscle attachment. The triradiate shape of the acetabulum seen in pelycosaurs (Sumida et al, 2013) cannot be examined for this specimen because of dorsoventral compression. The pubis is poorly preserved, and thus lacks information.

The femur is a slender and elongated sigmoidal bone, similar in morphology to those of *Heleosaurus* and *Microvaranops* (Reisz & Modesto, 2007; Botha-Brink & Modesto, 2009). It is 21.61 mm long, which is slightly less than the average length of the femur of the juvenile varanopids described by Botha-Brink and Modesto (2009), i.e., 24 mm. Compared to the humerus, the femur is slightly longer, with a difference of approximately 2 mm. The proximal and distal ends have a width of 6.28 mm and 4.57 mm, respectively. It is dorsoventrally wider than it is mediolaterally. The length to distal width ratio is 3:1 (Pelletier, 2013; Reisz & Dilkes, 2003) as it is in *Microvaranops* (Botha-Brink & Modesto, 2009). An anteriorly projected greater trochanter is visible (**Figure 15**). A fourth trochanter is absent, which is also a feature of most

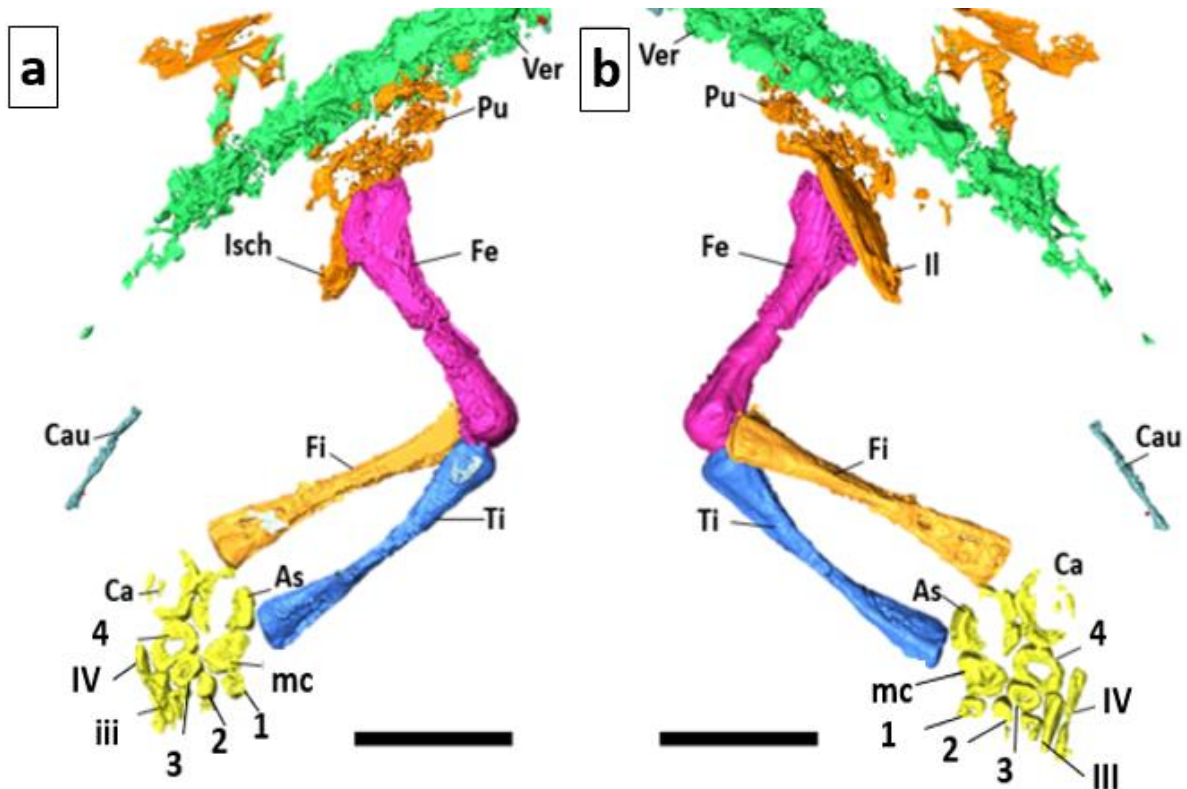


Figure 16. Left hindlimb of specimen BP/1/8499 in (a) ventral and (b) dorsal views. **Abbreviations:** 1-4, distal tarsals; III-IV, metatarsals. Scale bar = 30 mm.

varanopids (Botha-Brink & Modesto, 2009). The femoral head is damaged on both the ventral and dorsal margins. It lacks a visible intercondylar fossa. The distal articular surface of the femur is smooth, and it possesses a fibula articular surface that is visible in dorsal view (**Figure 15a**).

The tibia and fibula are subequal in length, with 23 mm and 23.5 mm, respectively. The tibia is slender and slightly curved on the shaft (**Figure 16**) as in other pelycosaurs (Sumida et al, 2013), including the varanopids *Archaeovenator* (Reisz & Dilkes, 2003), *Varanops* (Campione & Reisz, 2010), *Mycterosaurus* (Berman & Reisz, 1982) and *Microvaranops* (Botha-Brink & Modesto, 2009). The ventral ridge of the tibia is slightly visible on the shaft of the bone and is broad at the proximal end and narrow towards the distal end. The distal end is ovoid in posterior view. The distal and proximal facets for articulation of the astragalus and femur cannot be determined. The tibia and fibula are longer than the femur, with the shaft of the femur being twice as thick as the shafts of the fibula and tibia contrary to the situation in other varanopids. The fibula is an almost straight bone and shows little curvature than the tibia (**Figure 16**). Unlike the tibia, the fibula is slightly broader at the distal end. Similar to *Aerosaurus* and *Archaeovenator*, the fibula has a

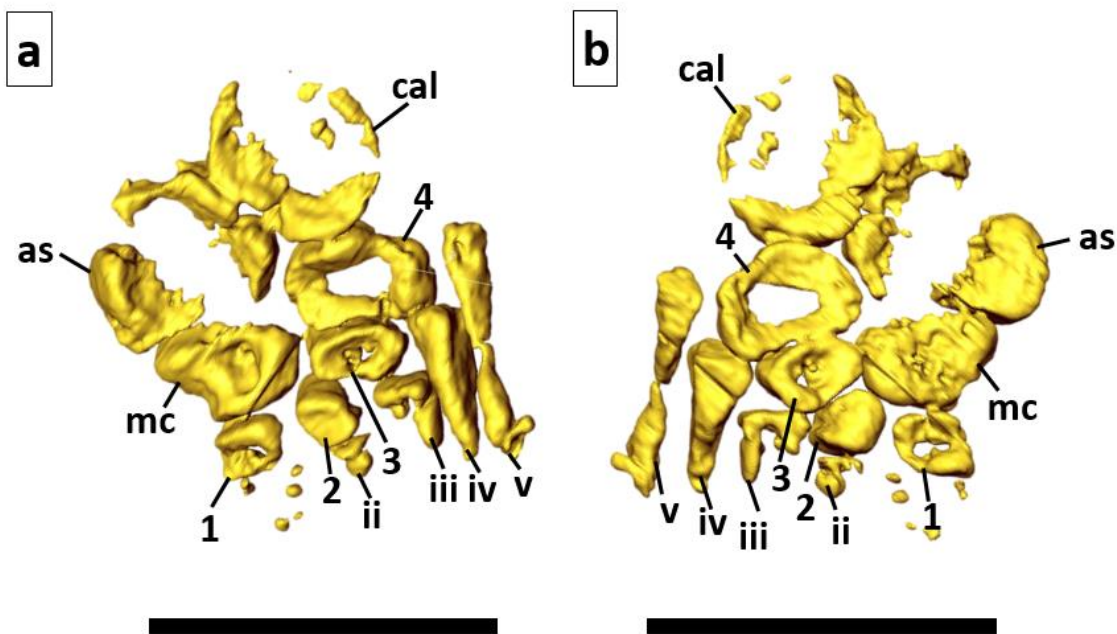


Figure 17. Specimen BP/1/8499 pes in (a) dorsal and (b) ventral views. **Abbreviations:** 1-4, distal tarsals; as, astragalus; cal, calcaneum; III-IV, metatarsals; mc, medial centrale. Scale bar = 10 mm.

narrow ridge that runs from the middle shaft to the medial end of the distal fibula (Pelletier, 2013). The distal end is dorsoventrally flattened.

The pes of BP/1/8499 is partially preserved and articulated. It retains the astragalus, calcaneum, medial centrale, four distal tarsals and two visible metatarsals. As in *Varanops* and *Aerosaurus*, the pes is more robust and larger than the manus (Williston, 1911; Langston & Reisz, 1981). The astragalus is almost square in dorsal view (**Figure 17a**) as in *Aerosaurus* and *Microvaranops* (Langston & Reisz, 1981), and not L-shaped as presented in other pelycosaurs (Botha-Brink & Modesto, 2009). Its dorsal surface appears slightly concave in dorsal view (**Figure 17a**), similar to that of varanopids, including *Microvaranops* (Botha-Brink & Modesto, 2009), *Varanops* (Williston, 1911; Campione & Reisz, 2010) and *Mycterosaurus* (Berman & Reisz 1982). The articular surface for the tibia is slightly convex in ventral view (**Figure 17a**). The articular surface for the fibula on the astragalus is unclear. Medial to the calcaneum and astragalus, there is a foramen that is positioned on the midlength of the elements (**Figure 17a**), this morphology is similar to other varanopids such as *Varanops* (Williston, 1911) and *Aerosaurus* (Pelletier, 2013). In dorsal view, the astragalus has raised edges adjoining the articular surfaces (**Figure 17a**), like the condition observed in *Aerosaurus* (Pelletier, 2013) and *Microvaranops* (Botha-Brink & Modesto, 2009).

The calcaneum is almost rounded and has a convex lateral surface as in other varanopids (Pelletier, 2013) (**Figure 17**). It is preserved as an outline and lacks the inner portion of the bone. The calcaneum is subequal to the astragalus. The medial centrale is posteroventrally long on the lateral border (**Figure 17a**). It has a lateral ramus pointing proximally, next to the astragalus. In dorsal view, it possesses a concave surface and a narrow ridge distally (**Figure 17a**).

All the metatarsals are preserved with only the fifth distal metatarsal missing. The fourth metatarsal is the largest, while the size of the distal metatarsals decreases from the fourth to the second. Most of the inner surfaces of the pes bones are weathered. Each distal tarsal has a lateral curvature which fits the convexity of the one next to it. The first distal tarsal is sub-rectangular and slightly larger than the second distal tarsal in dorsal view (**Figure 17a**). Distal tarsal 2 is more cuboidal than it is rectangular. It is a robust element. The articular surface for metatarsal two is oblong. In ventral view, it has a convex ventral surface (**Figure 17b**). The first and second

digits do not preserve any metatarsals and phalanges. The dorsal and ventral surfaces of distal tarsal 3 are oblong and concave (**Figure 17**). The metatarsals are mediolaterally flattened and the proximal ends for the third digit is dorsoventrally widened and narrows distally. Similar to the other distal tarsals, the fourth one retains an oblong shape. It is the largest out of the three and has a similar concave ventral and dorsal surfaces (**Figure 17**). Metatarsal four is also dorsoventrally wide, but not to the same extent as the third metatarsal (**Figure 17b**). Its distal end is also wide, giving a narrow shaft.

Table 4. Cranial and postcranial measurements in mm to compare the sizes of the newly discovered specimens described in this project. These measurements indicate that specimen TM-1483 (*Elliotsmithia* holotype) followed by SAM-PK-1070 (*Heleosaurus* holotype), CG-RMS353 and BP/8499, respectively. Measurements for SAM-PK-K8305 taken from Botha-Brink & Modesto (2009).

Measurements	SAM-PK-1070 (<i>H. scholtzi</i>)	TM-1483 (<i>E. longiceps</i>)	CG- RMS353	BP/1/849 9	SAM- PK- K8305 (Adult)	SAM-PK- K8305 (juvenile)
Cranial measurements						
Skull						
Maximum length	50.78	~ 60.2	~ 48.25	36.06	>49.2	40
Width	31.73	~ 22	-	-	-	-
Length (snout to orbit)	-	-	24.60	-	-	-
Length of orbit	-	~ 15	-	-	15.5	11.9
Width of orbit	-	~ 23	13.91	-	-	-
Length of temporal fenestra	-	~ 9	-	-	-	-
Width of temporal fenestra	-	-	6.43	-	7.2	-
Postcranial measurements						
Clavicle						
Maximum length	-	-	-	9.53	30.7	-
Width	-	-	-	1.38	6.2	-

Scapulocoracoid	-	-	-	9.67	18.3	-
<i>Humerus</i>						
Maximum length	-	-	-	20.63	35.5	-
Proximal width	-	-	-	4.08	12.8	-
Midshaft width	-	-	-	1.74	3.7	-
Distal width	-	-	-	6.52	11.6	-
<i>Radius</i>						
Maximum length	-	-	-	16.49	29.4	-
Proximal width	-	-	-	2.59	4.6	-
Midshaft width	-	-	-	1.09	2.6	-
Distal width	-	-	-	2.24	-	-
<i>Ulna</i>						
Maximum length	-	-	-	15.88	-	-
Proximal width	-	-	-	3.63	4.9	-
Midshaft width	-	-	-	0.60	3.3	-
Distal width	-	-	-	2.44	-	-
<i>Femur</i>						
Maximum length	44.89	-	-	21.75	-	-
Proximal width	-	-	-	5.81	-	-
Midshaft width	-	-	-	4.32	-	-
Distal width	-	-	-	2.66	-	-
<i>Tibia</i>						
Maximum length	-	-	-	22.38	-	-
Proximal width	-	-	-	4.81	-	-
Midshaft width	-	-	-	1.52	-	-
Distal width	-	-	-	3.94	-	-
<i>Fibula</i>						

Maximum length	-	-	-	22.73	-	-
Proximal width	-	-	-	3.38	-	-
Midshaft width	-	-	-	1.73	-	-
Distal width	-	-	-	4.13	-	-
<i>Pelvis</i>						
Ilium length	-	-	-	11.71	-	-
Ischium length	-	-	-	-	-	-

3.3 Cladistic Analyses

3.3.1 Ford & Benson 2020 matrix

i) Changes in the Ford & Benson data matrix

No changes were made to the characters used on this matrix, except for the scoring of *Heleosaurus*, *Elliotsmithia* and the addition of *Microvaranops*. The scoring of the first two genera included characters from specimens CG-RMS353 and BP/1/8499, respectively (7.4 Appendix). The scoring of *Heleosaurus* and *Elliotsmithia* was made on a combination of adult and juvenile characters where applicable.

ii) Consensus tree reconstruction

To investigate the placement of varanopids within Synapsida, I conducted phylogenetic analyses using the Ford and Benson (2020) data matrix with no constraints. The heuristics search recovered 1573 best trees, which is also the tree length using ACCTRAN optimisation. The following indices were recovered, consistency index = 0.2339, homoplasy index= 0.7661 and retention index of 0.5990. A Bayesian analysis was also conducted and recovered a consensus tree with no major differences to the maximum parsimony tree (see Appendix 1).

The results of the consensus shown in **Figure 18** are interpreted as follows: the major clades, Synapsida and Captorhinidae are collapsed into polytomies such that the results show no knowledge on the placement of both clades among Amniota. The node that groups amniotes have a Bremer index of 2. Diapsids are supported and include all varanopids, which are grouped

as a sister taxon to Neoreptilia with a Bremer score of 3, similar to the results by Ford and Benson (2020). Support for this node is based on 10 unambiguous characters that are 24) a height of a dorsoventral preorbital process that is twice that of the anterior orbital margin, 52) small to absent contribution of the lacrimal to the orbital margin in lateral view, 74) a narrow height of the zygomatic bar, 151) absent ectopterygoid dentition, 170) the presence of a retroarticular process, 239) absent supraglenoid foramen of the scapula, 247) poorly developed capitulum and trochlea of the humerus, 258) absent olecranon process of the ulna, 282) a tibia with a low cnemial crest.

The Bremer support for the South African varanopids node is 3, while the Bayesian posterior probability is 0.99, with *Heleosaurus* and *Microvaranops* forming a sister group with the node that comprising *Elliotsmithia* and *Mycterosaurus*. The sister relationship of *Heleosaurus*, *Elliotsmithia* and *Microvaranops* has the following synapomorphies: 136) an extensive contact of the vomer and pterygoid on the medial margin, 145) absence of median contact between pterygoids, 191) the anterior extension of the surangular terminating posteriorly and 227) the presence of dorsal osteoderms. While *Mycterosaurus* and *Elliotsmithia* are joined by the following synapomorphies: 32) greater than two caniniform teeth, and 42) the posterior termination of the maxilla being at the level of the posterior margin of the orbital rim. *Heleosaurus* and *Microvaranops* share several synapomorphies: 213) an anteroposteriorly long centra of the dorsal vertebrae, 214) a longitudinal keel of the dorsal centra on the ventral surface, 223) a flat dorsolateral surface of the dorsal vertebrae, 253) the presence of an ectepicondylar foramen of the humerus and 273) an ilium that lacks a mediolateral expansion on the dorsal surface. *Elliotsmithia* has the autapomorphy of the presence of coronoid dentition (189), while *Heleosaurus* showed an unambiguous character that is 276) a greater than 1.2 ratio of the length of the femur to humerus.

3.3.2 Spindler 2018 matrix

i) Changes in the Spindler et al. (2018) data matrix

The updated dataset consists of 13 changed characters. Character 14 was revised and modified and character 99 removed, respectively. Characters 8, 11, 12, 36, 42, 49, 65 and 114 were re-

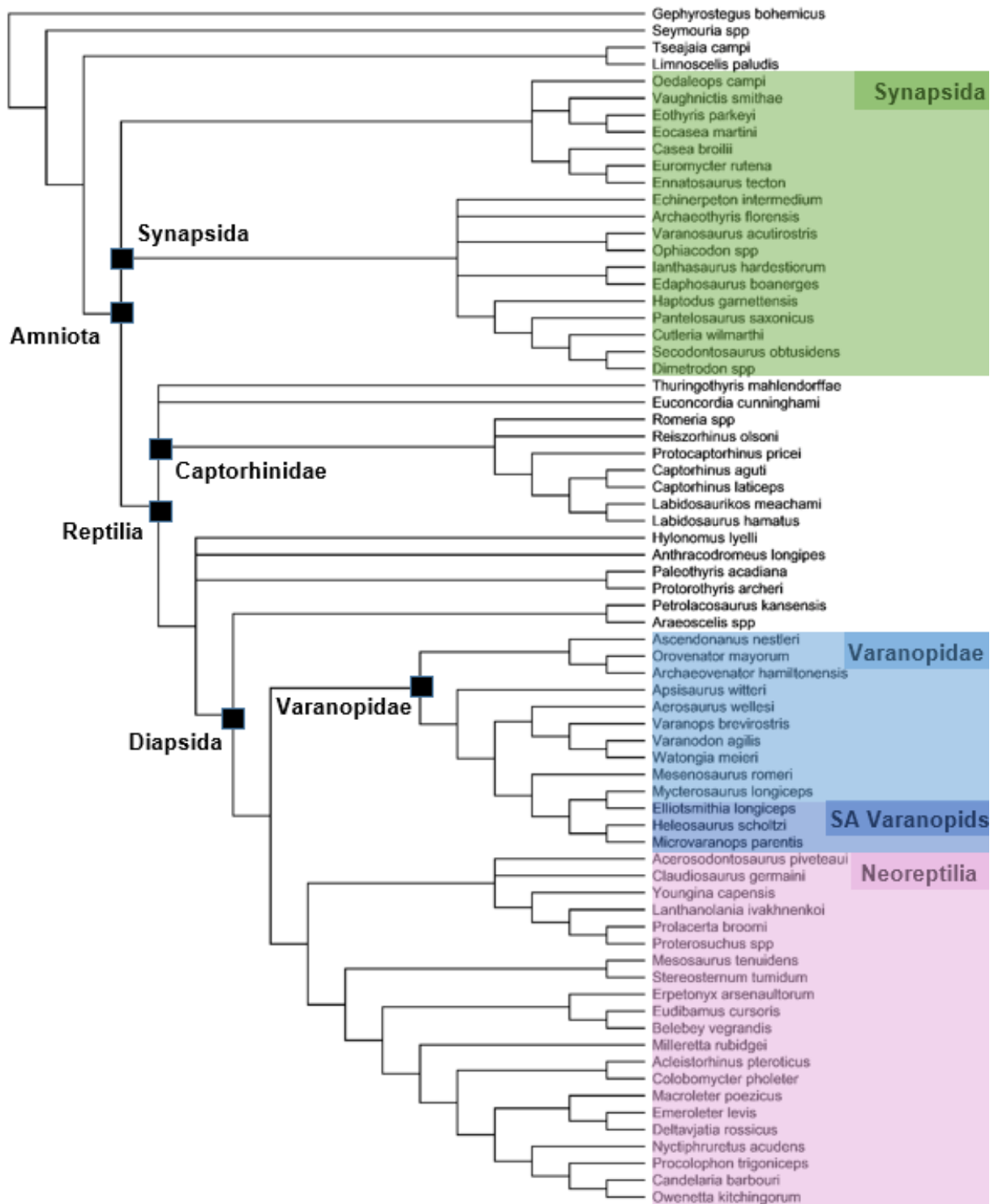


Figure 18. Consensus tree showing the phylogeny of amniotes recovered using the Ford & Benson (2020) character matrix on PAUP*v4.0a.

added to the new data set from the original dataset of Benson (2012). While the character states of 6, 10, 29, and 32 were modified. The inclusion of these particular characters was predicated

upon their observed morphological traits in varanopids. Furthermore, the character states were subsequently simplified, thus rendering them easily discernible and amenable to scoring within the matrix. The new dataset includes the following:

8. Temporal fenestra morphology: narrower dorsally than ventrally (0), ventral and dorsal margins of similar length, oblong (1), narrower ventrally than dorsally (1).

10. Lateral temporal fenestra size: approx. $\frac{1}{2}$ skull height (0), approx. $\frac{3}{4}$ skull height.

11. Skull, ventral outline of temporal bar in lateral view: (0) straight or weakly concave, (1) strongly anteroposteriorly concave, (2) straight but inflected posterovertrally relative to tooth row.

12. Skull, circumorbital tuberosities ornamenting jugal and prefrontal: (0) absent, (1) present.

14. Longitudinal position of posterior most portion of skull (occipital embayment); (0) approximately at the level of the occipital condyle, (1) far posterior to occipital condyle, resulting in a significant embayment in dorsal view.

29. Maxillary tooth number: between 15 and 25 (0), more than 15 (1), more than 25 (2).

31. Maxilla, precaniniform teeth count: zero to three (0), four to five (1), six or more (2).

32. Maxilla, Caniniform teeth: absent, maxillary teeth almost subequal in size (0), caniniform region present (1), large caniniform tooth, or two teeth distinctively larger than other maxillary teeth (2), more than two distinct caniniforms (3).

36. Lacrimal contribution to orbital margin in lateral view: large (0), small, restricted by a prominent ventral process of the prefrontal (1).

42. Prefrontal-maxilla contact: absent (0), present, anterodorsal to lacrimal (1).

49. Jugal, anteroposterior thickness of dorsal ramus: broad, temporal fenestra only weakly emarginates the jugal (0), narrow, jugal strongly emarginated (1).

65. Occiput slope: approximately vertical, inclined anterodorsally by 10-50 degrees (1), strongly inclined anterodorsally by >60 degrees (2), inclined posterodorsally (3).

99. Marginal tooth curvature: (0) largely absent, (1) distinctly present in the midpoint of marginal teeth.

114. Cervical ribs: absent (0), present (1).

ii) Consensus tree reconstruction

To reconstruct the phylogeny of South African varanopids in comparison to other varanopids, a similar technique to the one mentioned above was used. The heuristic search method was employed to identify the most parsimonious results. Using the delayed transformation (DELTRAN) optimisation strategy, PAUP produced a tree length of 599, with a consistency index of 0.3132, a homoplasy index of 0.6845, and a retention index of 0.6027. From this, 63,180 trees were ultimately retained. A strict consensus of all the retained trees was then condensed (**Figure 19**).

South African varanopids are grouped in a single clade. They form a taxon sister to Varanodontinae and are gathered into the subfamily Mesenosaurinae along with *Mesenosaurus*. The node that gathers all varanopids is supported by two unambiguous characters: 343) state 1 of distinctively pronounced caniniform teeth size, and 54) state 1 of a long postorbital-squamosal contact. The South African varanopids are supported by only one apomorphy 65) an occiput slope that is strongly anterodorsally inclined, and the decay index of 1. This support is weak, as it takes only one step to collapse this node. Varanopids among pelycosaurs have 3 unambiguous apomorphies, which include 113) a short length of the cervicals, 123) shallow neural excavation of the dorsal vertebrae and 176) distal articular surfaces of the femur positioned on the same level. The current tree also branches *Paleothyris*, *Protorothyris*, and *Captorhinus* more closely to eupelycosaurs than in Spinder et al's analysis.

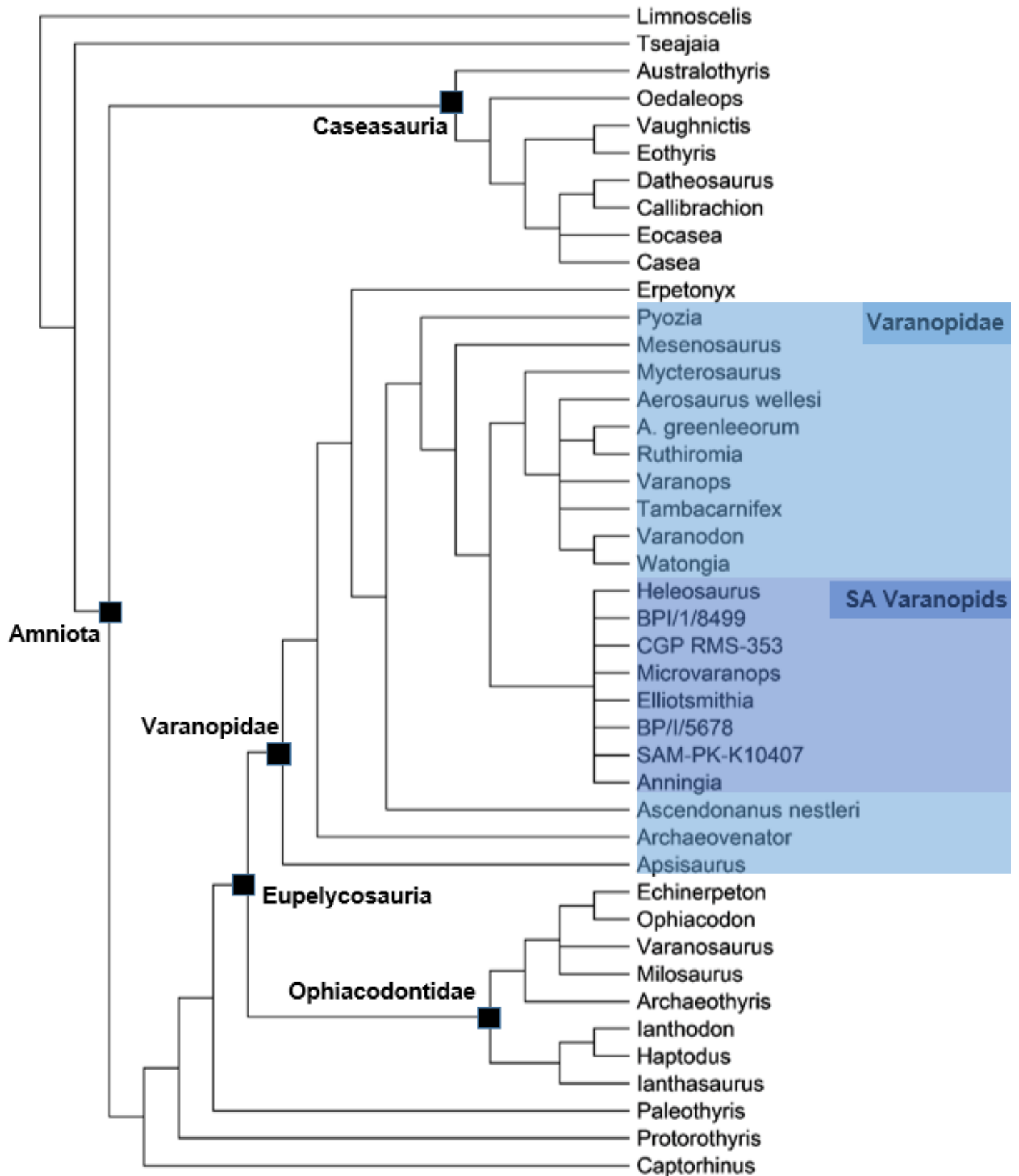


Figure 19. Consensus tree showing the phylogeny of amniotes recovered using Spindler et al. (2018) character matrix on PAUP*4.0a.

4. DISCUSSION

4.1 Comparisons and identification

4.1.1 Identification of CG-RMS353 as a varanopid

The skull of specimen CG-RMS-353 has i) strongly recurved teeth which are labiolingually compressed, ii) a lateral temporal opening that is anteroposteriorly elongated and occupies a significant portion of the postorbital region, iii) a prominent boss on jugal and postorbital bones, iv) a slender ventral temporal bar made up of the jugal and quadratojugal and v) exclusion of the splenial from the jaw symphysis (Reisz et al, 1998; Ford & Benson, 2020). The palate of this specimen also resembles that of *Heleosaurus* with a long and slender vomer, alveoli in the basiptyergoid neck, as well as posteroventrally recurved dentition of the transverse process of the pterygoid (**Figure 3**). These characters enable the classification of this specimen as a varanopid. The ornamentation on the posterior angular and surangular of this specimen is less pustulous than that of the holotype of *Heleosaurus*, suggesting an intermediate stage of development (see below). The presence of a distinct horizontal protuberance of the postorbital bone is shared with the adult specimen of *Microvaranops* (Botha-Brink & Modesto, 2009), and is more developed than that of the juveniles. Specimen CG-RMS353 also has a lateral ridge on the dorsal process of the jugal that extends ventrally to form a boss, similar to that seen *Heleosaurus* (Carroll, 1976), and not on *Microvaranops*. The posterior ramus of the maxilla slightly contacting the quadratojugal on this specimen is shared with *Elliotsmithia* and not in the juvenile specimens of *Microvaranops* (Reisz et al, 1998; Botha-Brink & Modesto, 2009). These observations along with the fact that the skull of CG-RMS353 is about 48.25 mm long, making it intermediate between the juvenile *Microvaranops* (which ranges from 40 to 43 mm) and the adult specimen (which is longer than 50 mm), suggest that CG-RMS353 may be a sub-adult (**Table 4**).

4.1.2 Identification of BP/1/8499 as a varanopid

Specimen BP/1/8499 has a poorly preserved skull and is thus best identified by postcranial features that include i) lateral excavations at the base of the dorsal neural spine (**Figure 8**), and ii) a slender femur that is three times longer than distally wide (Pelletier, 2013; Reisz & Dilkes 2003), which is shared with *Microvaranops* (Botha-Brink & Modesto, 2009). BP/1/8499 shares with *Heleosaurus* a midventral groove found parallel to two ridges on the centrum of the dorsal vertebrae (**Figure 9c**) (Reisz et al, 1998). The overall morphology of the specimen resembles

that of the holotype of *Heleosaurus* and juveniles of *Microvaranops*. The maximum length of the cranium from the snout tip to the posterior-most bone is smaller than that of the smallest juvenile described by Botha-Brink and Modesto (2009; table 1) (**Table 4**). Therefore, the specimen is the smallest known varanopid from South Africa and is here considered a juvenile. In addition to its small size, the juvenile status of BP/1/8499 is supported by the absence of osteoderms on the cervical vertebrae and poor ossification observed mostly in the manus and pes (**Figure 13 & Figure 17**, see discussion below) (Botha-Brink & Modesto, 2009). This is further supported by the extent of the curvature of the radius, unfused neuro-centrum sutures on the cervical vertebrae and the dimensions of the limb elements that are comparable to those of the juvenile *Microvaranops* (**Table 4**) (Botha-Brink & Modesto, 2009).

4.1.3 Comparison of both newly described specimens to Heleosaurus (Broom, 1907)

Broom (1907) described *Heleosaurus* as a lizard-like reptile with a long triangular shaped skull. More recent work by Reisz and Dilkes (1998) established that *Heleosaurus* was in fact the first South African Karoo varanopid ever named. Broom (1907) noted some cranial features and provided a brief description of the palate, shoulder girdle, axial skeleton and pelvic girdle. The second known *Heleosaurus* specimen described was SAM-PK-K8305 (Botha-Brink & Modesto 2009), which was later renamed *Microvaranops* by Spindler et al. (2018). This specimen comprises an aggregation of five individuals, an adult specimen with four juveniles.

In the reappraisal of the holotype of *Heleosaurus* by Reisz and Modesto (2007) the diagnostic characters given by them included the pustulous ornamentation on the angular and surangular (**Figure 20**). This character is also observed in CG-RMS353, though on the posteromedial surfaces of the elements (**Figure 4a**). The pustules are smaller in CG-RMS353 than in the reconstruction of the holotype made by Carroll (1976). The smoothness of the angular and surangular lateral surfaces of the latter specimen and *Microvaranops* is likely a result of overpreparation rather than ontogenetic variation. The available evidence suggests that the acquisition of such ornamentation along with osteoderms most likely took place during the subadult stage and subsequently continued growing during ontogeny.

Reisz & Modesto (2009) consider that the slight elongation of the largest marginal tooth in *Heleosaurus* is not a strong enough diagnostic character of *Heleosaurus*. Varanopids have homodonty, and the extent of preservation of the maxilla on the *Heleosaurus* holotype suggests that the preserved teeth are possibly post caniniform teeth. It is also possible that this elongation in *Heleosaurus* may be the result of different stages of dental eruption. As is evident in the varanopid *Mesenosaurus* from the Richards Spur Lagerstätte, varanopids experience tooth replacement throughout their life (Maho et al, 2022). Maho et al. (2022) also found that teeth replacement is independent of ontogenetic development in early terrestrial vertebrates. Therefore, the differences in the teeth sizes cannot be used to infer ontogeny.

The presence of a median groove dividing a longitudinal ridge on the ventral surface of the centrum of the dorsal vertebrae in *Heleosaurus* is also visible in BP/1/8499 (**Figure 20 & Figure 9**). This is because BP/1/8499 is the only other specimen that has the ventral surfaces of the centra of the dorsal vertebrae preserved and prepared. This feature is indeterminate in *Microvaranops* (SAM-PK-K8305) and *Elliotsmithia* (TM-1483) due to the absence of exposure of the ventral surface of the vertebrae and lack of preservation of the dorsal vertebra, respectively (Botha-Brink & Modesto, 2009; Reisz et al, 1998).

The presence of osteoderms in adult specimens of *Microvaranops* and *Heleosaurus*, but not in the juvenile *Microvaranops* and in BP/1/8499, is consistent with interpreting dermal ossicles as a character that appears at a late stage in the ontogenetic development of varanopids. The fact that there are adult specimens of *Microvaranops* and *Heleosaurus* with osteoderms provides insight on the extent of osteoderms along the axial spine. These osteoderms extend from the most anterior cervical vertebrae to the third or fourth sacral vertebrae. This developmental pattern of osteoderms is also replicated in modern crocodilians, wherein these bony structures emerge post-hatching and initially form in a dorsal position adjacent to the cervical vertebrae (Vickaryous & Hall, 2008). The holotype of *Heleosaurus* is about the same size as the adult *Microvaranops*, with a skull length greater than 50 mm (**Table 4**).

Therefore, the large *Microvaranops* specimen may be an adult of *Heleosaurus*, as originally hypothesised by Both-Brink and Modesto (2009). Similarly, the holotype of *Elliotsmithia* is even larger than all the specimens discussed above, as its skull length is approximately 60 mm

(**Table 4**). The larger size of the skull of *Elliotsmithia*, accompanied by the presence of osteoderms on the cervical vertebrae, is consistent with the interpretation of osteoderms as an adult feature (Reisz et al, 1998; Botha-Brink & Modesto, 2009). As presented above, characters such as the absence of osteoderms on BP/1/8499 (which otherwise preserves all the postcranial bones in articulation, even gastralia), suggest that this specimen is a juvenile and is consistent with its interpretation as a juvenile of *Heleosaurus*. Specimen CG-RMS353 lacks postcranial elements and therefore, the presence of osteoderms cannot be determined, but its intermediate size suggests that it is a sub-adult (**Table 4**).

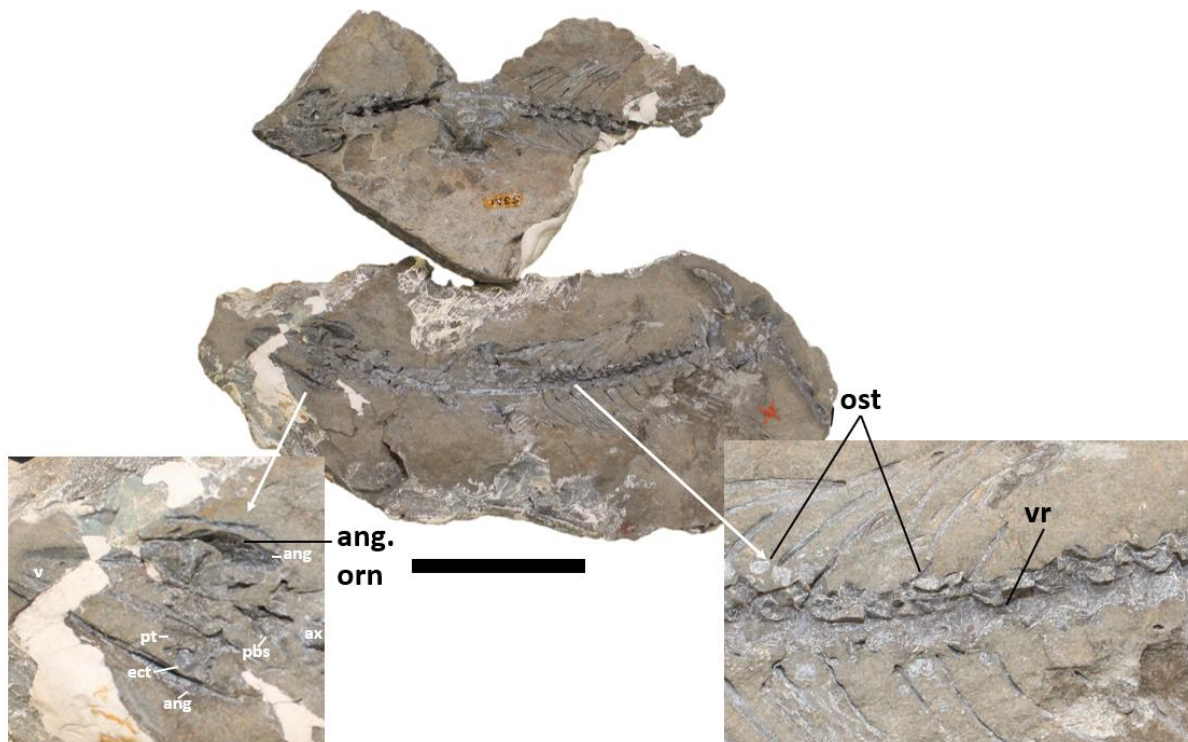


Figure 20. Photograph of the holotype of *Heleosaurus* SAM-PK-1070 showing its diagnostic features which include: the angular and surangular ornamentation (**ang.orn**), the ventral ridges parallel to a ventral groove on the centra (**vr**) and the presence of osteoderms (**ost**). Scale bar = 100 cm.

4.1. 4 *Elliotsmithia longiceps* (Broom, 1937).

Elliotsmithia was named and briefly described by Broom (1937) (**Table 1**) as a reptile, and he noted its similarity to the pelycosaurs *Anningia* and *Mycterosaurus*. He described TM-1483 as having a large pineal foramen positioned between anteriorly narrow parietals, a large orbit, a long and slender postfrontal, recurved teeth and a long single angular. Dilkes and Reisz (1996)

added a slender and long paroccipital process of the opisthotic, a neural spine of the cervical vertebra that is anteriorly inclined, an anteriorly inclined occiput and the presence of osteoderms on the cervical vertebrae (**Figure 21**) (Dilkes & Reisz, 1996; Reisz et al, 1998). The revised diagnosis by Reisz et al. (1998) compared *Elliotsmithia* to *Mycterosaurus* and the Varanodontinae, *Aerosaurus*, *Varanops* and *Varanodon* only.

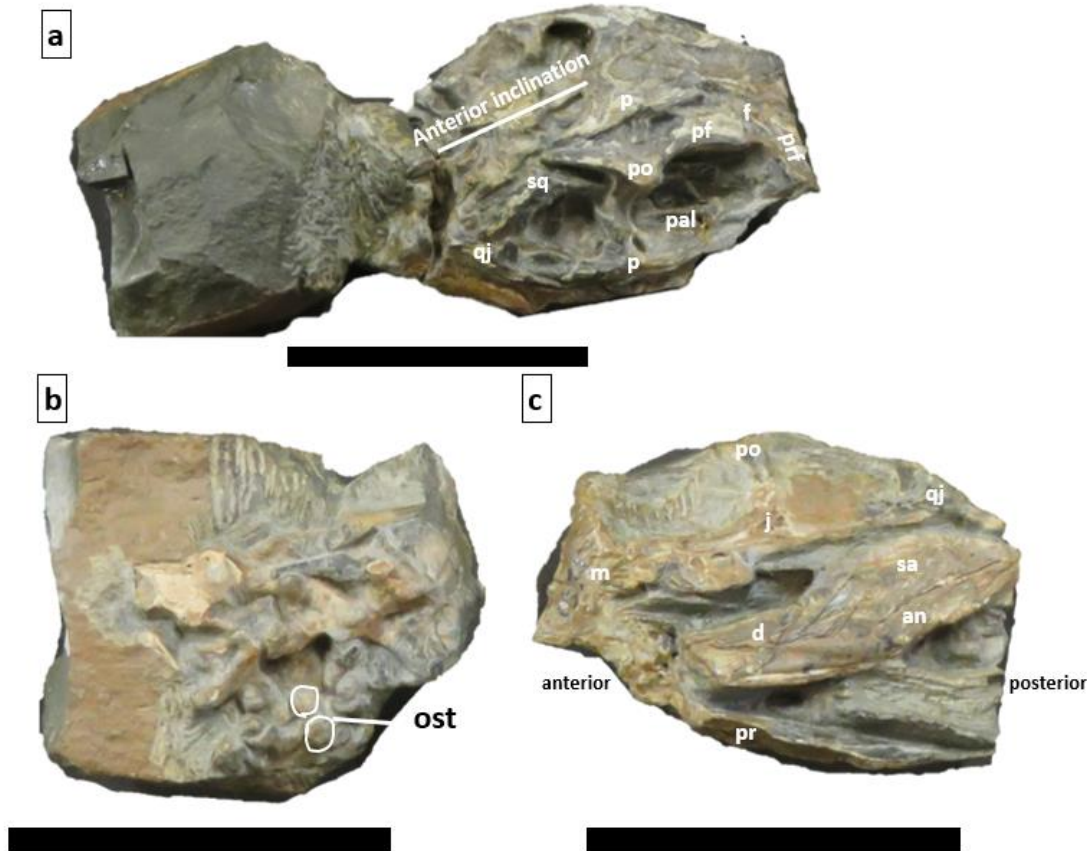


Figure 21. Photograph of holotype of *Elliotsmithia* (TM-1483) showing its diagnostic features in a) oblique dorsal view of skull, b) dorsal view of cervical vertebrae showing the presence of osteoderms, c) left lateral view of the skull and lower jaw. Scale bar = 110 mm.

However, some of the diagnostic features above are not unique to *Elliotsmithia*, as they are also found in other South African varanopids. The second *Elliotsmithia* specimen (BP/1/5678) described by Modesto et al. (2001) has a similar dentition to the holotype. This specimen comprises a skull with vertebrae 1-3 and shares the same preservation style as the holotype. Based on its large size (**Table 4**) and the presence of osteoderms (**Figure 21**) it appears that

the holotype of *Elliotsmithia* is an adult specimen (**Figure 21**) and is the largest described varanopid from South Africa.

The anteriorly sloping occiput of *Elliotsmithia* and the presence of osteoderms are similar to adult *Microvaranops*, but not the juveniles (**Figure 21 & Figure 22**) (Spindler et al, 2018; Botha-Brink & Modesto, 2009). The morphology of the opisthotic is indeterminable for the other varanopids, as the opisthotic is rarely preserved or prepared. The diagnostic feature of the anterior inclination of the axial neural spine in *Elliotsmithia* is only comparable to BP/1/8499 as the other specimens do not preserve a vertebral column. Although the axis of BP/1/8499 is poorly preserved, other vertebrae preserve distinguishable anteriorly inclined neural processes.

Based on the evidence above, there are no small individuals of *Elliotsmithia longiceps* and the ones known display anatomical features that are consistent with an interpretation of them as being large adults of *Heleosaurus*. I here suggest that the two genera may be synonymous.

4.1.5 *Microvaranops parentis* (Spindler et al, 2018).



Figure 22. Photograph of SAM-PK-K8305 *Microvaranops* holotype demonstrating its coronoid area.

Abbreviations: 2-5; juveniles, 1- adult. Scale bar = 100 mm.

Spindler et al. (2018) re-described SAM-PK-K8305. They argued that it did not belong to *Heleosaurus* and erected the new genus *Microvaranops*. The diagnostic traits recognised by Spindler et al. (2018) included the absence of serrations on the dentition, a flat coronoid, and that it differs from *Heleosaurus* in having a longer skull. The characters used to erect this new genus are, in my opinion, not very strong. The presence of unserrated teeth is not a reliable trait, as serrations can easily be lost during preservation and preparation. Serrations are also not visible on the teeth of CG-RMS353 which otherwise shares synapomorphies with both *Heleosaurus* and *Elliotsmithia*.

The distinction between *Microvaranops* and *Heleosaurus* as proposed by Spindler et al, (2018), based on the short skull in the former, is not accurate. Specimen SAM-PK-K8305 (adult *Microvaranops*) and the holotype of *Heleosaurus* are actually of a similar size. A flat coronoid does not support *Microvaranops* being different to the other described varanopids from South Africa, as the coronoid eminence is not flat but rather anteriorly positioned such that it is enclosed by the quadratojugal (**Figure 1**) and is covered by matrix on SAM-PK-K8305. This is also observed in CG-RMS353 (**Figure 1**). Therefore, based on this evidence, *Microvaranops* cannot be considered a valid species or a genus but rather a synonym of *Heleosaurus*.

4.1.6 *Anningia megalops* (Broom, 1927)

Broom (1927) described and named *Anningia megalops* based on a partially preserved skull with a skull roof that preserves a large pineal foramen similar to that of other varanopids. It also preserves the right lateral side of the skull with a large temporal fenestra, an orbital and postorbital region. Unfortunately, the specimen cannot provide any further information as it was destroyed through serial sectioning. However, the holotype of *Anningia* shares with other varanopids (including CG-RMS353) a triradiate jugal with a slender ventral bar, a dorsoventrally tall lateral temporal fenestra.

The illustration by Reisz and Dilkes (1992), shows the morphology of the postorbital and squamosal to be similar to that seen in *Elliotsmithia*. The dorsal ramus of the squamosal contributes most to the dorsal margin of the lateral temporal fenestra, almost excluding the

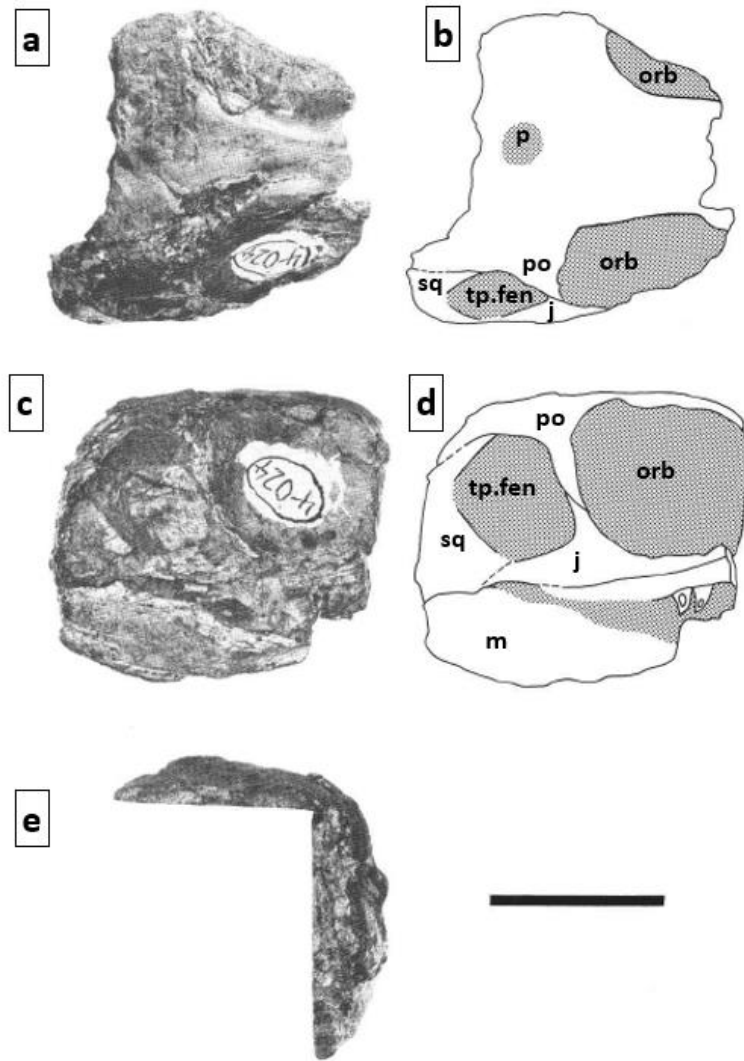


Figure 23. Holotype of *Anningia megalops* (Transvaal Museum N. 4024). (a) Photograph and (b) illustration of skull in dorsal view, (c) photograph and (d) illustration of skull in right lateral view, and (e) occipital view. **Abbreviations:** orb, orbit; tp.fen, temporal fenestra. Scale bar = 4 cm. Taken from Reisz & Dilkes (1992).

posterior postorbital process. This coincides with the ventral process of the squamosal making contact with the posterior process of the jugal.

The lack of information on the specimen as a result of poor preservation and serial sectioning led to an inability to diagnose *Anningia* as a valid taxon and was therefore declared as *nomen vanum* by Reisz and Dilkes (1992). I concur with this conclusion as *Anningia* lacks diagnostic features that separate it from the other varanopid species.

4.2 Conclusion on South African varanopids

Most varanopid specimens from the Abrahamskraal Formation are quite fragmentary. As a result, of all four species described in SA, only two are likely valid *Heleosaurus scholtzi* and *Elliotsmithia longiceps*. In addition, the two new varanopid specimens described here show a combination of anatomical traits that overlap between the two varanopid genera:

- Posterior ornamentation on angular and surangular
- Anterior inclination of occiput
- Anterior inclination of vertebral neural spine
- Midventral groove on the centrum is parallel to two ventral ridges
- Elongate skull

The re-examination of the holotypes of *Heleosaurus* and *Elliotsmithia* supports the idea that none of these specimens possess unique diagnostic characters which can be used to characterize the different genera. Many of these diagnostic features appear to be linked to the ontogenetic status of the specimens on which the diagnosis is based. Features found in larger specimens include a prominent postorbital boss, a large rugose jugal boss, osteoderms present, jugal and squamosal contact, quadratojugal and maxillary contact and angular and surangular ornamentation. These features coincide in TM-1483, except the latter which can only be seen on SAM-PK-1070. In contrast, these features cannot be found in smaller specimens which have open neurocentrum sutures such as the juvenile in SAM-PK-K8305 and BP/1/8499. The fusion of the opisthotic to the rest of the braincase is only seen on the largest specimen TM-1483, therefore, it is likely an ontogenetic feature as seen in dicynodonts and other therapsids such as *Lystrosaurus* (Cluver, 1971) and *Lumkuia fuzzi* (Benoit et al,2022). Therefore, an ontogenetic series can be hypothesised based on these features:

- Presence of osteoderms
- Horizontal protuberance of the postorbital bone
- Neuro-centrum sutures
- Orbit size relative to skull size
- Angular and surangular posterior ornamentation
- Body proportions
- Opisthotic fusion to the braincase
- Quadratojugal and maxillary contact

- Jugal and squamosal contact (exclusion of the quadratojugal from the ventral surface of the lateral temporal fenestra).

These characters strongly suggest that the SA varanopids, firstly, are not separate genera and species, and secondly, that the differences observed between the different specimens are ontogenetic rather than taxonomic. This is consistent with the result of the analysis of the updated Spindler et al. (2018) matrix, which recovers all South African varanopids as a clade. These varanopids share a single unambiguous character: (66) the strong anterior inclination of the occiput. This character is one of the diagnostic features of *Elliotsmithia* described by Reisz et al. (1998), but it is also present in SAM-PK-K8305 (*Microvaranops*, but formerly *Heleosaurus*, Botha-Brink & Modesto, 2009) and CG-RMS353.

Based on the above, it is sensible to regard all South African varanopid genera and species as synonymous. The first varanopid species discovered and named in South Africa was *Heleosaurus scholtzi*, which was named by Broom in 1907. Consequently, the remaining three varanopid species ought to be viewed as synonyms to *Heleosaurus scholtzi*. The morphological differences observed among these taxa are best attributable to ontogeny.

4.3 A hypothetical ontogenetic series of varanopids

The adult specimens of the described varanopid specimens from South Africa have a skull length greater than 50 mm, the largest being TM-1483. Although it is difficult to build a complete sequence of ontogenetic changes for South African varanopids due to poor preservation of the specimens and non-overlapping preserved elements, several cranial and postcranial ontogenetic morphological stages can be hypothesised.

The remarkable preservation of SAM-PK-K8305, which preserves both adults and juveniles on a single block, allows for a number of observations to be made based on dimensions in cranial and limb elements and the presence of osteoderms. As expected, body size increases with the progression of the ontogenetic stages, such that juvenile specimens have smaller skeletal elements. The skull size of the smallest known South African varanopid is 36.06 mm, which is the newly described specimen BP/1/8499. The juvenile skull sizes range from 36 – 43 mm, while the sub-adult stage is reached when the skull size is greater than 45 mm. TM-1483, with a skull length of more than 60 mm, has the largest skull of all the specimens, while the minimum skull

length of an adult individual is that of SAM-PK-1070 which is 51mm long (**Table 4**). In all the specimens where the skull is preserved, the orbit size also becomes relatively smaller as the skull increases in size.

The hypothetical juvenile stage is recognised by the lack of the following features: osteoderms, a postorbital protuberance, angular and surangular ornamentation and fusion of the opisthotic to the rest of the braincase. Open neuro-centrum sutures are present in all the juvenile specimens. The character of the posterior extension of the maxilla not reaching the jugal is evident in the smallest individuals of specimen SAM-PK-K8305. In the hypothesized subadult stage, the pustules on the angular and surangular occur on the posteromedial and ventral surfaces of both elements and are small as observed in the subadult CG-RMS353 (**Figure 4 & Figure 23**). The jugal boss also begins to appear and become more rugose as seen on CG-RMS353. The maxilla is beginning to extend posteriorly to reach the quadratojugal (**Figure 1**) at the same time the squamosal also extends anteriorly to contact the subtemporal process of the jugal. Skeletal evidence of the hypothetical intermediate stage (subadult stage) is not documented by preserved skeletal material but such a specimen it is hypothesised, would have osteoderms and cranial ornamentation (**Figure 24**).

The final ontogenetic stage is the adult stage which is exemplified by specimen TM-1483 as it contains all the hypothesised adult features and is the largest. During this stage, all sutures have fused, including the opisthotic to the braincase and the neuro-centrum sutures. The cranial bosses along with the dermal ossicles have fully developed. As observed on specimen TM-1483, the maxilla extends further posteriorly to make contact with the quadratojugal (Reisz et al. 1998) and the ventral process of the squamosal is in contact with the subtemporal process of the jugal. Botha-Brink and Modesto (2009) noted that the dorsal process of the squamosal to form a third or less of the dorsal surface of the temporal fenestra on SAM-PK-K8305. However, they did not specify whether this observation was based on adults or juveniles. As the dorsal process of the squamosal of TM-1483 extends further anteriorly to exclude the posterior postorbital process from the dorsal margin of the lateral temporal fenestra, it is probable that anterior extension of this process is also an ontogenetic feature. Hypothetically, both the dorsal and ventral processes of the squamosal would extend anteriorly as the animal grew (**Figure 24**). The co-occurrence of the morphological characters of the dorsal and ventral processes in the squamosal of *Anningia*

supports this hypothesis.

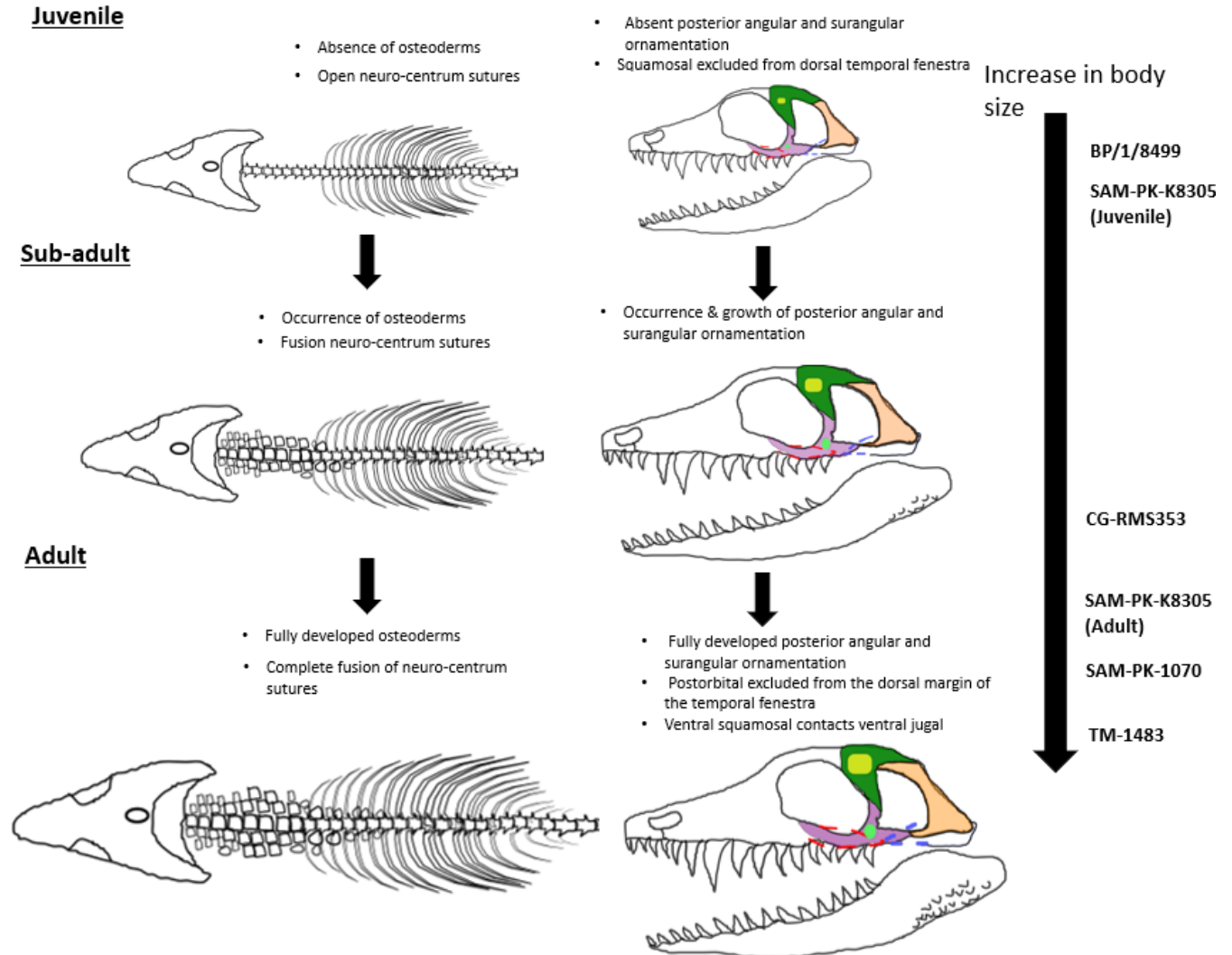


Figure 24. Illustration of a hypothetical South African varanopid ontogenetic series. Demonstrated in **orange** is the squamosal which shows the anterior extension of its rami to contact the jugal ventrally and excluding the postorbital from the temporal fenestra ventrally as the stages progress. The **green rectangle** demonstrates the horizontal postorbital boss that grows as the animal grows, while the **green oval** represents the jugal boss which also grows with the animal. The dotted lines demonstrate the medial contact between the maxilla (**red**) and the quadratojugal (**blue**) through ontogenetic development.

4.4 Relationship to other amniotes: Are varanopids synapsids?

The current consensus tree updated from Ford and Benson (2020) supports the hypothesis put forth by Ford and Benson (2020) that varanopids may be diapsid. This may be due to the design of the matrix which focuses on diapsid interrelationships, therefore sampling characters and taxa

with a bias towards diapsids while under-sampling synapsid characters (Simoes et al., 2022). Therefore, it branches the varanopid clade within diapsids and collapses synapsids into a polytomy. Varanopids possess only 9 synapsid features listed in the matrix, only three being unambiguously shared with other synapsids (when the clade is forced to be monophyletic). These characters include a free posterior margin of the jugal which results from the lack of an upper temporal fenestra (76), posteroventral contact between the jugal and the squamosal (90) and long and thin neural spines on the dorsal vertebrae (216). There are 5 unambiguous synapomorphies shared between varanopids and diapsids and include, an edentulous ectopterygoid (151), holocephalous ribs (211), a long posterolateral ramus of the frontal (66), occipital flange of the squamosal absent (92) and a low dorsoventral height of the axial neural spine (204).

The combination of both diapsid and synapsid synapomorphies within this group highlights the complexity of reconstructing varanopid evolutionary history. Despite this, there is strong comparative anatomical evidence suggesting that varanopids may be pelycosaur-grade synapsids, supported by the unequivocal synapsid feature of the lateral temporal fenestration (Sues, 2020). Ford and Benson (2020) stated that the morphology of the lateral temporal fenestra was a result of post-hatching heterochrony. With the current ontogenetic evidence, this idea is not supported as there are no observed modifications on the jugals of the juvenile specimens of SAM-PK-K8305 and CG-RMS353.

Benoit et al. (2021) further supported this conclusion with soft tissue evidence demonstrating the pattern of the maxillary canal in CG-RMS353 to conform with the pelycosaur condition. This complex pattern was further studied by Sibiya (2021) in an unpublished honors project. The results indicated that a simple and tubular maxillary canal, similar to diapsids, may be ancestral for amniotes. Thus, making the complex condition in synapsids synapomorphic to the group. Thus, the evidence suggests that varanopids should be classified as synapsids, which is further supported by the latest phylogenetic report on amniotes which group Varanopidae with

Synapsids (Simões et al., 2022). Based on the available evidence, it is preferable to classify varanopids as synapsids.

To conclude, despite that the cladistic analysis undertaken in the current study supporting the hypothesis of Ford and Benson, the classification of varanopids remains questionable and more data is needed to settle the debate.

4.5 Aspects of varanopid paleobiology

Most recent studies on South African varanopids have focused mainly on their taxonomy, with little attention to their posture. However, as more varanopid specimens have been collected and accessioned in collections in recent years, it is becoming more apparent that the posture and gait of the group warrants investigation. The recently discovered specimens offer valuable insight into varanopid biology, as they are the first CT scanned specimens of South African varanopids. The newly described specimen BP/1/8499 is especially noteworthy, as it preserves almost complete fore and hind limbs, including an almost complete manus. This can offer a deeper understanding of the taxa, its gait, posture, diet and paleoenvironments. According to Spindler et al. (2018), *Ascendonanus*, *Tambacarnifex*, and an unnamed Thuringian varanopid all display a greater curvature in their terminal phalanges, suggesting that they were adapted to an arboreal existence. While the terminal unguals of BP/1/8499 are not entirely intact, they do exhibit some curvature, suggesting that South African varanopids possessed claw-like unguals that allowed them to cling to trees.

According to current interpretations, the anatomical features of pelycosaurs, particularly terminal position of the femoral head and the ventrally positioned distal femoral condyles suggest that they were obligate sprawlers (Romer & Price, 1940; Blob, 2001; Jenkins, 1971). The proximal and distal ends of the femur on specimen BP/1/8499 are not sufficiently well preserved to observe these characters. However, the horizontal positioning of the femur of BP/1/8499 closely resembles that of pelycosaurs (Romer & Price, 1940). In his description of *Heleosaurus*, Carroll (1976) described this animal as a bipedal reptile, based on the configuration of the pelvis and femur. Carroll (1976) further described the ischium of the specimen to resemble that of a semi-erect diapsid *Proterosuchus*. In contrast, Botha-Brink & Modesto (2009) considered the ischium to be similar to the synapsid condition with it being flat and blade-like, and anteroposteriorly

elongated, and the femur being similar to that of the sprawling *Varanops* and *Mycterosaurus*. A reduced ischium is found on animals with a semi-erect posture (Blob, 2001). Accordingly, the anterior elongation of the ischium is indicative of a sprawling posture (Sidor & Hopson, 1998). In contrast, the limb proportions in BP/1/8499 which has a longer distal hind than fore limbs along with a robust pes resembles a condition similar to that of the bipedal reptile *Eudibamus* (Berman et al, 2000). The longer hindlimbs are used to lengthen the stride and increase the speed of the animal (Berman et al, 2000). In doing so, the shorter forelimbs would be lower, which would mean that the animal would assume a bipedal posture (Carroll, 1976).

The hypothesis regarding the possible bipedal posture requires further testing. Nevertheless, it seems like a stretch to consider varanopids as bipedal based on the observation of specimen BP/1/8499. Although the hindlimbs are proportionally longer than the forelimbs, the difference is not significant enough to support this claim. The length of the hindlimb of this specimen is 44.48 mm, while the forelimb is 37.12 mm, when compared to each other the difference is not significant enough to infer bipedalism. The early Permian bipedal reptile *Eudibamus* is calculated to have a forelimb length of 82% relative to trunk length, and the hindlimb to trunk length ratio being 135% (Berman et al, 2000). When *Eudibamus* is compared to BP/1/8499, with a forelimb and hindlimb to trunk ratio of 32% and 37% respectively, it is evident that BP/1/8499 most probably did not have a bipedal posture.

5. CONCLUSION

This research focuses on South African varanopids that have been found in the middle Permian Abrahamskraal Formation and presents additional specimens of this scarce fauna that enhance our understanding of varanopid taxonomy and comparative anatomy. Re-scoring of these varanopids on the data matrices of Spindler et al. (2018) and Ford and Benson (2020) were undertaken using the newly described specimens. The analysis of the former matrix points to these four described varanopid taxa possibly being synonymous. The results of the second phylogenetic analysis support the hypothesis that varanopids may not be synapsids.

The current study provides detailed descriptions of the cranial and postcranial elements of the newly discovered varanopids, including a full palate description, which shows that the palate of CG-RMS353 is similar to that of the holotype of *Heleosaurus*, and has also enabled a full

description of the lower jaw. New features are described which add to the phylogenetic dataset of varanopids to better understand the taxonomy of this group. Anatomical descriptions of CG-RMS353 and BP/1/8499 reveal a mosaic of features shared with all currently accepted species of South African varanopid. These features are interpreted as being adult and juvenile anatomical traits of an ontogenetic nature rather than being of instead of taxonomic significance. The holotype specimens of *Heleosaurus*, *Elliotsmithia*, and *Anningia* are here interpreted as being adult specimens, with *Elliotsmithia* being the most fully developed adult. This conclusion is drawn based on the presence of osteoderms, the morphology of the squamosal, the extent of cranial bosses, and the size of the specimens.

Accordingly, this study concludes that there is only one valid middle Permian varanopid species in southern Africa, *Heleosaurus scholtzi*, from the Abrahamskraal Formation of the Beaufort Group. The study of specimen BP/1/8499, which preserves fully articulated forelimbs and hindlimbs, indicates that the manus has morphological specialisation suggestive of an arboreal lifestyle and that the hypothesis of *Heleosaurus* being bipedal is unlikely.

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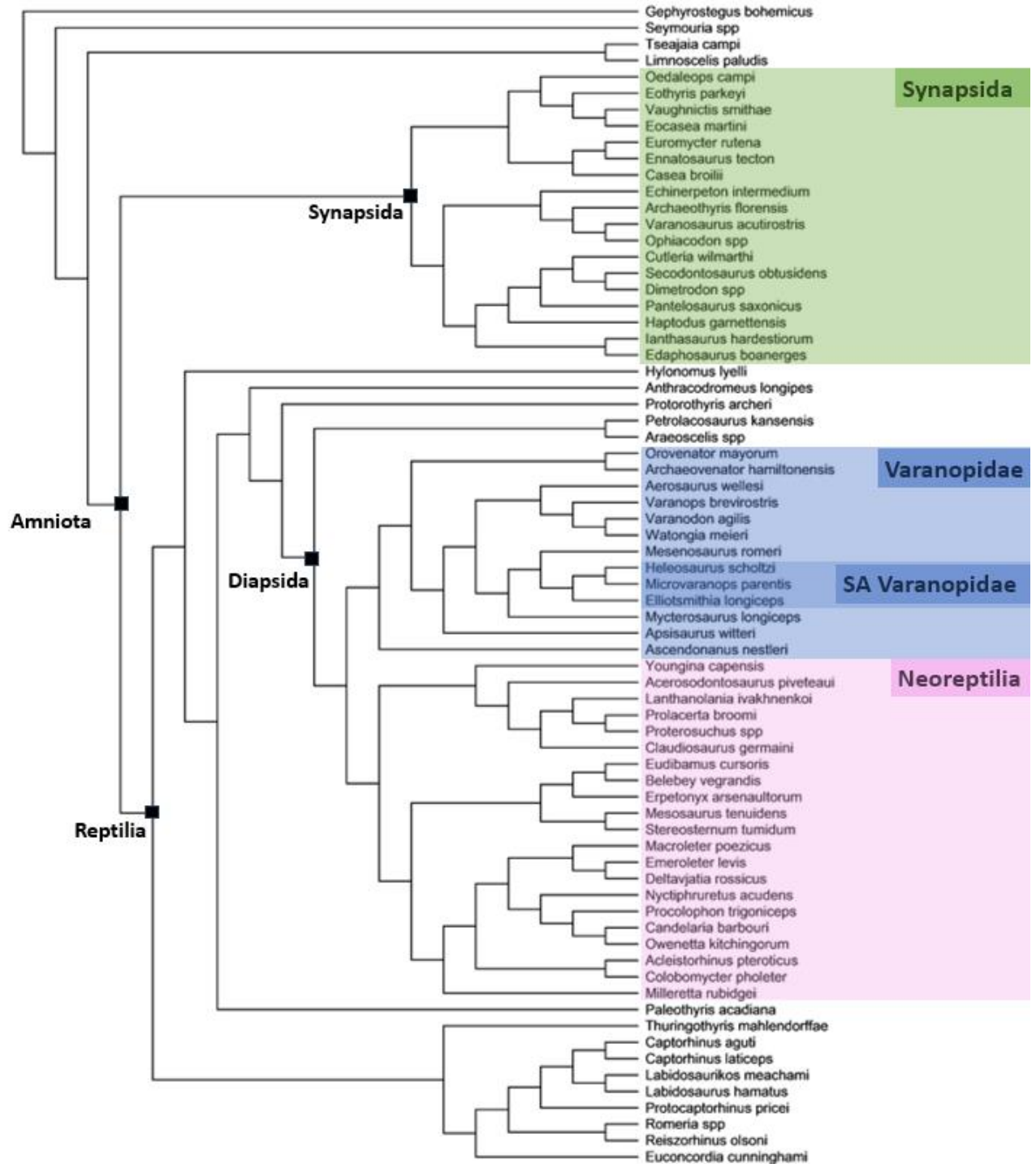
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7. APPENDICES

7.1 Appendix 1



Extended Data Figure 2. Bayesian analysis tree showing the phylogeny of amniotes recovered using the Ford & Benson (2020) character matrix.

7.2 Appendix 2

Table 5. Characters scored using Ford & Benson (2020) matrix.

Taxon	Characters (1-237)
<i>Gephyrostegus_bohemicus</i>	0000000000-00000000-00---0??000000-00000100?000--0000?0-0000--000000000-?0?0-000000??0000????????00?00?00?0-00000?1?0000-0?????1000??00111000??00000?0000-?01?00?0000000-0???00?????-?????????0?0?????????????????0????-??-0-?????
<i>Seymouria_spp</i>	000000?0000-00000000-0110000?0000100-0000000010000--0000?0-0000--000001000-00?0-000000?00000?100????00000000001100000100?00?1000?1?1-1000100001111000?00000????10?01?0000?010?1-0100000000101-00000000?000000110000000000?00?0?11?-00-0-00100
<i>Tseajiaia_campi</i>	00100000011000?10000-0111000???01110-000001000?00--000001-0000--000001100-1??0-000100?00?01?01-0000000?00101?0-11000?0?0100-000000?01000--0011001?0?101000000?00100??00000000?01001000000?1000000000000000011000000010?0000000?0-00-0-??0?
<i>Limnoscelis_paludis</i>	001001?0010-00011000-0100000???01110-000001000?00--011001-0000--000001100-0000-0001000001000000??0000??001110110100110?0100?0000?0?01000--001101000110100?0000-00100?00?0?00-01001000?00100000000000?00000011?100000101000000010-?0-0-??001
<i>Oedaleops_campi</i>	1001-000011000?11000-01111000-110100-010000100-000010111010010?-1000001011000?0-00?10?0?01000??????? ?????????????????????????0??0??0????????????0????????????????????????0????????????00001-100????100?00??????000?0?1?0001????????????
<i>Eothyris_parkeyi</i>	10?1-000011000011000-0111101??110000-01001-100-00001011001001011000000101100?00-0001000000000100??1?0????00??1?????00?10????0-0000??00100--0????001??1?1?000000-??
<i>Vaughnictis_smithae</i>	?010000001????11????0????????????0??????1-10????0?01110100101001?00010111??0-00?10?????????????????01?????01??0100?0????????????0?0??0?0??00?0??00?0??0-????????????10?????0????????????????? ??????????????????1?0001????????????
<i>Eocasea_martini</i>	??0???0????????????0????????0????????????????11001??10??01?0?????????0-00110?0000010?????? ?????????????????????????000?0????00--0????????????0?00??000?0000?000-00??00000????????????? ?????????????001001?0?0???1?0???0??
<i>Euromycter_rutena</i>	1001-000110-00000001000---00-110000-01000010??00001011101001011010000101000000-001100?001001100??10111?0000?????0100?10????0-000010000?0--0?????1?010?0100?????0?00?0001?????????0???00?0????????? ????0110000001????????????????????????
<i>Casea_broilii</i>	1001-000110-00000000-00---00-110000-01?0?-10?0000?01??01001011010000?010000?0-001100??01000100??101010000?01?0-0100010?0?0-0?0010000100--0001?11?001?1010000?00100?00001001-0000010101?0001-0?010001000?00100000100?00000001110010110?000
<i>Ennatosaurus_tecton</i>	1001-000110-00011001000---00-110000-010001100-?00100111110010111100000010?0?00-00110?0?0000111-??101?1??00?0110-010001001010-00?0???00100--00011110010?101?0000?0????0???1?01?0?00?101???0001-0???000? ?00???1???001????0???0???0010100?000

<i>Echinerpeton_intermedium</i>	???1-?000???????0???011100?1000?0????0????????????????010???????????????????????????? ????????????????????????????1?????????0????????????????00?01??0?10?0????010????????1 00????????????0??????11??????
<i>Archaeothyris_florensis</i>	0?000?100?0-????0???011100?10?0?0?-00?011?????1?0???100100-??000010111?0?0-0??1????01???????1? ????????????????????????0?0?1????1????0???1?????????0???0000?011-00?00?0?0???????????1 000??????0???00?0?00??????1?????
<i>Varanosaurus_acutirostris</i>	01000000000-11111000-011101111000110-000101100-0111000110100100-100100101110010-010100000000001-??01 000010010111??1100000?1100-00?000010000--100110001?11111?0010?000?0????01-0110?00?0????????1001? ????????????0001?0?0?001001011????1
<i>Ophiacodon_spp</i>	011000?0000-10011000-010001011000110-000001100-0111101110100100-100100101110010-010100000100000-0001 00001100?110-1100?1011?00-000000110000--10011000101011100001000000000001001-001100000000110001010011 00010000100010001000?0000000100100111
<i>Cutleria_wilmarthi</i>	0110010101????0???0?0111000?0?0?0????1??110?0??1?001101?0100-1100???0110?0?0-01?100?1010????????? ????????????????????????1?????1?01???01---10????????000-?0??10?100?0???0???00???1???01??01?0?1 0????0????????????????????????
<i>Pantelosaurus_saxonicus</i>	01110000000-0?00100?0?0101000?0000110-00010110?0?0??110011?1?0100-100010-0110?0?0-01?10???0????????? ????????01??010???0?????10?0???10001?0?0???100?????????????1????10????-00???00??110?1?0?01?0?1 00?00?0000?1?01?1?0?????01???????
<i>Haptodus_garnettensis</i>	01000000000-00011000-011101010000110-000101100-0101100010110100-110010-01100000-010100?1????0?0???00 ?00010000110-0100000111?0-1000001000110001---10000?101?000-1?0?0000000001-0000000?1101101011011 00000000?001100?01?0000??0?11110?0?1
<i>Secodontosaurus_obtusidens</i>	01100100000-00011000-011101010000110-001-01100-0101100010100110-110010-0110000100101001101000000?00 00001100111?0?010000011100-0000001100011101---0001001111?00?-10?01?100?01?-00010?01?????0100011011 ?0?????????????1?0?1001???1?1?????
<i>Dimetrodon_spp</i>	01100111010-00011000-011100110000110-001-01100-0101101110100110-100010-01100000-0101001101000000?00 0000110011111010000011000-1000001100011101---1000000111?000-1?001??10010?1-00010001?110?-0100011011 000100001001100101000?0010001111?0111
<i>Ianthasaurus_hardestiorum</i>	0??1-1?00?0-????000-011?0?0?000100-000001100-00?110001?110100-110010-0110?0?0-01?100????????????? ?????????1?????0?01?????1100???0?0???0???10?0???1????00?1?0???0???0?10-1000000?0?????????1???1 00?????????0???1?0?????????1??????
<i>Edaphosaurus_boanerges</i>	0111-110000-00000000-00----00-001100-00000110100001100010110110-110010-01100001001010001?1000100??00 1000100001?0-01?000011010-11000010010100001111100000101?000-1????00??1?11-10010101?110?0000010011 000100101?011000010000011000110100001
<i>Hylonomus_lyelli</i>	0011-000000-0001?000-01100000-000100-00000010??00010000001-0000--100000000-0??0-???10???0000???????? ?11???0001???0100??00???0???00?10?????????0?1???0??????000000?0?000??-00??0?0?01?????????0?1 10-?????????00010000?11???100001???

<i>Anthracodromeus_longipes</i>	0?0????????????????0???????0????????????????????00001-0000--1?001000-00?0-010100?0000001-??00 ????????????????????0-???????0????????????????????000?000001001?00?0000?0???????????1 10?00???????1?????0?01?????11?0?1?00
<i>Paleothyris_acadiana</i>	0001-000000-00000000-01110100-000000-000000100-00?10000001-0000--100001001-0010-01?100100000?1-??10 0?1??000010??0100?0000?0-0?0000?000?0--0????000?01?11100000-000000000001000?0?000001?011?0010?0?00?1 1000010101??10??10000111101111101000
<i>Protorothyris_archeri</i>	0001-0000?0-00?01000-0111010?000000-00000010??0010000001-0000--100001001-0010-01?100?000000?1-??10 0???000011100100100?00?0-00?0?0?00000--00101000101?1?0?000-00??000001010?0?00001?0100101000?10?? ?0-???????????0????????????????????
<i>Petrolacosaurus_kansensis</i>	00000000000-00011001001110100-000100-00000010??0001000010101100-110000?010010110010100100000001-0000 011??000010110100100000110000000?00000--0????00?101101000000-00100011011100-011?000?0001110110011011 10110101001?0111010011?1011111101011
<i>Araeoscelis_spp</i>	0011-000000-1?000000-0111000?000100-000000100-00010001101-1000-??00001001-100100101001000000000?00 00000000?1????00?10?00010100000100010--01---00?1000111000?0-00??011010110-010?000000?0010110011111 101?0?0100??001001001101011100101011
<i>Orovenator_mayorum</i>	00100000000-10100001100----011010101000011-101000110?????111100-1?00??01?????1001?1??????????????? ?1100000010110100110000110000?01-0000??00011001101011000101100????0???????????0????????????????? ????????????????????????????????
<i>Archaeovenator_hamiltonensis</i>	01100000010-00100001100----01?010101100001-10??001100111?110100-110000101101??0-00?10?1?00?0??????? 00??0000?101?010011000110-0?00??000010?0001100110101100000?0000?000000010000??10010001011-000????? ???????????????1?0?0?11?1?111101011
<i>Ascendonanus_nestleri</i>	0?10000000????0000?0110?000-00010?0?0?0010??0?0?0010?110100-11000010110?1?0-01?10??0000??????? 1????000????0100?0?????00?????0?0?10?0??00???????????????0??0?????0?0?0100000?01?????0??? 1??0111?1111??0?0?01??1?11010??100
<i>Aerosaurus_wellesi</i>	01101101010-00101001001000000-0?0000-00000010?00?10?????110101011?0010100?00-010?0?11?????00?0000 011??010???????0?10?????0?00?000?0?100000110001?1??00010110000?0?1001000?00?000001?0001?1010001 00010110?11010??01000??00010110??11
<i>Apsisaurus_witteri</i>	???000000????????????????????1?????????????????????1?100-1110001?11?10?????1????????????????? ?????00?????????00?100?1?0??0???????????0?????????????0001011?0???000?0?0???1?0???0???1?0?0?00?1 10110?????????????1110?????????????
<i>Mesenosaurus_romeri</i>	01101111000-1010001100110000?0001010001-1-10100011010101110100-101000101101100-01?10100000000????00 011??01101011010000000100-000001-00001000????0011011110000011000????100?0?0?00??100?0?????????00?? 0?0?011???1010?00?1??1???1?????????1?
<i>Mycterosaurus_longiceps</i>	011011?1010-?010?011?01000000?0000010001-??1010001101?1111101010101000101101??0-01?1???0010000????0? ?110000101???0100?0?0???0?000000000??0?????0?????111001011?0???01000000000??1?????????1-000??0?? ?0??0????????001?0?0?110?0?10?00???

<i>Heleosaurus_scholtzi</i>	011011110?0-00?00011101100?0?-0001010001-??10??00?101110?11010?-101000100101100-01??01?00000?0????? ?11??00101?1001000100???0-0??0??0?001000???0????1?1?100?????01?001000010?00?0101100??0?1-0?0?00?1 1?110111?010000?10?1111?0?00100??1??1
<i>Elliotsmithia_longiceps</i>	0?10111101????0001110100000?00000??1?1-1010?0110111111010101010001?0101100-01010?100????????? ????????01010?000100?110-0?00??000010001--?0?1101?10100?????01?0?????????????1????????????? ????????????????????????????????
<i>Microvaranops_parentis</i>	01101111010-00?0001110110000?-0001010001-??10??00?101110?110101-101000100101100-01?1????????????? ???????????????????????0-???0??00001000???00?1?1?1?100?????01?001000010?00?0101??0????1?0?0?00?1 1?110111?01?000110?0111?0?001?0?????1
<i>Varanops_brevirostris</i>	01101101000-00001101001100110-0000011000000100-001100101011010101?1000100001000-0101000101?0??0000?1 011?0000?1?????0?10????0-0000000010-1000001100?1?10110?01011000??1100?000100?00000?0001-?101010001 000?011011?0100110101000000010010?11
<i>Varanodon_agilis</i>	11101101000-0??0110??0110011??0000011000000100-001101?0?011010101100001000010?0-01?1??010???000??? ????????1?????0?0?0?????0?00??010-1000????0?????????010??00?1?110010?0100110000000????0?0??1 00?10?1??11010???????0??????????11
<i>Watongia_meieri</i>	???011010?0-????????????????????????????????1?? ??00?000?0011?????0?????0?0??01 00?00110110?1????????????????????
<i>Youngina_capensis</i>	00100000010-00000010-00----?000100-001-00100-1001000110111100-110000101001?111010100000010?0010110 00000000011110100?10001110000001-00????0???00?1?1?1?00??0-?01??000000000-0010101?0010?01-010001?1 10111?11?11?1010001111?00111100?01111
<i>Acerosodontosaurus_pivet eaui</i>	0??000000???????01??0???????00?1?????1-00100-??010??11??1?100-11?010??100???????1????????????? ?????????1?????????????????00?????010???????????11??10??0100?0?0?000?001?100?0????????????? ?0111110000??110??1????0??????????
<i>Lanthanolania_ivakhnenko i</i>	00?00??0?0-?????001000----0??00000??1-0010??100100??101-?100-110010??10???????1????????????? ?0100????1???????1?????????????0????????????????11???????????????????????????????? ????????????????????????????????
<i>Claudiosaurus_germaini</i>	0011-?00000-10000000-00----0??000100-101-1-10??000110011?1-1100-110010-010010?1101-11-0?1----01-??00 000??000011110100110?011100000??00000--00011000101011????0-??11?000001010-00??100100?0?1????000?1 1011?11010?011????1101100101100101011
<i>Prolacerta_broomi</i>	00101101001100000001100----011000100-101-00100-1001000010111100-110010-01001101101-11-001----0011110 00000000011110100110001110001011-01001100???010101111011??0-?11?11001?101-0111100110?1101-01000??1 11110??1?0??11100010111?001110?111?11
<i>Proterosuchus_spp</i>	00101111001110000001100----0??0?0000-101-0010??11?1000110011100-1000?0-010011?1101-11-0?0100??0?11?0 ?0000??00111101001?00?11100?1011-110?1101????010??1?11011??0-?1?1?111010101?001?100110?1001-00000?? ?1?10??????110?0?1?1100??10??1101?

<i>Thuringothyris_mahlendorffae</i>	0011-000010-00001000-00---0??0?0000-000001100-00000000101-0000--10000100?-0010-010100100010??1-??00 ?000??0?1111?0100?0?1?1????0000?0?0--????0000????????????10?0?0??1010?00?0000???001????????1 00-00?10011?1?????010?0???01?100110?
<i>Captorhinus_aguti</i>	1001-000010-01011000-11110000-001100-000001101-00000000001-0000--100000100-0010-01-11-100010001-??00 00?0000011111010010000--110000001011010000111010001111100000-00100000100010-010000000010000000010001 00-?0110000?101010000001100010110100?
<i>Captorhinus_laticeps</i>	1001-000000-01011000-01110000-001100-000001101-00000000001-0000--100000100-0010-01-11-100010001-??00 0000?00011111010010000--11000000?011010000111010001111100000-0011?????0???-01??0000?0????????????? ???????0?????????????????????0?????????
<i>Labidosaurikos_meachami</i>	0001-0000?0-01?11000-10---0??011100-00000110??00001000101-0000--100000100-0010-01-11-100?10001-???? ?00??00011111100100??--110?00001011010000111000011111?010-0????????????????????????????????? ???
<i>Labidosaurus_hamatus</i>	0001-0010?0-01011000-00---0??001100-00000110??00001000001-0000--100000100-0010-01-11-100010001-??00 000??00111110100100?0101100000?111010000111100011111?010-0????????????????1????0????????????????? ???????0?????????????????????0?????????
<i>Protocaptorhinus_pricei</i>	1001-000000-01011000-0111000?001000-00000110??00000000001-0000--100001001-0010-01-11-?00010001-???0 0????????1?????00?0?0--110?0000?001?10?0???0????1?1????????????0???01?1????01?0?00?0???01????????1 ??-????0?????????????????????0?????????
<i>Romeria_spp</i>	1001-?000?0-01011000-0111000?001000-00000110??00001000001-0000--000000000-0010-01-11-?000?00?1-??0 00?????11?100100100?0--110??000?00100--0????0100?1?111???0-????????????????1????0????????????????? ???????0????1?????????????0?????????
<i>Euconcordia_cunninghami</i>	?001-100000-01?00000-0100000??00100-00000110?-00000000001-0000--100???00?-0010-01-11-100010001-???? ?110000001???0100110?0??1100?000100?0--0????00?1??? ???
<i>Reiszorhinus_olsoni</i>	000000?1000-01011000-0110000??111000-00000110?-00000000001-0000--000000000-0010-01-11-1000000?-???? ?????????????????????????????00?0???00100--001101000?11111000010????????????????????????????????? ???
<i>Eudibamus_cursoris</i>	??11-00001?????????100---????????????0????1?11???10???0??1?10????000?01?01??1--1????????0????? ?00?????11???1111?0?0?1?????0?????10--?0????????????????????1????????????0?0?-0000????1?????0?1 0?1???????0??????11111?000?111-?1110
<i>Mesosaurus_tenuidens</i>	0011-000000-00-00000-00---00-0?0100-000-00100-00000000?01-0000--100001001-1010-001100000001?01-??00 ?00??00101?11010000000--??00?0?0?000?11001---0010?0?11000000-??00?000?10010-000010010000101-110000?1 10110?10?0000?000001?1100100100101001
<i>Stereosternum_tumidum</i>	00100000000-00?10000-00---00-0?0100-000-??100-??000??????????0-??0?0?10??-?0?0-00?1??00????????????? ?????????????????????????????00?????000110101---001?0?0???000?00-??0000?00100?????0100100?0?1-1-110000?1 10110?0100?0???001011?0?0?110?101001

<i>Erpetonyx_arsenaultorum</i>	??1000000???????0???00----?0-??0?0???????1?????010???????10?????0???????0???00110?0?00?1?0?????0? ?????????0???01?00???????1???0?????11?????????1?????0?00????0???0???????????01001?1???0?????????1 ?0?1010?01?????00?00110010?1110????0
<i>Belebey_vegrandis</i>	0011-000010-00000000100----0??000100-0000011011000100?10011?1011-10000100110010-1--100??00?1?01-??01 ?00010??11?0-111101001101100?0??00010--00011100101011100010-????????????????????????????????? ??1?????????1?????????1?????????????????
<i>Macroleter_poezicus</i>	00000100000-00001001101000000-000100-001-0010110000011110110101101000000001??00-00-100100?01??0???11 ?00??0001?1101000100111110??1?1-?0??10?00101??1?1?1?00001?????????????????????????????????1??01??0?0? ?01?????????????????????????0?????11?0?
<i>Milleretta_rubidgei</i>	0000000?010-?000?000100----0??000100-00001-1011?001000110100100-010000001010000-001100000000??1-??00 0111-???011??0100?10?0101100?001-000110100101000?011110?1?0-?11?0??????0?00?0100?0?0011-??00?0?1 0010??0???1?1?????11110?001?????1???
<i>Acleistorhinus_pteroticus</i>	00000000010-0?000010100----0??000000-001-0010??00001011000101010010000100001010-00010?0?0100?101??00 ?11????0011110100?10?01?1101?00??0??1010?????01?1?1?100????????????????????????????????????? ?????????????????????????????????????
<i>Colobomycter_pholeter</i>	0001-100010-00011110101110000-000000-011-?-1011000110?100110101101000010100?0?0-00-11-??0001??????? ?11???0?011110100011?110?0?00??000?10?001100001????1?0000????????????????????????????????? ?????????????????????????????????????
<i>Nyctiphruretus_acudens</i>	0001-000000-00000000100----0??000100-001-1-101100000010101-0100--10011-000-1000-00?1001?010100????? ?00??00001?110100010?01?110??1???00011100???000101???100?10-?????????????????????0??1????0?????0?1 ?0?????0?????????????1????101??00?0?
<i>Emeroleter_levis</i>	00000000000-00000001100----0??000000-101-00101100010011101-00010-100000000-?0?0-00?10??0??1??????? ???????001??0100?1??1111??1?????10?0?????????1??0???1????0??000?0??0??100?1???????1??0?1 1???0??1?00?1??????111?00011??10011
<i>Deltavjatia_rossicus</i>	1001-001110-00010001100----00-000100-1000000011000--111101-00011-100001100-1000-0011001001011?01??11 000111000110-01100?0011011110101-0?101010011111000111000010-0?1?0??00?0?01-0???101101?0?0?0?11?0?1 ?0?00?0?0?0?1????0000??10001???1??01
<i>Procolophon_trigoniceps</i>	0011-000011100000000100----00-001100-011-00101100000010?01-0010--10001-110-0000-00-11-101---100-??00 0?01-0?00111101010100010111101?1-001011000111010101111100010-??000?000010??-00??100?01?0101-0?0100?1 00100?10?0011100000001101?0111?11?0?
<i>Candelaria_barbouri</i>	10100000000-0000000010100000?00?100-001-0011?????1001110010100-010011-0000?0?0-00?1????????????????? ?????????011?01???????????0?0???1??? ?????????????????????????????????????
<i>Owenetta_kitchingorum</i>	00100000000-0000000010100000?000100-011-001111?0000010000-0100--10011-000-0000-00-11-100001010-??01 000??000011110101010001?110001????01101100010001010111100000-??0???000010?0-00?00?0101?0?01-??01?0?1 ?11?0???????1??????11?0?0???????????

7.3 Appendix 3

Table 6. Characters scored using Spindler et al. (2018) matrix

Taxon	Character states (1-183)
<i>Limnoscelis</i>	0000010- 00000001110000?001100100000000000110?000?000000?00?00?010010010001100?01?000000?100000001000000?010001000?0110?0011 000110010100???1?00000001101001??1000100001?00000010???00
<i>Tseajaia</i>	0000010?- 00000001110000?0?0001000000010000000?1?0?101100?10?10?000010110?010?0?0110000001100000001000?001?10001110?0110?0011 000?0?110000001100101000110100???1?00101000100?0?00???1?
<i>Australothyris</i>	?010?0100?0001???0?00?0?010?0?10?1??00?01?00010?11000001001100000001??00?100?11100101?10000????10000??0??1?????1? ???0?01???110??
<i>Erpetonyx</i>	011??0????????????????00??00??0?0?1?11000? ???????0? ???????00????????????0000??0?00??1???011000??0?0?1??0???1000 1011????????????100??0?00110?01????011?1110100001?0?1100010
<i>Paleothyris</i>	0000000?- ??000?0000000??0?011100?0000??010?01?000?101011?00?00?000000011?100?10000???100?00?0??1???0?000000011110?00?0?000001 010001010?100?100?000110000?00?110010010001?11001101010
<i>Protorothyris</i>	0000000?- 00000100010000?0?01010100000000001?100?000?100010?00?00?000000001?100?10000??0000000001????10?000??101??10??100?00010 1000001010011????0?010????0??00110000???????????????????
<i>Captorhinus</i>	0010000?- 00000100110000?0001101000000000010000?000?100001?00?00?0???001110010?1000001000001000001100?0?001010011100?0010?0000 000110010100100110001000100001000110000110100001000111010
<i>Oedaleops</i>	?01001111000001011100010000100101000100010110110001000100010100010001????????????????????1?0?0?0?????00?0??0?0??0?1? 0?0?0?0?011100??1?110?0?00?????100??010010??????0110???????
<i>Vaughnictis</i>	?11???100?0?1????1?????????1?????0?0?0?1?01?00010?01001?010001?????11?????10??????000?0?0?001???000????????0????0?0 0?1????????????????????????0??????????????????011????????
<i>Eothyris</i>	??10001010?001001110001001?1011010001000001101000000001000101000100000?01?00100?0?11011100?10000????0?000? ?????????? ???
<i>Datheosaurus</i>	?110??1????1????????11????????????????????0? ???????1 ?????????????????????????????????????1?0? ?????????0? ???1?0? ??????????1? ?00? ??????????????1?101100????0001?????????????1?001?
<i>Callibrachion</i>	?1????????????????????11??????01??1?0? ?????????00? ??????1? ???????01?? ??0 ?1?????1?1??????1?0?01????00111?????10???????????

<i>Eocasea</i>	0?????1??0?00?1???????????1????????????????00000?0000101?01?00000???????????0??0?0??0000?????????001000001?00??100?0 00100???????????1??????0??0101????????????????0??11??010
<i>Casea</i>	011001101000001001100?11?00101??000?1?000??0100000000100010?00110?01101010010100001110101?00000?0??0?001?10011100? 0100?100111?00?10?0?1011?11000001000?0000000010????0?00000111110
<i>Echinerpeton</i>	????????????????????100?1?1?000????????????????????????????????0?0????????????0?0????????01??000?11?0100?1000 ???001??????0?0????????????????0100??????????????10101?
<i>Archaeothyris</i>	?00???10??0??10?????0100?1?10100??????111010?????110?11000??0??1?0????????0?0??1?10??0??????0010??1011110?0100?1 000????0???????????1?00??110??1?0001100??????00????00?1?
<i>Varanosaurus</i>	00011010000011010001100?0110101000010110110100001110111000000110000101000110?01010001100000111000?0?00100000111 0?0110?000000????1???0010001100??110011110????001???????01011101111
<i>Ophiacodon</i>	0001011000001?000000?010001010010?010?1?11110100000010111000000110010101100110?000100011010001110000000?1?01001111 ?0100?110000000011000?10001?000011001101001000010111100001010101001
<i>Ianthodon</i>	?001001001?10000001??00?000100000000?00011110101001000111000?1?001010??1110??0?????00000001?0?10?000?????01?11?01 ?101000?????01001?1????????????????00?0000???????????????????
<i>Ianthasaurus</i>	0001??100101000?0????00??0?010100000?00001101010100111011100001?0??1??111?0????????000?00010??11?00??1111?1?000 111000?0???????011?1?00??0??0???0000100??0?1?0??0000?1??1??
<i>Haptodus</i>	00010010010100000101000??00010000000001001111010100111011100001?00??00111110?0?00111?00000000100011110001??1?0?111? 010111000?00010010101111?0010?01010?011000010010??1???001001111110
<i>Milosaurus</i>	??00?0??0??1?????0?0?0?0?? ??????????00??????????110????????????????0?0?110111?
<i>Archaeovenator</i>	01011111000000010??1100??00010???10001001100011010001100?00?0100001000001010100?000????100000010?00?0000??00011110? 1100?0?10010001?0??00?10??01?110???10?0????????????????11?01101110
<i>Pyozia</i>	?1?????1??????1??1?????0?01????????????????????????????????000?0??011??00?1011??0??100??0?01?????000?1?0?11????????? ???0110???
<i>Apsisaurus</i>	??????11??0??1????????????0?0?????????????1????????????01000??????0?01??0?0?0??0?0000?????000????11?1?0??1?10000 0??000101100??0??01????10??0?0??11011??????1110???????
<i>Ascendonanus_nes tleri</i>	010??0110??0001??00??00??0001001??00?10?101?01?00001110100100?00001?00001???101100?00??100?0?00?????100010000?1?10??1 00?0010000000??????01100????0010001?????1111110100111???11?0010
<i>Mesenosaurus</i>	0101111100100011000??111000010010110010111100110010111110110100001100011010101011101000000?1100??11101000????0 ??100?001001????0??1???1100?0??1110110??0?0100000010?111111110?001
<i>Mycterosaurus</i>	?001111100100011000??11100?011010?1?0101111?0110010?111?10?10100101?10????010101111?0100?0?0????????1111?0?1?111?11 0100010?????00??1010?1?1?101?00??001?1100????????0101?10001?

<i>Heleosaurus</i>	11????11?01?0?1????????????0??01????0?????1????????????0?0?0??001010101010?1?1?1??001?1?00??111?10?01?110??100?0 010??0??000??1??0??01110????????????????????1?????????
<i>BP/1/8499</i>	?10????11???????10???????0????????????????????????????????0????????????????????????????111???10000?11??1?0- 001000???????????0??
<i>CGP-RMS353</i>	?101??1110?0??1??01??0??1??10011?10??0?0?1??11??1???????????000????00100?0???????????0?00101011???111????????????????? ??
<i>Microvaranops</i>	110111110010000?000??11100?0001101?0010011000110011011100110100001100?????????????0111?100?1?????????1111???0?0?0??1 0??00100?0?0?0?????1????1??11001???????11111100000111???10?00?
<i>Elliotsmithia</i>	110????1100100011???????????0??1???100111?0110111011110110100101?00?0?????????101??0?00?????0??1111?1?0???????1??? ??
<i>BP/1/5678</i>	110????1100?000?????????????0?1101???1???1??01?00?1?111?01?0?0?????????????????????????1?0?0?????????111???????????1????? ??
<i>SAM-PK-K10407</i>	???1?????????????????1110??0?1?0?????????????????1?????011?1????????????????????10000??1?????111?????????????????1?? ??
<i>Anningia</i>	??????110?0000????????????????????????????????01?0?1??11?101?01?0?????????????????????1?????1?????????1????????????????????? ??
<i>Aerosaurus_welles</i> <i>i</i>	00010111101011110010?011?000110100?00000110?0111?1??111110??11011010??01?0010111011110100001001??001110??01?01?11? ?101100001111100110?1?011?0??0?00101100110?000101101011000?0111001
<i>A._greenleeorum</i>	??1110????????????????????????10111??????0????? 1???111????111?????????????01110?0??????0??????1?0??
<i>Ruthiromia</i>	??1????????????????????110??????1?0????00?????????0??11?11?110???0 ??????1?????11?00?01??0011?0111?000?????????000??1111?
<i>Varanops</i>	001111111010111100011011110011010000000011000111?0?01101100??101101010?1?00??11?1?1110100011101?000011100?01101111? 110110000?01010011001101110110101001100000?000100101?1101010111001
<i>Tambacarnifex</i>	0??010????10?111?111110?00? ?????????????1??????0100111??0010001??1010110??01?1010
<i>Varanodon</i>	00111111100011110001101111?0110100?0000011?10111?1??110?000011011????1???????????1111?100?1100??0???1110?10110111?11 0101100000?0?????0?11??????????0111?000?00011010?111??????????
<i>Watongia</i>	??????1110????1???????????0???????????111?1????1?1???????01????????????????????0???????110?????01?11?1?101100 ??001?????0??????????????01100000?000100101110??????????

7.3 Appendix 4

The character state (–) stands for unapplicable, as it represents the features that are not preserved on the specimens or features not found in the specific taxa. The term Afrothyra, represents all South African varanopids (Spindler et al, 2018).

Table 6. Character state changes made on the Ford and Benson data matrix.

Character	Taxon	F&B State	New state
78	<i>Microvaranops</i>	0	1
79	<i>Elliotsmithia</i>	0	1
82	<i>Microvaranops</i> & <i>Elliotsmithia</i>	0	1
82	<i>Heleosaurus</i>	0	?
132	<i>Elliotsmithia</i>	?	0
134	<i>Elliotsmithia</i>	?	0
135	<i>Afrothyra</i>	?	1
136	<i>Afrothyra</i>	?	0
137	<i>Elliotsmithia</i>	?	0
138	<i>Elliotsmithia</i>	?	1
144	<i>Afrothyra</i>	?	0
145	<i>Afrothyra</i>	?	2
146	<i>Elliotsmithia</i>	?	1
148	<i>Elliotsmithia</i>	?	0
151	<i>Elliotsmithia</i>	?	1
152	<i>Elliotsmithia</i>	?	1
153	<i>Afrothyra</i>	?	0
154	<i>Afrothyra</i>	0	-
164	<i>Elliotsmithia</i>	?	0
166	<i>Microvaranops</i>	?	0
167	<i>Elliotsmithia</i>	?	0
168	<i>Elliotsmithia</i>	?	0
169	<i>Afrothyra</i>	?	0
175	<i>Elliotsmithia</i>	?	1
176	<i>Elliotsmithia</i>	?	-
180	<i>Elliotsmithia</i>	?	1
181	<i>Afrothyra</i>	?	0
182	<i>Elliotsmithia</i>	?	1
183	<i>Elliotsmithia</i> & <i>Microvaranops</i>	?	1
185	<i>Elliotsmithia</i>	?	1
187	<i>Elliotsmithia</i>	?	1
190	<i>Elliotsmithia</i>	?	3
191	<i>Elliotsmithia</i>	?	1
192	<i>Elliotsmithia</i>	?	0
200	<i>Heleosaurus</i>	?	1
223	<i>Heleosaurus</i> & <i>Microvaranops</i>	?	0
224	<i>Heleosaurus</i> & <i>Microvaranops</i>	?	0
228	<i>Heleosaurus</i>	?	1
229	<i>Heleosaurus</i>	?	0
231	<i>Heleosaurus</i>	?	1