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# Revision of the Scylacosauridae (Therapsida: Therocephalia)

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The abundant, primarily middle Permian therocephalian family Scylacosauridae is comprehensively reviewed and revised. The 33 nominal scylacosaurid species from the *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa are reduced to seven: *Alopecodon priscus*, *Alopecognathus angusticeps*, *Glanosuchus macrops*, *Maraisaurus parvus*, *Pardosuchus whaitsi*, *Pristerognathus polyodon*, and *Scylacosaurus sclateri*. The scylacosaurid records from the earlier *Eodicynodon* Assemblage Zone (previously referred to *Glanosuchus* and *Ictidosaurus*) are recognized as a new taxon, *Eutheriodon vandenheeveri*. Scylacosaurid records from the later *Endothiodon* Assemblage Zone consist of two long-snouted taxa (the long-ranging species *A. angusticeps* and *P. polyodon*) and a short-snouted taxon (*Hyorhynchus platyceps*) possibly restricted to this zone. The revised identifications presented herein demonstrate that there was substantial scylacosaurid turnover between the *Tapinocephalus* and *Endothiodon* AZs, corresponding to the end-Guadalupian extinction.

**Keywords**: Synapsida, Karoo Basin, Permian, taxonomy, biostratigraphy.

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## INTRODUCTION

Therocephalians were one of the major subclades of non-mammalian therapsids, and encompassed a broad range of body sizes and inferred ecologies throughout their lengthy evolutionary history (middle Permian–Middle Triassic) (Angielczyk & Kammerer 2018). Therocephalians first appear in the Wordian *Eodicynodon* Assemblage Zone of the South African Karoo Basin (Abdala *et al.* 2008), with the earliest known records belonging to a group of mid-to-large-sized, large-fanged predators called Scylacosauridae. Scylacosaurids are one of the two therocephalian families often called 'early therocephalians' or 'basal therocephalians' (the other being Lycosuchidae), that is, those therocephalians outside of the diverse subclade Eutherocephalia. Despite being an abundant component of middle Permian faunas (Smith *et al.* 2012) and having high diversity (at least nominally), scylacosaurids have received little research attention relative to coeval therapsid groups.

The earliest-discovered specimen that can confidently be identified as a scylacosaurid is NHMUK PV R 872, the holotype of *Hyorhynchus platyceps* Seeley, 1889, which was collected by Thomas Bain in the Gouph Tract (Western Cape Province of South Africa), then purchased by the British Museum in 1880 (Boonstra 1969). Seeley (1889) considered *Hyorhynchus* most similar to *Aelurosaurus* (a gorgonopsian), but at the time, very few therocephalian fossils were known, and the distinction between members of this group and other theriodonts had not yet been established. Owen (1876) had previously described three theriodont taxa currently considered therocephalians (*Scaloposaurus*, *Theriognathus*, and *Tigrisuchus*), but two of them were based on highly incomplete material (*Theriognathus* and *Tigrisuchus*, the former of which was at first mistakenly described as an anomodont related to *Oudenodon*), so there was limited basis for comparison. Owen (1876) attempted to subdivide the Theriodontia based on compartmentalization of the external naris, but his categories largely reflected preservational artefacts and included a random assortment of gorgonopsians, therocephalians, and cynodonts (as well as the parareptile *Procolophon*). Seeley (1894) refined theriodont taxonomy, abandoning Owen's naris-centric system and recognizing cynodonts as a group separate from the other theriodonts. However, he retained therocephalians and gorgonopsians together in a group named Lycosauria (note, though, that this group did not include *Gorgonops* itself, which he considered the sole member of the new taxon Gorgonopsia). In the same work, Seeley named the second taxon now recognized as a scylacosaurid, *Pristerognathus polyodon*.

Broom (1903a) described the first well-preserved, largely complete skull of an early therocephalian, the holotype (US D173) of *Lycosuchus vanderrieti*. Shortly thereafter, he (Broom 1903b) described four additional taxa of early therocephalians (notably *Scylacosaurus sclateri*), beginning a half-century-long explosion in the alpha taxonomy of this group. Between 1903 and 1954, 44 new species of early therocephalians were described from the Karoo Basin, mostly based on poorly prepared, incomplete cranial

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material (e.g. Broom 1904, 1907, 1908; Boonstra 1953). Following this period, work on early therocephalians dropped to near non-existence, with only two new South African taxa named subsequently (*Zinnosaurus paucidens* Boonstra, 1964 and *Crapartinella croucheri* Mendrez, 1975). The deaths of Broom (in 1951) and Boonstra (in 1975) brought an end to the 'explosive period' in the taxonomy of Karoo therocephalians (and indeed, of Karoo tetrapods generally), with subsequent researchers beginning the arduous work of revising their nomenclatorial excess. However, while the 1970s and '80s witnessed major advances towards resolving the taxonomy of several major therapsid groups (e.g. Dicynodontia [Keyser 1973, 1975; Cluver & Hotton 1981; Cluver & King 1983; King 1988], Gorgonopsia [Sigogneau 1970; Sigogneau-Russell 1989], and Cynodontia [Hopson & Kitching 1972; Grine *et al*. 1978]), therocephalians were, for the most part, not among them. The tragic early death of the researcher tasked with revising the Therocephalia (Christiane Mendrez-Carroll, 1937–1978) arrested for some time serious work on African members of the group (although this period did witness important contributions to the Russian fauna, e.g. Tatarinov [1974]).

Interest in therocephalian systematics was slow to resume, and until recently, substantive works on the topic were few and far between. Van den Heever (1980) re-examined *Lycosuchus*, recognizing the apparent double canines of this taxon as an artefact of replacement, and as such considered this taxon to be fundamentally similar to other early therocephalians. Accordingly, he considered the family Lycosuchidae to be invalid, and included *Lycosuchus* in the family Pristerognathidae. Hopson & Barghusen (1986) presented the first (hand-drawn) cladistic phylogeny of Therapsida, and within Therocephalia recognized a fundamental split between early therocephalians and later Permian forms, the latter forming the subclade Eutherocephalia. They followed van den Heever (1980) in recognizing only a single family of early therocephalians (Pristerognathidae), which they placed in the monofamilial higher taxon Pristerosauria Boonstra, 1953. However, van den Heever (1994) later showed Lycosuchidae to indeed be distinct from other early therocephalians (the latter forming the family Scylacosauridae Broom, 1903c, a name with precedence over Pristerognathidae Haughton, 1924), representing the earliest-diverging therocephalian lineage. He established the taxon name Scylacosauria for the least inclusive clade uniting Scylacosauridae and Eutherocephalia. Abdala (2007) included seven therocephalian operational taxonomic units (OTUs) in his analysis of eutheriodont phylogeny, recovering a paraphyletic Therocephalia in which *Theriognathus* is the sister-group to cynodonts, reviving in a cladistic framework a hypothesis previously advanced by Kemp (1972). However, therocephalian monophyly was reaffirmed by Huttenlocker (2009), who published the first computer-assisted cladistic analysis primarily focused on therocephalians (rather than including a few therocephalian exemplars in broader-scale analyses). Variations on Huttenlocker's (2009) matrix have been used in almost all subsequent phylogenetic work on the group (Huttenlocker *et al*. 2011, 2015; Sigurdsen *et al*. 2012; Huttenlocker 2014; Huttenlocker & Sidor 2016; Huttenlocker & Smith 2017; Liu & Abdala 2017, 2019, 2020; Maisch 2017; Kammerer & Masyutin 2018; Brocklehurst 2019; Grunert *et al*. 2019).

Although the large number of recent papers on Therocephalia attest to a renaissance in work on this group, it should be noted that these papers mostly concern higher-level phylogeny, palaeobiology and morphological disparity, or the description of new species. Alpha taxonomic revision of the extensive existing set of nominal therocephalian species has largely remained in a state of stasis, with only a few published exceptions (e.g. Ivakhnenko 2011; Abdala *et al*. 2014a; Huttenlocker & Abdala 2015). Among unpublished works, however, there is an important exception, namely the Ph.D. thesis of van den Heever (1987) on the (primarily South African) record of early therocephalians. The descriptive section of this thesis, presenting detailed anatomical coverage of new, well-prepared lycosuchid and scylacosaurid specimens from the collections of the Council for Geoscience (Pretoria), was later incorporated into a published monograph (van den Heever 1994). The larger section of the thesis, a comprehensive taxonomic revision of early therocephalians, was never published, but is widely known to Karoo workers. Most aspects of this revision have gone uncontested in the literature, and it still represents the 'state of the art' for early therocephalians, generally being cited whenever the lower-level taxonomy of this group needs to be addressed (e.g. Abdala 2007; Abdala *et al*. 2008; Suchkova & Golubev 2019; Pusch *et al*. 2020).

Van den Heever (1987) greatly reduced the number of valid South African species in both Lycosuchidae (previously 13 nominal species) and Scylacosauridae (previously 33 nominal species). In Lycosuchidae, he recognized only two species of *Lycosuchus*: the type (*L. vanderrieti*) and a new species based on the specimen CGS C60. Later, however, he declined to formalize the latter as a new taxon, referring to it only as a 'lycosuchid' (precise taxon not specified) (van den Heever 1994). More recent work on lycosuchids (Abdala *et al*. 2014b) has also recognized two valid species, but with the other corresponding to the historical taxon *Simorhinella baini* Broom, 1915b rather than CGS C60 (which Abdala *et al*. referred to *L. vanderrieti*). In Scylacosauridae, van den Heever (1987) recognized six valid species: *Alopecodon priscus*, *Glanosuchus macrops*, *Ictidosaurus angusticeps*, *Pardosuchus whaitsi*, *Pristerognathus polyodon*, and *Scylacosaurus sclateri*. Differentiation between these taxa was based entirely on tooth count, specifically that of the upper anterior (pre-canine) dentition. All known scylacosaurids have either six or seven upper incisors and a variable number of precanines (small, typically incisiform maxillary teeth anterior to the canine), and van den Heever's (1987) taxonomic scheme treats the combination of these counts as diagnostic: I6/PrC0=*Glanosuchus macrops*, I6/PrC1=*Ictidosaurus angusticeps*, I6/PrC2=*Pardosuchus whaitsi*, I7/PrC0=*Pristerognathus polyodon*, I7/PrC1=*Scylacosaurus sclateri*, and I7/PrC2=*Alopecodon priscus*.

Although reasonably straightforward, there are a number of pitfalls to this system for scylacosaurid identification. First and foremost, by being entirely reliant on a small portion of the anatomy, it excludes a large portion of the scylacosaurid fossil record from identifiability (including many holotypes). One could have an otherwise complete and well-preserved scylacosaurid skull, but missing the tip of the snout consigns it to indeterminability under this system. Second, it ignores the possibility of individual variation in tooth count, including possible changes during growth (as seems to be the case in some other eutheriodonts, see e.g. Anderson 1968). Examination of small scylacosaurid specimens, interpreted as juveniles, indicates that this is a real concern. As an example, take UCMP 42659, a very small (basal skull length 9.61 cm) therocephalian specimen from *Tapinocephalus* AZ sediments in Weltevreden, Beaufort West. The weakly ossified occiput, broad intertemporal region without a distinct sagittal crest, and very large interpterygoid vacuity of this specimen indicate that it is a juvenile, and the highly dentigerous pterygoid boss and serrated upper incisors, canines, and postcanines indicate that it is a scylacosaurid. The taxonomic identity of this specimen is uncertain, as it does not fit cleanly into the van den Heeverian paradigm for scylacosaurid identification. In the left premaxilla and maxilla, there are 10 tooth crowns preserved anterior to the canine (Fig. 1A). The first three tooth crowns are definite incisors and are the largest of the preserved anterior teeth (although I1 is damaged and may not have been fully erupted; Fig. 1B). What are here interpreted as I4 and I6 are very short and apparently still in the process of eruption, whereas I5 appears fully erupted (although still shorter than I1–3). All fully erupted incisors have distinct distal carinae and serrations are present in at least I2 and I3. Also, I1–6 are all weakly recurved and slightly posteriorly canted. The three teeth posterior to I6 appear to be fully erupted, but lack carinae or serrations and the first two are anteriorly canted, similar to the first precanine when it is present in larger scylacosaurid specimens. Here, these three teeth are all considered to be precanines. The final anterior tooth is strongly recurved and bears large serrations and is interpreted as the erupting tip of a replacement canine in the anterior canine alveolus.

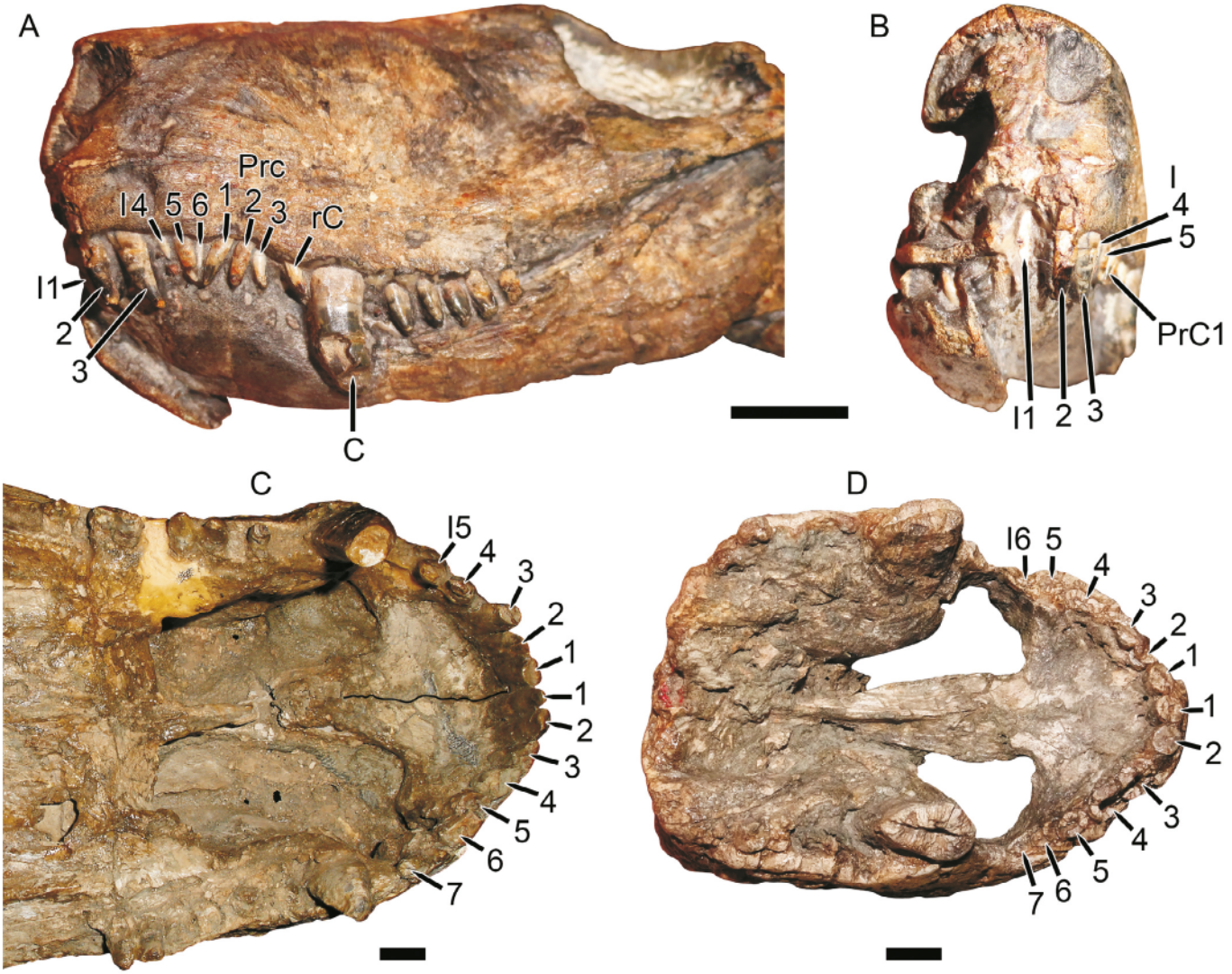



**Figure 1.** Scylacosaurid anterior dentition, showing variation in incisor and precanine counts. UCMP 42659, an indeterminate juvenile scylacosaurid, in **(A)** anterolateral and **(B)** anterior views. **C**, SAM-PK-11942, holotype of *Ptomalestes avidus* (=*Glanosuchus macrops*), in ventral view. **D**, NHMUK PV R 2581, holotype of *Pristerognathus polyodon*, in ventral view. *Abbreviations*: C, upper canine; I, upper incisor; PrC, upper precanine; rC, replacement canine. Scale bars equal 1 cm.

The dental formula of I6/prC3 is otherwise unknown among scylacosaurids. The possibility that the seventh anterior tooth is an incisor (yielding the dental formula of I7/prC2 that van den Heever [1987] considered diagnostic for *Alopecodon*) must be considered, although the differences in angulation and crown morphology between it and the preceding incisors would tend to contradict such an interpretation. Furthermore, these three teeth all appear to legitimately originate in maxillary alveoli, unlike I5 and 6 that originate in premaxillary alveoli overlain laterally by the maxilla. It is of course possible that UCMP 42659 represents an unknown taxon of therocephalian, in which the adult also had an unusually high anterior tooth count. But, especially considering that several of the incisors and the canine are clearly in the process of replacement, it seems more likely that this specimen is capturing a transitory state in the dental development of this individual, potentially with more precanines than would be present in the adult.

While incisor count seems to be less prone to ontogenetic variation than precanine count in theriodonts (at least taking cynodonts as a point of comparison; see Anderson 1968; Hopson & Kitching 1972), it is clear that it is not totally fixed in scylacosaurid species, as there can be variation in incisor number even within single individuals. Historically, *Pristerognathus polyodon* was thought to have six upper incisors (e.g. Seeley 1895; Broom 1932; Boonstra 1954), based on the condition in the holotype (NHMUK PV R 2581). Additional preparation of the specimen detailed by Mendrez (1972; see also Mendrez 1974, 1975) revealed the presence of a tiny seventh incisor in the left maxilla, and van den Heever (1987) considered the presence of seven incisors and no precanines to be diagnostic for *P. polyodon*. However, while seven upper left incisors are present in this specimen, there are only six incisors in the right premaxilla, and although this bone is more poorly preserved than its counterpart, the presence of a thick alveolar rim posterior to the sixth incisor indicates that it was indeed the last tooth in the series (Fig. 1D). As such, an incisor count of six, on its own, cannot rule out possible identification of a scylacosaurid skull as *Pristerognathus*, and given the minuscule size of I7 and the known history of NHMUK PV R 2581, it is clear that this tooth would not be visible in a less thoroughly prepared specimen (i.e. the vast majority of scylacosaurid specimens).

Another scylacosaurid specimen with variation in the incisor count is SAM-PK-11942, holotype of *Ptomalestes avidus*. Seven incisors are preserved in the left maxilla but only five in the right (Fig. 1C). The mid-premaxillary suture is very well exposed ventrally in this specimen, so there can be no doubt as to the identity of I1 on each side; this is not a case where taphonomic deformation has shifted an incisor to an uncertain position. Van den Heever (1987) considered *P. avidus* referable to *Pristerognathus polyodon* based on the presence of seven incisors and no precanines, but this only applies to one side of the skull. Furthermore, SAM-PK-11942 differs from NHMUK PV R 2581 and other specimens of *P. polyodon* in snout proportions, being broader.

Examples such as these indicate that anterior tooth count cannot be taken as the final word on scylacosaurid species determination. While van den Heever's (1987) review of the group was a major step forward in our understanding of early therocephalian diversity, his paradigm of strict incisor/precanine count-based diagnoses are limiting and of questionable biological value. Although anterior tooth counts in scylacosaurids are not random and have some diagnostic value, they are not without variability and must be incorporated into a broader, holistic view of their cranial anatomy, which I have endeavoured to accomplish here. Poor preparation of many scylacosaurid fossils necessarily means that some of the synonymies proposed here (see Table 1) are tentative, and changes to the identifications of certain specimens will almost certainly occur as better preparation (or CT-scanning) provides more information on their anatomy. However, it is hoped that this work generally provides a robust framework for interpreting the expansive scylacosaurid record, allowing incorporation of a greater number of specimens into studies of the biostratigraphy, geographic distribution, and palaeoecology of this group.

## MATERIAL AND METHODS

Comparisons were made based on first-hand examination of all surviving scylacosaurid holotypes and plaster casts of BSPG 1936-II-9 (the holotype of *Pristerognathus peyeri*, which was destroyed during World War II). Unless specified otherwise, all specimens referenced below were found in rocks of the Beaufort Group in the Karoo Basin of South Africa.

## SYSTEMATIC PALAEONTOLOGY

**Synapsida** Osborn, 1903
**Therapsida** Broom, 1905
**Therocephalia** Broom, 1903c
**Scylacosauria** van den Heever, 1994

**Scylacosauridae** Broom, 1903c
1924 Pristerognathidae Haughton, p. 74
1932 Alopecodontidae Broom, p. 65
1932 Ictidosauridae Broom, p. 64
1975 Crapartinellidae Mendrez, p. 382
*Type genus*. *Scylacosaurus* Broom, 1903b.
*Diagnosis*. Early therocephalians characterized by the combination of the following primitive character states for Therocephalia: absence of a mandibular fenestra, presence of serrated incisors and canines, paired vomers, a separate postfrontal bone, and a contact between the tabular and opisthotic on the occipital plate; as well as the following derived character states for Scylacosauria: absence of teeth on the transverse process of the pterygoid, presence of a well-developed crista choanalis, ventromedian crest on palatines, and a medial squamosal contribution to the pterygo-paroccipital foramen (van den Heever 1994; Huttenlocker 2009). There are few recognized autapomorphies of Scylacosauridae (in large part due to the poor preservation/preparation of most

**Table 1**. Taxonomic history of Scylacosauridae.

| Specimen number | Original identification | van den Heever (1987) | Present study |
|---|---|---|---|
| AMNH FARB 5502 | *Pristerognathus platyrhinus* Broom, 1912 | Scylacosauridae indet. | *Glanosuchus macrops* |
| AMNH FARB 5559 | *Alopecognathus angusticeps* Broom, 1915a | *Glanosuchus macrops* | *Alopecognathus angusticeps* |
| AMNH FARB 5560 | *Scylacorhinus falkenbachi* Broom, 1915a | *Scylacosaurus sclateri* | *Scylacosaurus sclateri* |
| AMNH FARB 5569 | *Alopecodon priscus* (Broom, 1915a) | *Alopecodon priscus* | *Alopecodon priscus* |
| BP/1/276 | *Lycosuchus* (Abdala, 2007) | – | *Pristerognathus polyodon* |
| BP/1/278 | *Glanosuchus macrops* (present study) | – | *Glanosuchus macrops* |
| BP/1/1100 | *Walteria skinneri* Brink & Kitching, 1951 | *Glanosuchus macrops* | *Glanosuchus macrops* |
| BSPG 1934-VIII-30 | *Cynariognathus seeleyi* Broili & Schröder, 1936a | Scylacosauridae indet. | ?*Alopecognathus angusticeps* |
| BSPG 1936-II-9 | *Pristerognathus peyeri* Broili & Schröder, 1936b | *Glanosuchus macrops* | *Pristerognathus polyodon* |
| CGP/1/779A | *Glanosuchus macrops* (present study) | – | *Glanosuchus macrops* |
| CGS GM 74 | *Glanosuchus macrops* (present study) | – | *Glanosuchus macrops* |
| CGS M 796 | *Glanosuchus macrops* (van den Heever, 1987) | *Glanosuchus macrops* | *Alopecognathus angusticeps* |
| CGS MJF 211 | *Alopecognathus angusticeps* (present study) | – | *Alopecognathus angusticeps* |
| CGS RMS 335 | *Alopecognathus angusticeps* (present study) | – | *Alopecognathus angusticeps* |
| CGS RMS 893 | *Alopecognathus angusticeps* (present study) | – | *Alopecognathus angusticeps* |
| CGS RMS 1058 | *Hyorhynchus platyceps* (present study) | – | *Hyorhynchus platyceps* |
| CGS RMS 1287 | *Pardosuchus whaitsi* (present study) | – | *Pardosuchus whaitsi* |
| CGS RS 329 | *Glanosuchus macrops* (present study) | – | *Glanosuchus macrops* |
| CGS RS 330 | *Pristerognathus polyodon* (present study) | – | *Pristerognathus polyodon* |
| CGS RS 424 | *Alopecognathus angusticeps* (present study) | – | *Alopecognathus angusticeps* |
| GPIT-PV-116189 | ?*Alopecognathus angusticeps* (present study) | – | ?*Alopecognathus angusticeps* |
| MB.R.996 | *Glanosuchus macrops* (present study) | – | *Glanosuchus macrops* |
| MMK 449 | *Lycedops scholtzi* Broom, 1935 | Scylacosauridae indet. | *Pardosuchus whaitsi* |
| MMK 5139 | *Pristerognathus vanderbyli* Broom, 1925 | *Glanosuchus macrops* | *Alopecognathus angusticeps* |
| NHMUK PV R 872 | *Hyorhynchus platyceps* Seeley, 1889 | Scylacosauridae indet. | *Hyorhynchus platyceps* |
| NHMUK PV R 2581 | *Pristerognathus polyodon* Seeley, 1894 | *Pristerognathus polyodon* | *Pristerognathus polyodon* |
| NHMUK PV R 4055 | *Scylacosaurus sclateri* (Broom, 1914) | *Scylacosaurus sclateri* | *Alopecodon priscus* |
| NHMUK PV R 4096 | *Crapartinella croucheri* Mendrez, 1975 | – | ?*Glanosuchus macrops* |
| NHMUK PV R 4100 | *Scymnosaurus watsoni* Broom, 1915b | Scylacosauridae indet. | Scylacosauridae indet. |
| NHMUK PV R 5750 | *Alopecodon minor* Broom, 1925 | Scylacosauridae indet. | *Alopecodon priscus* |
| NMQR 2908 | *Glanosuchus macrops* (Abdala *et al*. 2008) | – | *Eutheriodon vandenheeveri* |
| NMQR 2910 | *Ictidosaurus angusticeps* (Abdala *et al*. 2008) | – | *Eutheriodon vandenheeveri* |
| NMQR 3488 | *Eutheriodon vandenheeveri* (present study) | – | *Eutheriodon vandenheeveri* |
| SAM-PK-583 | *Pristerognathus baini* Broom, 1904 | *Glanosuchus macrops* | Scylacosauridae indet. |
| SAM-PK-630 | *Ictidosaurus angusticeps* Broom, 1903b | *Ictidosaurus angusticeps* | Scylacosauridae indet. |
| SAM-PK-634 | *Scylacosaurus sclateri* Broom, 1903b | *Scylacosaurus sclateri* | *Scylacosaurus sclateri* |
| SAM-PK-637 | *Glanosuchus macrops* Broom, 1904 | *Glanosuchus macrops* | *Glanosuchus macrops* |
| SAM-PK-920 | *Alopecodon priscus* Broom, 1908 | *Alopecodon priscus* | *Alopecodon priscus* |
| SAM-PK-921 | *Alopecodon rugosus* Broom, 1908 | Scylacosauridae indet. | ?*Pardosuchus whaitsi* |
| SAM-PK-1069 | *Arnognathus parvidens* Broom, 1907 | Scylacosauridae indet. | Scylacosauridae indet. |
| SAM-PK-1077 | *Pardosuchus whaitsi* Broom, 1908 | *Pardosuchus whaitsi* | *Pardosuchus whaitsi* |
| SAM-PK-3415 | *Alopecognathus minor* Haughton, 1918 | *Glanosuchus macrops* | *Pristerognathus polyodon* |
| SAM-PK-3435 | *Pristerognathoides minor* Boonstra, 1954b | *Glanosuchus macrops* | *Pristerognathus polyodon* |
| SAM-PK-3611 | *Pristerognathoides parvus* Boonstra, 1954b | Scylacosauridae indet. | ?*Pristerognathus polyodon* |
| SAM-PK-4321 | *Blattoidealestes gracilis* Boonstra, 1954a | – | Scylacosauridae indet. |
| SAM-PK-4997 | *Alopecideops gracilis* Broom, 1932 | Scylacosauridae indet. | *Alopecognathus angusticeps* |
| SAM-PK-6533 | *Pristerognathus vanwyki* Broom, 1925 | Scylacosauridae indet. | *Alopecognathus angusticeps* |
| SAM-PK-9083 | *Pristerosaurus microdon* Boonstra, 1954 | Scylacosauridae indet. | *Maraisaurus parvus* |
| SAM-PK-9342 | *Alopecognathus angustioriceps* Boonstra, 1953 | *Glanosuchus macrops* | *Alopecognathus angusticeps* |
| SAM-PK-9356a | *Pristerognathus roggeveldensis* Boonstra, 1953 | *Glanosuchus macrops* | *Alopecognathus angusticeps* |
| SAM-PK-11460 | *Ptomalestes avidus* (Boonstra, 1954b) | *Glanosuchus macrops* | *Glanosuchus macrops* |
| SAM-PK-11560a | *Cynariognathus paucioridens* Boonstra, 1954b | Scylacosauridae indet. | *Glanosuchus macrops* |
| SAM-PK-11689 | *Pristerognathoides vanwyki* (Boonstra, 1954b) | Scylacosauridae indet. | *Pristerognathus polyodon* |
| SAM-PK-11695 | *Scymnosaurus* sp. (Boonstra, 1964) | – | *Glanosuchus macrops* |
| SAM-PK-11843 | *Glanosuchus macrops* (Boonstra, 1954b) | ?*Glanosuchus macrops* | *Glanosuchus macrops* |
| SAM-PK-11888 | *Therioides cyniscus* Boonstra, 1953 | *Scylacosaurus sclateri* | ?*Scylacosaurus sclateri* |
| SAM-PK-11893 | *Pristerognathoides vanwyki* (Boonstra, 1954b) | *Glanosuchus macrops* | *Alopecognathus angusticeps* |
| SAM-PK-11942 | *Ptomalestes avidus* Boonstra, 1954b | *Pristerognathus polyodon* | *Glanosuchus macrops* |
| SAM-PK-11944 | *Maraisaurus parvus* Boonstra, 1953 | Scylacosauridae indet. | *Maraisaurus parvus* |
| SAM-PK-K223 | *Pardosuchus whaitsi* (present study) | – | *Pardosuchus whaitsi* |
| SAM-PK-K312 | *Pristerognathus polyodon* (present study) | – | *Pristerognathus polyodon* |

*Continued on p. 56*

**Table 1** (continued)

| Specimen number | Original identification | van den Heever (1987) | Present study |
|---|---|---|---|
| SAM-PK-K7809 | *Glanosuchus macrops* (Fourie & Rubidge, 2009) | – | *Alopecognathus angusticeps* |
| SAM-PK-K10540 | *Pristerognathus polyodon* (present study) | – | *Pristerognathus polyodon* |
| SAM-PK-K11360 | *Pardosuchus whaitsi* (present study) | – | *Pardosuchus whaitsi* |
| TM 266 | *Cynariognathus gallowayi* Broom, 1936 | *Glanosuchus macrops* | ?*Alopecognathus angusticeps* |
| TM 1491 | *Alopecognathus megalops* Broom, 1937 | Scylacosauridae indet. | *Alopecognathus angusticeps* |
| UCMP 42395 | Lycosuchidae indet. (Huttenlocker, 2009) | – | *Glanosuchus macrops* |
| UCMP 42581 | *Glanosuchus macrops* (present study) | – | *Glanosuchus macrops* |
| UCMP 42659 | Scylacosauridae indet. (present study) | – | Scylacosauridae indet. |
| UCMP 42669 | cf. *Glanosuchus* (Huttenlocker, 2009) | – | *Scylacosaurus sclateri* |
| Unnumbered | *Ictidoparia brevirostris* Broom, 1925 | Therocephalia indet. | Therocephalia indet. |

specimens), but appear to include the presence of a preorbital depression and reduction of the interpterygoid vacuity in adults (Huttenlocker 2009).

*Phylogenetic definition*. *Scylacosaurus sclateri* Broom, 1903b and all taxa more closely related to it than *Lycosuchus vanderrieti* Broom, 1903a, *Hofmeyria atavus* Broom, 1935, *Akidnognathus parvus* Haughton, 1918, *Theriognathus microps* Owen, 1876, *Bauria cynops* Broom, 1909, or *Galesaurus planiceps* Owen, 1859.

*Alopecodon* Broom, 1908

*Type species*. *Alopecodon priscus* Broom, 1908.

*Etymology*. 'Fox tooth', from the ancient Greek ἀλώπηξ ('fox', Latinized *alopex*) and ὀδών ('tooth', Latinized *odon*).

*Diagnosis*. As for type and only species.

***Alopecodon priscus*** Broom, 1908

Figures 2, 3

1925 *Alopecodon minor* Broom, p. 319

*Holotype*. SAM-PK-920, a laterally crushed partial skull (missing the temporal region) and lower jaws found 9 miles northwest of Zeekoegat, Prince Albert (Fig. 2A,C,D).

*Referred material*. AMNH FARB 5569, a partial snout and lower jaws from Fraserburg Road Station (=Leeu-Gamka), Prince Albert (Figs 2E, 3B); NHMUK PV R 4055, a partial skull (missing most of the temporal arches) and lower jaws from Fraserburg Road Station (=Leeu-Gamka), Prince Albert (Figs 2B,G, 3A); NHMUK PV R 5750 (holotype of *Alopecodon minor*), a very poorly prepared partial snout and lower jaws from Abrahamskraal, Prince Albert (Fig. 2F).

*Etymology*. Latin *priscus* ('ancient'), presumably in reference to its appearance in the (at the time) oldest known strata of the Beaufort Group.

*Diagnosis*. Mid-sized (estimated maximum skull length 26 cm, based on SAM-PK-920, estimated with reference to the proportions of NHMUK PV R 4055) scylacosaurid with the dental formula I7/PrC2/C1/PC8, upper post-canines recurved, elongate, and mesially thickened, proportionally shorter snout than *Pristerognathus* or *Scylacosaurus*, and dentary lacking the 'hourglass' morphology of *Scylacosaurus*.

*Remarks*. Broom (1908) distinguished *Alopecodon priscus* from other therocephalians on the basis of its high incisor count. Broom originally considered the holotype (SAM-PK-920) to have eight incisors and one precanine, although he later reinterpreted this as seven incisors and two precanines (Broom 1925, 1932). Van den Heever (1987) also considered SAM-PK-920 to have seven incisors and two precanines and considered this count diagnostic for *A. priscus*.

The retention of two precanines even at relatively large skull size is notable in SAM-PK-920, although (as discussed in the Introduction) precanine count alone is here considered to be of limited diagnostic value. Establishing a more robust diagnosis for *Alopecodon priscus* is complicated by the poor nature of the holotype, which is badly weathered, laterally crushed, fragmentary, and still partially unprepared (the ventral surface of the specimen is still totally encased in matrix). However, SAM-PK-920 does differ in some notable regards from other scylacosaurids with seven upper incisors (i.e. *Scylacosaurus* and at least some specimens of *Pristerognathus*). The snout of SAM-PK-920 is proportionally shorter than that of *Pristerognathus* or *Scylacosaurus*, and this cannot be attributed to taphonomic distortion (as this specimen has suffered lateral rather than anteroposterior compression). Although the dentary of this specimen is broken, it clearly lacks the distinctive 'hourglass' shape of *Scylacosaurus*. The precanine region of the snout is proportionally shorter than that of *Pristerognathus*, and the incisors are smaller and more closely packed.

Three additional specimens, all smaller than the holotype, can be referred to *A. priscus*. AMNH FARB 5569 is a very poorly preserved partial snout with occluded jaw, referred to *A. priscus* by Broom (1915a; see also Boonstra 1935; van den Heever 1987). The exterior bone surface of this specimen is totally worn, but the upper dentition is preserved as tooth roots and clear impressions of the crowns (Fig. 3B). This specimen matches the holotype in having seven incisors (with the posterior two much smaller than the preceding five) and two precanines, of which the anterior precanine is angled more anteroventrally. Although only part of the lower jaw is preserved, it does not show the characteristic 'hourglass' shape of *Scylacosaurus*, and the snout is shorter and taller than that of *Pristerognathus* or *Scylacosaurus*. As such, Broom's (1915a) referral is upheld here. NHMUK PV R 4055 is a partially prepared skull and lower jaws (broken into two sections), referred to *Scylacosaurus sclateri* by Broom (1914) (see also Boonstra 1934, 1935; van den Heever 1987). The upper dentition of NHMUK PV R 4055

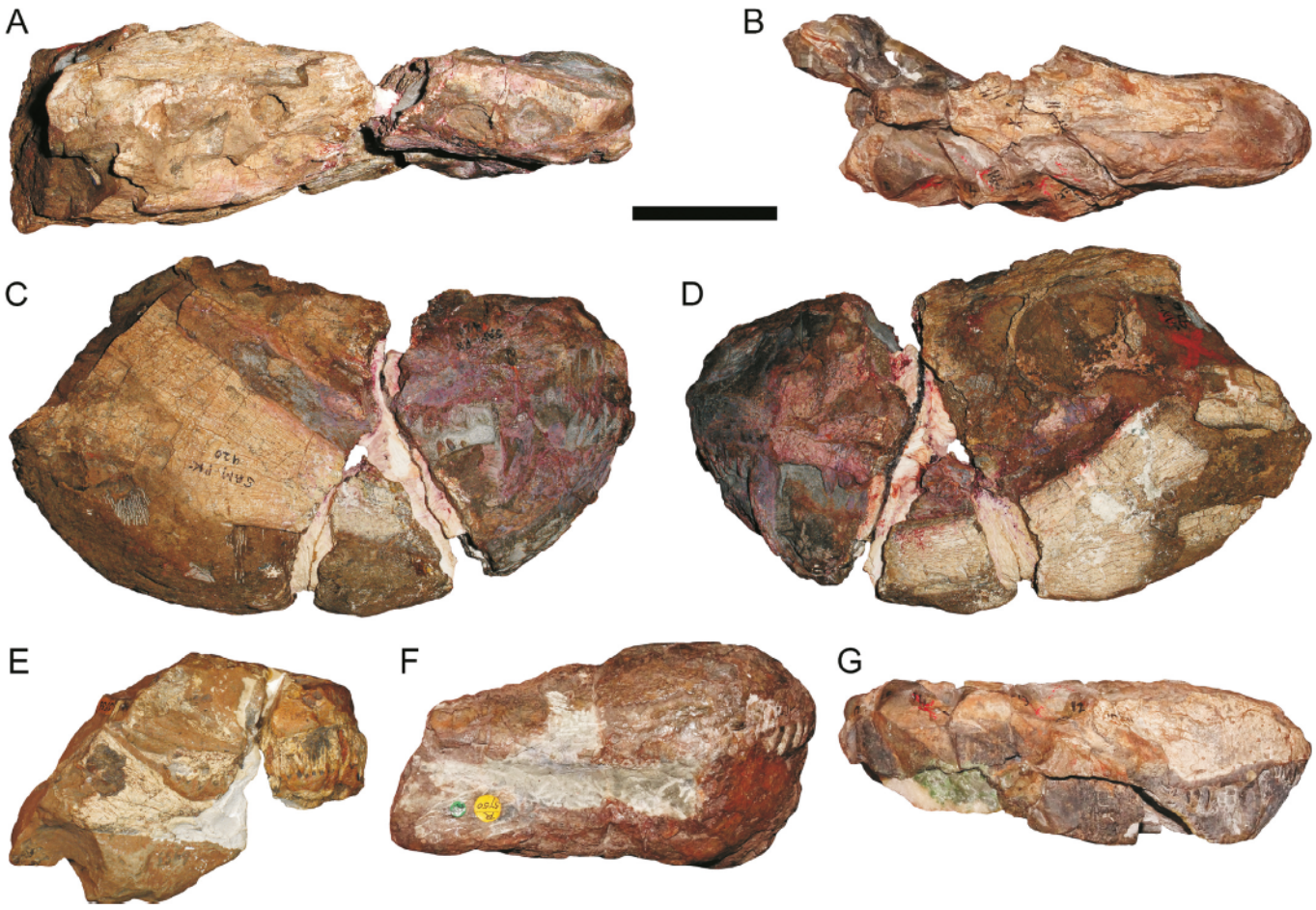



**Figure 2.** Specimens of *Alopecodon priscus* Broom, 1908. SAM-PK-920, holotype of *Alopecodon priscus*, in (**A**) dorsal, (**C**) right lateral, and (**D**) left lateral views. NHMUK PV R 4055 in (**B**) dorsal and (**G**) right lateral views. AMNH FARB 5569 in (**E**) right lateral view. NHMUK PV R 5750, holotype of *Alopecodon minor*, in (**F**) right lateral view. All specimens to scale; scale bar equals 5 cm.

closely matches that of SAM-PK-920 and AMNH FARB 5569: seven incisors are preserved, and although only the anterior precanine crown is present (in the same position and showing the same angulation as the other *A. priscus* specimens), there appears to be an alveolus for a second between it and the canine (Fig. 3A). The mandibular and snout morphology of NHMUK PV R 4055 is also more similar to that of SAM-PK-920 and AMNH FARB 5569 than *Pristerognathus* or *Scylacosaurus*, and it is here considered referable to *A. priscus*. NHMUK PV R 4055 has the only well-preserved postcanine crowns among *A. priscus* specimens: three postcanines from the middle of the right maxilla (probably PC2–4). These teeth are recurved, elongate, and notably thicker mesially than distally. Only distal serrations appear to be present. The upper canines and incisors of NHMUK PV R 4055 are also serrated (at least distally; mesial serrations may also be present, but are obscured by matrix), as expected for a scylacosaurid but not obviously the case in other *A. priscus* specimens. NHMUK PV R 5750 was initially described by Broom (1925) as a new species of *Alopecodon*, *A. minor*, but Boonstra (1934) considered this specimen referable to *A. priscus*. This specimen, a partial snout with occluded jaws, is exceedingly poorly prepared, and van den Heever (1987) considered it identifiable only as Scylacosauridae *incertae sedis*. However, it is clear that NHMUK PV R 5750 has a high anterior tooth count, and Broom's (1925) interpretation of there being seven incisors and two precanines appears accurate. The dentary in this specimen does not show the 'hourglass' shape of *Scylacosaurus* and the snout is comparable in proportions to those of other *Alopecodon* specimens. As such, Boonstra's (1934; see also Boonstra 1969) referral is accepted here.

Due to the poor condition of the known material, *Alopecodon* is one of the most incompletely known scylacosaurids, and a thorough understanding of this taxon's anatomy will likely have to await the discovery of new specimens. However, additional information could be gleaned even from the existing material with further preparation; NHMUK PV R 4055 in particular is a reasonably well-preserved skull (despite wear to the snout surface) and much of the palatal morphology is likely intact, though currently hidden beneath matrix. At present, only the tip of the left pterygoid boss and the blade of the parabasisphenoid are visible palatally, showing that the former was dentigerous but little else.

***Alopecognathus*** Broom, 1915a

1932 *Alopecideops* Broom, p. 66

*Type species*. *Alopecognathus angusticeps* Broom, 1915a.

*Etymology*. 'Fox jaw', from the ancient Greek ἀλώπηξ ('fox', Latinized *alopex*) and γνάθος ('jaw', Latinized *gnathus*).

*Diagnosis*. As for type and only species.

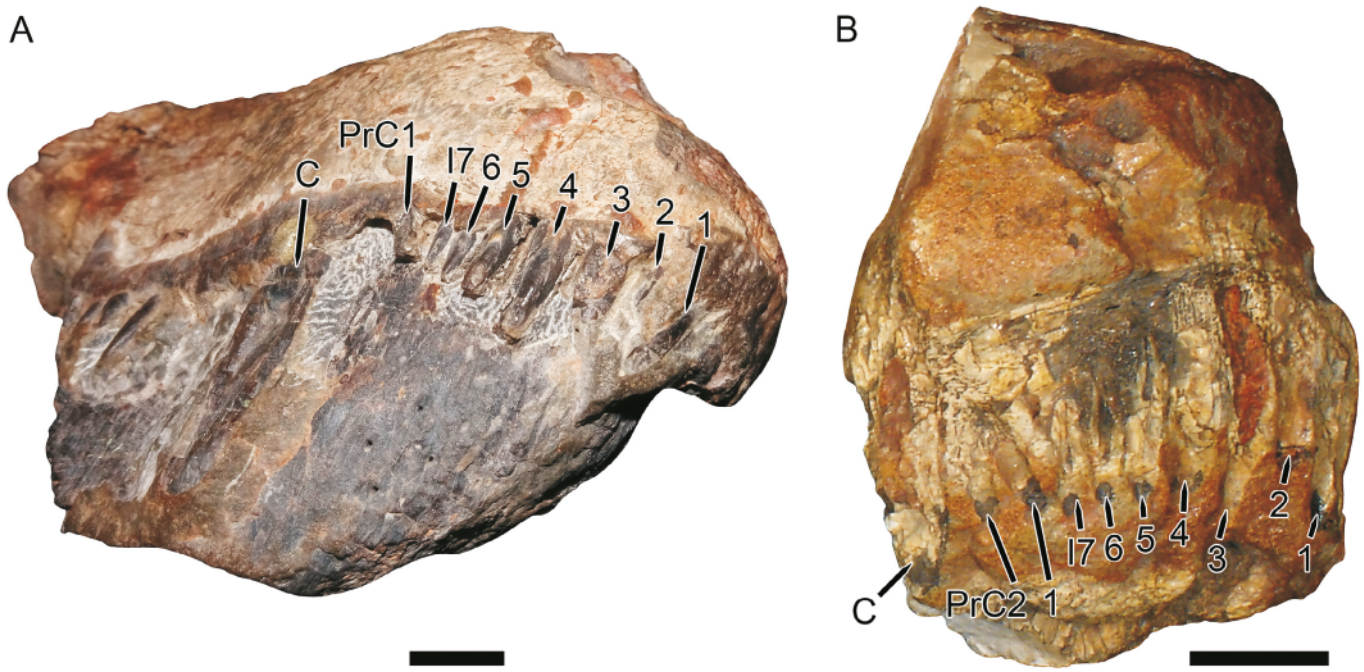



**Figure 3.** Anterior dentition of *Alopecodon priscus* Broom, 1908. **A**, Anterior snout portion of NHMUK PV R 4055 in right three-quarters view. Note alveolus behind the anterior precanine, presumably for PrC2. **B**, Anterior snout portion of AMNH FARB 5569 in right lateral view. Note anteroventral angulation of the anterior precanine in both specimens. *Abbreviations*: C, Upper canine; I, upper incisor; PrC, upper precanine. Scale bars equal 1 cm.

***Alopecognathus angusticeps*** Broom, 1915a
Figures 4–6, 7D,F, 8A

1925 *Pristerognathus vanderbyli* Broom, p. 316
1925 *Pristerognathus vanwyki* Broom, p. 318
1932 *Alopecideops gracilis* Broom, p. 66
1936 *Cynariognathus gallowayi* Broom, p. 356
1936a *Cynariognathus seeleyi* Broili & Schröder, p. 18
1937 *Alopecognathus megalops* Broom, p. 141
1953 *Alopecognathus angustioriceps* Boonstra, p. 63
1953 *Pristerognathus roggeveldensis* Boonstra, p. 60

*Holotype*. AMNH FARB 5559, a poorly prepared complete skull and lower jaws from Grootfontein, Beaufort West (Figs 4A, 5A,B).

*Referred material*. BSPG 1934-VIII-30 (holotype of *Cynariognathus seeleyi*), a partial skull (missing the surface of the right side of the skull and much of the temporal arches) and lower jaws from La-de-da, Beaufort West (Figs 4J, 5G); CGS M 796, a nearly complete skull and lower jaws from Booiskraal, Beaufort West; CGS MJF 211, a highly laterally crushed skull and lower jaws from Melton Wold, Victoria West (Figs 4E, 6C); CGS RMS 335, a dorsoventrally crushed complete skull and lower jaws from Bastardsberg 35, Sutherland; CGS RMS 893, a distorted complete skull and lower jaws from Putfontein, Beaufort West; CGS RS 424, a nearly complete but fragmented skull and associated autopodium from Klipplaatsfontein, Beaufort West; GPIT-PV-116189, a large, dorsoventrally crushed skull and lower jaws from an uncertain Karoo locality (Figs 7D, 8A); MMK 5139 (holotype of *Pristerognathus vanderbyli*), a complete skull and lower jaws from Abrahamskraal, Prince Albert (Figs 4F, 5F, 7F); SAM-PK-3435, a partial snout and lower jaws from Jakkalsfontein, Prince Albert; SAM-PK-4997 (holotype of *Alopecideops gracilis*), a badly eroded and dorsoventrally crushed skull and lower jaws from Stinkfontein, Prince Albert (Figs 4H, 6D); SAM-PK-6533 (holotype of *Pristerognathus vanwyki*), a very poorly-prepared partial skull (missing the right temporal arch) and lower jaws from Blaauwkranse, Prince Albert (Figs 4D, 5C); SAM-PK-9342 (holotype of *Alopecognathus angustioriceps*), a nearly complete but poorly preserved skull and lower jaws from Kroonplaas (=Heuningskopfontein), Beaufort West (Figs 4B, 5E); SAM-PK-9356a (holotype of *Pristerognathus roggeveldensis*), a very poor partial skull (missing parts of the orbital and temporal region) and lower jaws from Roggekloof, Sutherland (Figs 4G, 5H); SAM-PK-11893, a partial snout and lower jaws from Lammerskraal, Prince Albert; SAM-PK-K7809, a complete skull (Fig. 6B), jaws, and articulated skeleton (missing the tail and most of the hind limbs) from La-de-da, Beaufort West; TM 266 (holotype of *Cynariognathus gallowayi*), a partial skull (missing much of the temporal region) and lower jaws from Luttig, Beaufort West (Figs 4C, 5D); TM 1491 (holotype of *Alopecognathus megalops*), a dorsoventrally crushed partial skull (missing the anterior snout and part of the occiput) and lower jaws from Abrahamskraal, Prince Albert (Figs 4I, 6A).

*Etymology*. 'Narrow-headed', from the Latin *angustus* ('narrow') and *ceps* ('headed').

*Diagnosis*. Large (32.77 cm maximum basal skull length, based on GPIT-PV-116189) therocephalian with the dental formula I6/PrC0/C1/PC6–8, snout relatively long and narrow, equal in transverse width throughout postcanine-canine region, upper postcanines relatively small, pterygoid bosses reniform, broad, and oriented perpendicular to long axis of skull, and tooth row on pterygoid bosses arcing anteriorly.

*Remarks*. Broom (1915a) did not provide a differential diagnosis in his description of *Alopecognathus angusticeps*, but did note that the holotype (AMNH FARB 5559) had

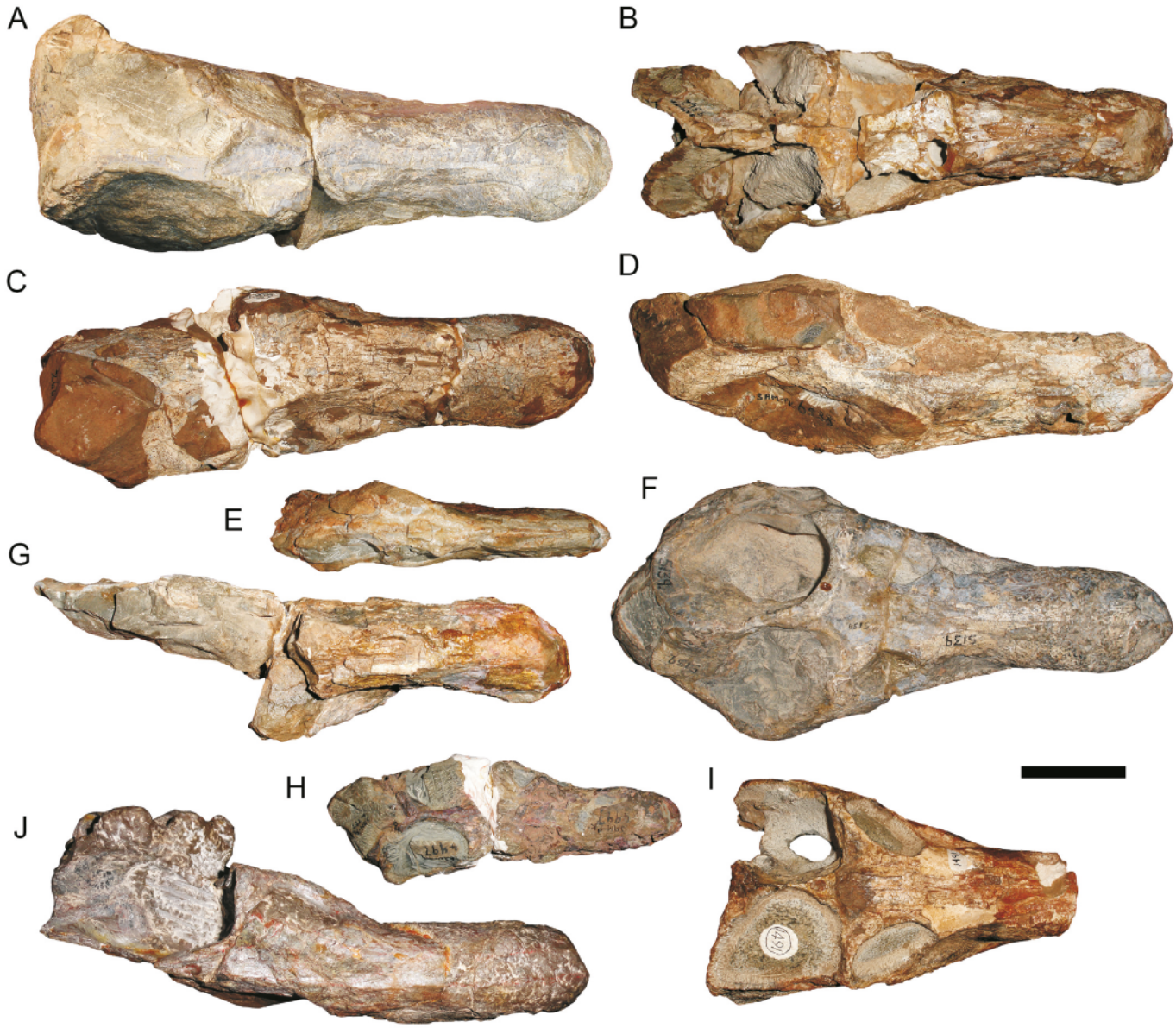



**Figure 4**. Specimens of *Alopecognathus angusticeps* Broom, 1915a in dorsal view. **A**, AMNH FARB 5559, holotype of *Alopecognathus angusticeps*. **B**, SAM-PK-9342, holotype of *Alopecognathus angustioriceps*. **C**, TM 266, holotype of *Cynariognathus gallowayi*. **D**, SAM-PK-6533, holotype of *Pristerognathus vanwyki*. **E**, CGS MJF 211. **F**, MMK 5139, holotype of *Pristerognathus vanderbyli*. **G**, SAM-PK-9356a, holotype of *Pristerognathus roggeveldensis*. **H**, SAM-PK-4997, holotype of *Alopecideops gracilis*. **I**, TM 1491, holotype of *Alopecognathus megalops*. **J**, BSPG 1934-VIII-30, holotype of *Cynariognathus seeleyi*. All specimens to scale; scale bar equals 5 cm.

relatively small orbits and an unusually narrow interorbital region. However, these proportions in AMNH FARB 5559 are comparable to those in a variety of other scylacosaurid skulls of similar size. The other characters in Broom's (1915a) description (skull narrow, orbits near midpoint of skull, sagittal crest present, six upper incisors) are either typical of therocephalians generally or present in other scylacosaurids (e.g. *Glanosuchus* and *Pardosuchus*, which also have six upper incisors). The proportionally long, narrow snout of AMNH FARB 5559 is notable, but a long snout is also present in the many scylacosaurid skulls that have been referred to *Pristerognathus* (see e.g. Broom 1925, 1932; Boonstra 1953, 1954, 1969).

*Alopecognathus* and *Pristerognathus* are indeed very difficult to differentiate from one another. Both taxa have long, narrow snouts, similar tooth counts (generally six incisors, no precanine, and six to eight postcanines), and overlap in size. These taxa are also among the most abundant scylacosaurids, so a wide range of taphonomic and individual variation is present among the known specimens. However, there are a number of slight but noteworthy differences supporting their distinction. The shape of the anterior snout differs between *Alopecognathus* and *Pristerognathus* in several regards. In *Alopecognathus*, the snout curves posterodorsally from the tip in lateral view, giving the snout a blunt, rounded appearance. By contrast, in *Pristerognathus* the snout tip is angled anterodorsally, comes to a point, and then is nearly horizontal posterior to it. In dorsal view, the snout of *Alopecognathus* narrows anterior to the orbits, then is of nearly consistent width throughout the postcanine and canine regions before finally narrowing again in the premaxilla. In *Pristerognathus*, the snout is narrowest around mid-length in the postcanine region, expanding anteriorly around the canines and with a relatively broad tip. The shape of the intertemporal region also differs




**Figure 5.** Specimens of *Alopecognathus angusticeps* Broom, 1915a in lateral view. AMNH FARB 5559, holotype of *Alopecognathus angusticeps*, in (**A**) right lateral and (**B**) left lateral views. **C**, SAM-PK-6533, holotype of *Pristerognathus vanwyki*, in right lateral view. **D**, TM 266, holotype of *Cynariognathus gallowayi*, in left lateral view. **E**, SAM-PK-9342, holotype of *Alopecognathus angustioriceps*, in right lateral view. **F**, MMK 5139, holotype of *Pristerognathus vanderbyli*, in left lateral view. **G**, BSPG 1934-VIII-30, holotype of *Cynariognathus seeleyi*, in left lateral view. **H**, SAM-PK-9356a, holotype of *Pristerognathus roggeveldensis*, in left lateral view. All specimens to scale; scale bar equals 5 cm.

between these taxa, being transversely wider in *Pristerognathus* than *Alopecognathus*. Finally, the skull of *Alopecognathus* is distinctly curved between the orbitotemporal region and the snout in lateral view, whereas in *Pristerognathus* it is essentially horizontal.

Unfortunately for the identification of fragmentary scylacosaurid remains, all of the above characters are subject to taphonomic distortion. Given that the majority of *Pristerognathus* specimens are dorsoventrally compressed, it must be considered whether the aforementioned differences could all just be taphonomically-induced artefacts. This certainly could be the case for some features (e.g. intertemporal width, which is likely also exaggerated in some *Pristerognathus* specimens due to erosion of the sagittal crest), and it is indeed likely that some of the more poorly preserved and prepared specimens herein referred to *Pristerognathus* might actually prove to be *Alopecognathus* (and *vice versa*). However, available evidence does not support *Alopecognathus* and *Pristerognathus* simply being taphomorphs of one another. The *Alopecognathus* specimen MMK 5139 (holotype of *Pristerognathus vanderbyli*) is instructive in this regard: this specimen is clearly dorsoventrally compressed, yet still shows the typical *Alopecognathus* snout morphology, being of equal width throughout the postcanine-canine regions and without an anteriorly-pointed tip. Although it is possible that a pointed snout tip was worn or broken off in specimens here referred to *Alopecognathus*, changing the appearance of the snout profile, the well-preserved and prepared specimen SAM-PK-K7809 shows that the *Alopecognathus*-style snout shape can be present naturally. MMK 5139 also shows several

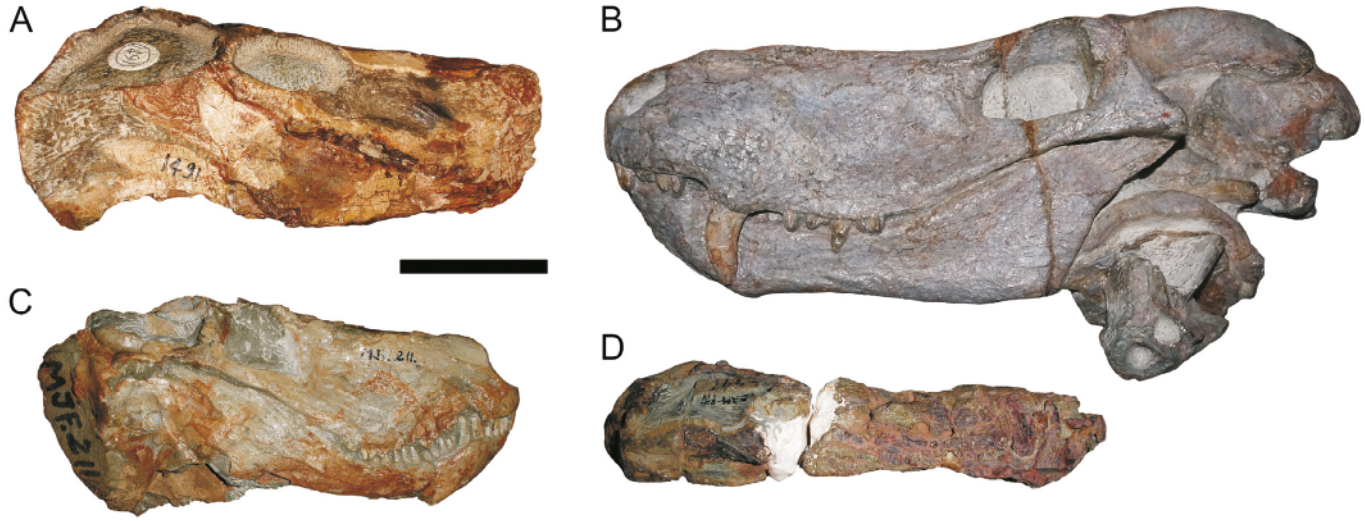



**Figure 6**. Additional specimens of *Alopecognathus angusticeps* Broom, 1915a in lateral view. **A**, TM 1491, holotype of *Alopecognathus megalops*, in right lateral view. **B**, SAM-PK-K7809 in left lateral view. **C**, CGS MJF 211 in right lateral view. **D**, SAM-PK-4997, holotype of *Alopecideops gracilis*, in right lateral view. All specimens to scale; scale bar equals 5 cm.

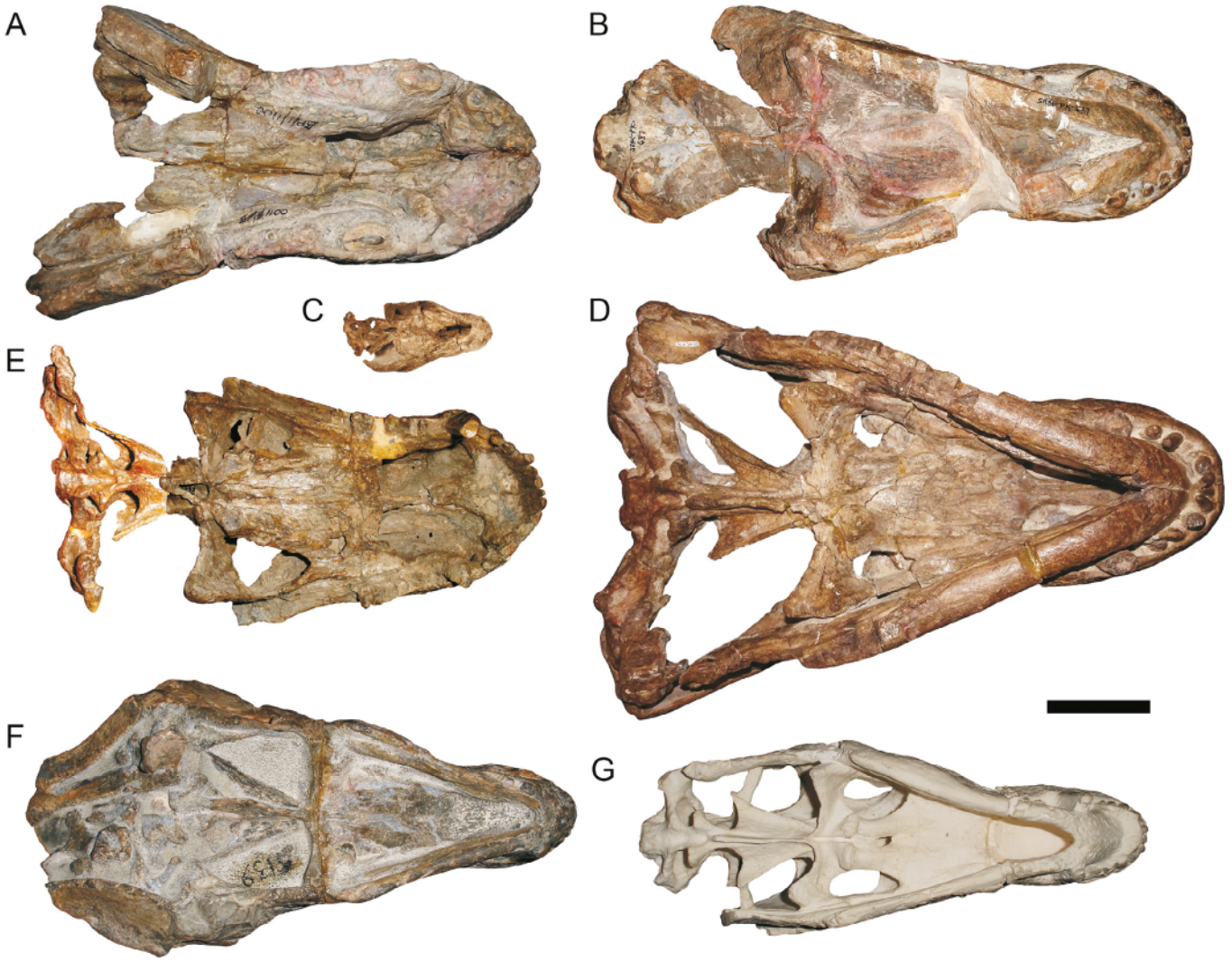



**Figure 7**. Scylacosaurids in ventral view. **A**, BP/1/1100, holotype of *Karroowalteria skinneri* (=*Glanosuchus macrops*). **B**, SAM-PK-637, holotype of *Glanosuchus macrops*. **C**, NHMUK PV R4096, holotype of *Crapartinella croucheri* (=*Glanosuchus macrops*). **D**, GPIT-PV-116189, referred specimen of *Alopecognathus angusticeps*. **E**, SAM-PK-11942, holotype of *Ptomalestes avidus* (=*Glanosuchus macrops*). **F**, MMK 5139, holotype of *Pristerognathus vanderbyli* (=*Alopecognathus angusticeps*). **G**, USNM 187095, cast of BSPG 1936-II-9, the destroyed holotype of *Pristerognathus peyeri* (=*Pristerognathus polyodon*). All specimens to scale; scale bar equals 5 cm.

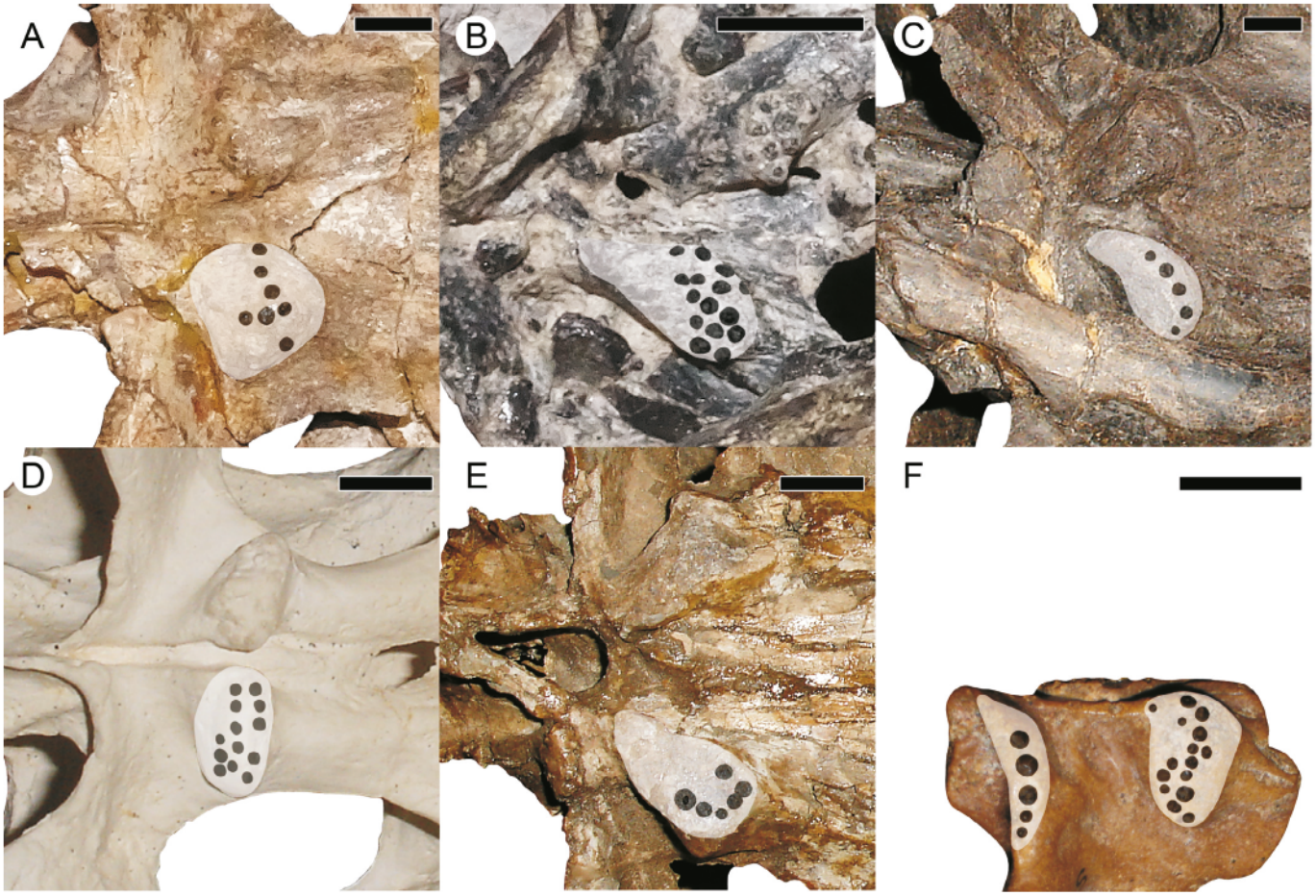



**Figure 8.** Early therocephalian pterygoid bosses in ventral view. **A**, GPIT-PV-116189, referred specimen of *Alopecognathus angusticeps*. **B**, NMQR 2910, holotype of *Eutheriodon vandenheeveri* gen. et sp. nov. **C**, UCMP 42669, referred specimen of *Scylacosaurus sclateri*. **D**, USNM 187095, cast of BSPG 1936-II-9, the destroyed holotype of *Pristerognathus peyeri* (=*Pristerognathus polyodon*). **E**, SAM-PK-11942, holotype of *Ptomalestes avidus* (=*Glanosuchus macrops*). **F**, PIN 157/683b, isolated left pterygoid of *Porosteognathus efremovi*. Dentigerous portions of pterygoid highlighted in white, with tooth positions marked in black; note presence of tooth rows on both the palatal boss and transverse process in *Porosteognathus*, unlike in scylacosaurids. Scale bars equal 1 cm.

features not easily explained as taphonomic artefact. The pterygoid bosses in this specimen are reniform, oriented perpendicular to the long axis of the skull, and each bear a palatal tooth row arcing anteriorly. In *Pristerognathus*, the pterygoid bosses are densely dentigerous (without a single distinct tooth row), elongate oval structures perpendicular to the long axis of the skull (Fig. 8D). Also, the postcanines of MMK 5139 are proportionally much smaller than those of *Pristerognathus* specimens, which is also the case in the holotype of *A. angusticeps* (AMNH FARB 5559) and most other referred *Alopecognathus* specimens (e.g. SAM-PK-6533, SAM-PK-9342, SAM-PK-K7809).

Van den Heever (1987) referred many of the specimens here considered to be *Alopecognathus* to *Glanosuchus macrops* on the basis of shared anterior dental formulae (six incisors, no precanines). A number of cranial characters support the distinction of these two taxa, however. Like *Pristerognathus*, the snout of *Glanosuchus* is expanded around the canine, but the snout of *Glanosuchus* is also massive and always transversely broader than in *Alopecognathus* specimens of equivalent skull length. The upper postcanines of *Glanosuchus* are larger and more recurved than those of *Alopecognathus*, with a thicker mesial margin. The pterygoid bosses are also distinct between these taxa, with those of *Glanosuchus* extending and expanding anterolaterally, unlike the transversely oriented, reniform bosses of *Alopecognathus*. In general, although *Alopecognathus* is more difficult to diagnose than highly autapomorphic scylacosaurids such as *Pardosuchus* and *Scylacosaurus*, it does seem to form a coherent morphotype and here is recognized as a valid taxon. The pterygoid boss morphology of this taxon may be autapomorphic, but unfortunately this region is not prepared in most *Alopecognathus* specimens (including the holotype of *A. angusticeps*). Further preparation of the majority of long-snouted scylacosaurid specimens from the *Tapinocephalus* and *Pristerognathus* AZs is needed to better understand morphological variation in *Alopecognathus* and *Pristerognathus* and their stratigraphic ranges.

A number of nominal scylacosaurid species are here considered synonymous with *Alopecognathus angusticeps*. Broom (1925, p. 317) established a new species of *Pristerognathus* (*P. vanderbyli*) for the specimen MMK 5139 based only on stratigraphy, as he believed it was 'certainly from a much lower horizon' than *P. polyodon*. As mentioned above, this specimen is here referred to *Alopecognathus angusticeps*. MMK 5139 exhibits the same sort of narrow snout of equal width through the canine-postcanine region, rounded snout tip in lateral view, and relatively small postcanines as AMNH FARB 5559. MMK 5139 also

exhibits reniform pterygoid bosses with anteriorly arcing tooth rows, which are not visible in the holotype but are shared with other *Alopecognathus*-morph specimens (and notably not present in *Pristerognathus*). In the same paper naming *P. vanderbyli*, Broom (1925) named a second new *Pristerognathus* species (*P. vanwyki*) based on a poorly preserved and prepared partial skull (SAM-PK-6533). The original diagnosis for *P. vanwyki* is limited to a few dubious proportional characters relative to MMK 5139: shorter absolute skull length, shorter absolute snout length, and relatively longer postcanine tooth row length in SAM-PK-6533. All of these characters are attributable to growth stage or individual variation, and are exceedingly minor in any case; Broom (1925) cites SAM-PK-6533 as having a snout 110 mm long *vs* 140 mm in MMK 5139. Despite the poor quality of the specimen, relative snout width and small postcanines in SAM-PK-6533 indicate it can also be referred to *A. angusticeps*.

Broom (1932) named *Alopecideops gracilis* for an extremely poorly preserved, highly dorsoventrally crushed skull and lower jaws (SAM-PK-4997), which he diagnosed based on its small size and apparent possession of six incisors and two precanines in the upper jaw. As previously noted by van den Heever (1987), SAM-PK-4997 is too poorly preserved to accurately determine its anterior tooth count. At least five incisors are present in the left premaxilla but no precanines are visible; a fragment anterior to the left canine that likely corresponds to one of Broom's 'precanines' appears to be bone rather than tooth. Based on its poor preservation, van den Heever (1987) considered *A. gracilis* to be a *nomen dubium*. However, the absence of transverse expansion of the snout around the canines in SAM-PK-4997 indicates that it can be referred to *A. angusticeps*. Notably, the extreme dorsoventral crushing in this specimen is further evidence that this distinction in snout shape is not entirely attributable to taphonomy (also, this specimen exhibits a relatively narrow intertemporal region, like larger *Alopecognathus* specimens but unlike *Pristerognathus*).

Broom (1936) established the species *Cynariognathus gallowayi* for a badly eroded skull (TM 266) that he distinguished from *C.* (originally *Pristerognathus*) *platyrhinus* by length of the upper incisor row (38 mm in *C. gallowayi vs* 32 mm in *C. platyrhinus*) and possession of eight postcanines (*vs* nine in *C. platyrhinus*). The snout of this specimen appears relatively tall, but this may be due to the clear lateral compression it has suffered (based on distortion of the right postorbital bar). The general snout morphology (width, curvature) of TM 266 matches that of *Alopecognathus*, and *C. gallowayi* is here considered synonymous with *A. angusticeps*. However, the postcanines of TM 266 are unusually large for an *Alopecognathus* specimen. This is probably attributable to erosion of the maxillary surface, showing the postcanine roots in cross-section and making the teeth appear larger than they would have been in life. Nevertheless, the possibility that TM 266 could represent a badly distorted skull of *Glanosuchus* cannot entirely be discounted, and preparation of the palate is needed for confirmation.

BSPG 1934-VIII-30, the holotype of *Cynariognathus seeleyi*, was thoroughly described by Broili & Schröder (1936a), a rarity for early work on scylacosaurids. Unfortunately, however, their diagnosis for the species mostly consisted of generalized early therocephalian characters. The one supposed autapomorphy of *C. seeleyi*, postorbital extending posterior to the level of pineal foramen, is not useful considering that sutures are not evident in most scylacosaurid specimens, rendering the posterior extent of the postorbital uncertain. This issue was noted by van den Heever (1987), who accordingly considered this species a *nomen dubium*. BSPG 1934-VIII-30 has a long, narrow snout, but also appears to have unusually large postcanines for *Alopecognathus*. Like TM 266, though, this may be artefactual: the maxillary surface is worn and overprepared and much of the exposed tooth surface is actually root. With this said, given the poor preservation of this specimen, characters supporting referral to *Alopecognathus* are few. It is here considered a specimen of *A. angusticeps* based on snout width (not expanded around the canine), but it could also represent *Pristerognathus*. Additional preparation to expose the palatal bosses is also needed for this specimen to clarify its relationships.

Broom (1937) named *Alopecognathus megalops* for a dorsoventrally crushed skull missing the snout tip (TM 1491). He distinguished this taxon from *Pristerognathus* based on the presence of eight postcanines, but oddly did not compare it to any other species of *Alopecognathus*. Haughton & Brink (1954) considered the referral of this species to *Alopecognathus* to be questionable, and van den Heever (1987) considered it a *nomen dubium*. Because of overpreparation of the palate and absence of the snout tip, identification of TM 1491 is difficult. It is referred to *A. angusticeps* here based on the relatively small postcanines and narrow intertemporal region.

Boonstra (1953, p. 63) described an additional species of *Alopecognathus* (*A. angustioriceps*) based on what he described as 'a well-preserved complete skull' (SAM-PK-9342) that unfortunately has substantially degraded as a result of acid preparation. Boonstra (1953) differentiated *A. angustioriceps* from the type species *A. angusticeps* based on smaller absolute size and a narrower skull; he did not compare it with *A. megalops*. Differences in absolute size between SAM-PK-9342 and AMNH FARB 5559 can be attributed to differences in age or individual growth rates. SAM-PK-9342 is only slightly narrower than AMNH FARB 5559, which is probably attributable to lateral compression. Van den Heever (1987) considered SAM-PK-9342 to be a specimen of *Glanosuchus macrops* based on the dental formula I6/PrC0, but the very slender snout of this specimen (both transversely and dorsoventrally) and relatively small postcanines are instead typical of *Alopecognathus angusticeps*. In the same paper, Boonstra (1953) also described a new species of *Pristerognathus* (*P. roggeveldensis*) based on a very poor partial skull and lower jaws (SAM-PK-9356a), and listed as its specific characters a dental formula of I6/C1/PC5, maximum skull length 255 mm, snout long and broader than high, orbit in posterior half of skull, and dentary with truncated, posteriorly-directed coronoid process. None of these

characters serves to distinguish SAM-PK-9356a from similar scylacosaurid specimens. The upper postcanine count in this specimen should be considered uncertain, as this region is very poorly preserved, and the presence of six incisors and no precanine is typical of *Glanosuchus* and *Alopecognathus* in addition to *Pristerognathus*. This specimen has clearly suffered left-right shear, so its exact snout proportions are somewhat questionable, but does not appear to be broader than high. The orbit is incompletely preserved, and as the temporal region is almost entirely missing, its position relative to total skull length is unknown. Finally, the dentary is not notably truncated (although it is distorted on the sheared right side of the skull) and its coronoid process is angled in a similar way as other scylacosaurids. Van den Heever (1987) considered SAM-PK-9356a to be another specimen of *Glanosuchus* based on anterior dental formula, but as with SAM-PK-9342, even taphonomic distortion is unlikely to account for the very narrow snout in this specimen. Here, SAM-PK-9356a is considered to be a specimen of *A. angusticeps*, based on the high degree of skull curvature between the snout and orbital region and relatively small postcanines.

Van den Heever (1994) comprehensively described a very well-prepared, partially disarticulated skull (CGS M 796) that he identified as *Glanosuchus macrops*. However, the snout proportions of this specimen instead indicate that it should be referred to *Alopecognathus angusticeps*. Similarly, Fourie & Rubidge (2009) referred SAM-PK-K7809, a spectacular specimen consisting of an intact skull and jaws in articulation with the majority of the skeleton, to *G. macrops*, again based on the dental formula diagnosis of van den Heever (1987). However, this specimen has a narrow snout of equal width throughout most of its length and relatively small postcanines, and is also better identified as *A. angusticeps*. A second, even more complete scylacosaurid skeleton (SAM-PK-K7808) is known from the same locality as SAM-PK-K7809 (La-de-da, Beaufort West), but this specimen was incompletely prepared at the time of study. This specimen has a relatively long snout and may also represent *Alopecognathus*, but there appears to be distinct constriction of the snout posterior to the canine, suggesting it could instead be *Pristerognathus*. Further preparation of the cranium is required for confident identification of this individual. In addition to CGS M 796, a number of other specimens currently housed in the Council for Geoscience (Pretoria) can be referred to *Alopecognathus angusticeps* (mostly from *Endothiodon* AZ exposures; see Discussion), as these specimens also exhibit the combination of a I6/PrC0 dental formula, long, narrow snout, consistent snout width through canine-postcanine region, relatively small postcanines, and skull curving in lateral view between snout and orbitotemporal region (e.g. CGS MJF 211, CGS RMS 983).

***Eutheriodon* gen. nov.**

*LSID*. urn:lsid:zoobank.org:act:57038D0A-5531-4641-8DAB-670DECF50883

*Type species*. *Eutheriodon vandenheeveri* sp. nov.

*Etymology*. 'True beast tooth', from the Ancient Greek εὖ ('true', Latinized *eu*), θηρίον ('beast', Latinized *therion*), and ὀδών ('tooth', Latinized *odon*), tooth. Named in reference to its status as the earliest known eutheriodont in the fossil record.

*Diagnosis*. As for type and only species.

***Eutheriodon vandenheeveri* sp. nov.**

Figures 8B, 9

*LSID*. urn:lsid:zoobank.org:act:C312E079-4E8C-4ED6-B0C1-B21E194A9F71

*Holotype*. NMQR 2910, a partial snout and lower jaws from Modderdrift, Prince Albert (Figs 8B, 9C–E).

*Referred material*. NMQR 2908, a partial snout and lower jaws from Modderdrift, Prince Albert (Fig. 9F–H); NMQR 3488, a partial skull (missing the temporal region) and lower jaws from Klein Wolwefontein, Jansenville (Fig. 9A,B).

*Etymology*. Named after Juri van den Heever (professor emeritus, University of Stellenbosch) for his contributions to our knowledge of early therocephalians.

*Diagnosis*. Mid-sized (estimated maximum basal skull length 25 cm, based on NMQR 3488; estimation based on the proportions of *Alopecognathus*) scylacosaurid distinguished by the following unique combination of characters: dental formula I6/PrC1/C1/PC9, snout relatively long and narrow, narrow interorbital region, pterygoid boss highly dentigerous, angled anterolaterally, and expanding anteriorly.

*Remarks*. Rubidge *et al*. (1983) initially noted the presence of therocephalians in the *Eodicynodon* AZ, the stratigraphically lowest assemblage zone of the Beaufort Group, based on a small partial snout and lower jaws (NMQR 2908) that they described as a 'pristerognathid' (=scylacosaurid). Later, Rubidge (1995) listed the scylacosaurid genera *Glanosuchus* and *Alopecodon* as being present in the *Eodicynodon* AZ, based on NMQR 2908 and an additional partial skull, NMQR 2910. Abdala *et al*. (2008) thoroughly described these two specimens, referring them to the species *Glanosuchus macrops* (NMQR 2908) and *Ictidosaurus angusticeps* (NMQR 2910) on the basis of incisor/precanine counts, following the diagnoses of van den Heever (1987). These identifications have been retained in subsequent studies (e.g. Smith *et al*. 2012; Day 2013), indicating extremely long ranges for these scylacosaurid genera, particularly *Glanosuchus*, which has been considered to range from the *Eodicynodon* through *Endothiodon* AZs (e.g. Day 2013; Day & Smith, 2020).

NMQR 2908 is a very small specimen (estimated total skull length 8.0 cm) and almost certainly juvenile, as determined by Abdala *et al*. (2008). NMQR 2910 preserves mostly the same parts of the skull as NMQR 2908, but its larger size (probably representing a mature animal) and more completely preserved palate make it more useful for comparisons with other scylacosaurids. NMQR 2910 has a relatively long, narrow snout, more similar to that of *Alopecognathus* or *Pristerognathus* than *Glanosuchus* or *Pardosuchus*. The upper postcanines are numerous (nine, the highest number known in scylacosaurids) and have somewhat lanceolate, serrated crowns directed ventrally, roughly similar to those of *Alopecognathus* and *Pristerognathus* but unlike the recurved, mesially thickened




**Figure 9.** Specimens of *Eutheriodon vandenheeveri* gen. et sp. nov. NMQR 3488 in (**A**) dorsal and (**B**) left lateral views. NMQR 2910, holotype of *Eutheriodon vandenheeveri*, in (**C**) dorsal, (**D**) left lateral, and (**E**) ventral views. NMQR 2908 in (**F**) left lateral, (**G**) right lateral, and (**H**) dorsal views. All specimens to scale; scale bar equals 5 cm.

postcanines of *Alopecodon* and *Glanosuchus*. Unlike *Alopecognathus* or *Pristerognathus*, however, the pterygoid bosses of NMQR 2910 are angled anterolaterally, expanding anteriorly (Fig. 8B), similar to those of *Glanosuchus* (Fig. 8E). Unlike in *Glanosuchus*, in which the pterygoid boss bears a single tooth row in an arc (curving around the anterior boss margin), in *Eutheriodon* this boss is densely dentigerous, with at least three tooth rows present. The presence of six incisors distinguishes NMQR 2910 from *Alopecodon* and *Scylacosaurus*, and it can also be distinguished from the latter taxon by the presence of a 'standard' (rather than 'hourglass'-shaped) scylacosaurid dentary. Although displaced, the frontals are preserved in NMQR 2910 and demonstrate that the interorbital region in this specimen was relatively narrow, unlike the condition in *Hyorhynchus* and *Maraisaurus*. In general, NMQR 2910 shows a mosaic of features present in other scylacosaurids without perfectly matching any of them. Although this specimen does concord with the holotype of *Ictidosaurus angusticeps* (SAM-PK-630) in terms of anterior tooth count (six incisors and one precanine), because this tooth count is observed in other scylacosaurid taxa with clearly distinct cranial morphologies, it is here considered insufficient to validate *Ictidosaurus* (see entry below) and allow referral of NMQR 2910 to that taxon. Given the unique combination of features in NMQR 2910, however, it can be recognized as a distinct scylacosaurid metataxon, here named *Eutheriodon vandenheeveri*.

NMQR 2908 accords with the morphology of NMQR 2910 in most regards other than in the absence of a precanine. Notably, NMQR 2908 exhibits the same unusually high postcanine count (nine uppers) and lanceolate, uncurved postcanine morphology of NMQR 2908. Combined with its discovery in the same strata at the same locality as NMQR 2910, this specimen is here regarded as most parsimoniously referred to the same taxon as the larger skull. The absence of precanines in the juvenile of a taxon that has them as an adult is unusual for a theriodont, but not unknown. One additional scylacosaurid specimen, mentioned by Modesto *et al.* (2001; misnumbered as NMQR 3484) and Kammerer & Rubidge (2022), may also be referable to *E. vandenheeveri*. NMQR 3488 is a snout, orbital region, and jaws showing the same unique combination of features as NMQR 2910 (although this specimen, like NMQR 2908, also lacks a precanine): nine uncurved postcanines (some tooth positions represented by empty alveoli), long, narrow snout, narrow interorbital region, and anterolaterally angled, highly dentigerous pterygoid bosses. However, this specimen is not from the classic *Eodicynodon* AZ exposures near Prince Albert, but rather from a farm (Klein Wolwefontein) near Jansenville in the Eastern Cape. The potential implications of this specimen for biostratigraphic correlation are addressed in the Discussion.

***Glanosuchus*** Broom, 1904

1931 *Cynariognathus* Broom, p. 161

1951 *Walteria* Brink & Kitching, p. 1218 (non *Walteria* Schulze, 1886)

1954 *Ptomalestes* Boonstra, p. 78

1958 *Karroowalteria* Kuhn, p. 382 (nom. nov. for *Walteria* Brink & Kitching, 1951)
1975 *Crapartinella* Mendrez, p. 382
*Type species*. *Glanosuchus macrops* Broom, 1904.
*Etymology*. 'Hyaena crocodile', from the ancient Greek γλάνος ('hyaena', Latinized *glanos*) and Σοῦχος (Greek name for the Egyptian crocodile god Sobek, Latinized *suchus*).
*Diagnosis*. As for type and only species.

***Glanosuchus macrops*** Broom, 1904
Figures 1C, 7A–C, E, 8E, 10, 11, 12A, 13A,B
1912 *Pristerognathus platyrhinus* Broom, p. 863
1931 *Cynariognathus platyrhinus* Broom, p. 161
1951 *Walteria skinneri* Brink & Kitching, p. 1218
1954 *Cynariognathus paucioridens* Boonstra, p. 93
1954 *Ptomalestes avidus* Boonstra, p. 79
1969 *Alopecognathus skinneri* Boonstra, p. 57
1975 *Crapartinella croucheri* Mendrez, p. 382
*Holotype*. SAM-PK-637, a partial skull (missing the temporal arches) and lower jaws from Knoffelfontein, Beaufort West (Figs 7B, 10C, 11A,B).
*Referred material*. AMNH FARB 5502 (holotype of *Pristerognathus platyrhinus*), a partial snout and lower jaws from Grootfontein, Beaufort West (Figs 10G, 11I); BP/1/278, a distorted partial skull (missing the temporal region and snout tip) from Antjiesfontein, Prince Albert; BP/1/1100 (holotype of *Karroowalteria skinneri*), a dorsoventrally crushed partial skull (missing the temporal region) and lower jaws from Elandsfontein, Beaufort West (Figs 7A, 10A, 11C); CGP/1/779A (=CGS RS 300), a partial skull (broken into several fragments), partial axial column (anterior 14 vertebrae), scapular spine, and proximal right humerus from Brandewyns Gat, Beaufort West; CGS GM 74, a laterally compressed complete skull and lower jaws from Danskraal, Alfred (Fig. 11F); CGS RS 329, a partial skull (missing the temporal region) from Brandewyns Gat, Beaufort West; MB.R.996, a distorted partial skull (missing part of the temporal region) and lower jaws from an uncertain Karoo locality; NHMUK PV R 4096 (holotype of *Crapartinella croucheri*), a partial skull (missing the temporal arches) and lower jaws from Weltevreden, Beaufort West (Figs 7C, 10F, 11J); SAM-PK-3435, an isolated snout and lower jaws from Jakkalsfontein, Prince Albert; SAM-PK-11460, a partial snout and lower jaws from Buffelsvlei, Beaufort West; SAM-PK-11560a (holotype of *Cynariognathus paucioridens*), a poorly preserved partial snout and right lower jaw from Kroonplaas (=Heuningskopfontein), Beaufort West (Figs 10H, 11H); SAM-PK-11695, a distorted snout and lower jaws from Celeryfontein, Fraserburg; SAM-PK-11843, a distorted partial skull (missing the temporal region) and lower jaws from Lammerskraal, Prince Albert (Figs 10E, 11E); SAM-PK-11942 (holotype of *Ptomalestes avidus*), a dorsoventrally crushed partial skull (missing the temporal arches) and lower jaws from Buffelsvlei, Beaufort West (Figs 1C, 7E, 8E, 10D, 11G, 12A, 13A,B); UCMP 42395, a partial skull (missing the snout tip, left postorbital bar, and right temporal arch) and lower jaws from Weltevreden, Beaufort West (Figs 10B, 11D); UCMP 42581, a partial skull (dorsal surface embedded in plaster) and lower jaws from Lammerskraal, Prince Albert.
*Etymology*. 'Long face', from the ancient Greek μακρός ('long', Latinized *macros*) and ὄψ ('face', Latinized *ops*).
*Diagnosis*. Large (estimated maximum basal skull length 37 cm, based on BP/1/1100, estimated with reference to the proportions of SAM-PK-637) scylacosaurid distinguished by the following unique combination of characters: upper dental formula I6/PrC0/C1/PC6–8, lower dental formula i3/c1/pc9, snout massive and relatively broad, narrow interorbital region, pterygoid boss angled anterolaterally and expanding anteriorly, with a single, 'C'-shaped tooth row.
*Remarks*. In recent years, *Glanosuchus* has taken over the role of 'archetypal early therocephalian' from traditional titleholder *Pristerognathus*, in large part due to van den Heever's (1987) referral of the majority of determinable (under his paradigm) scylacosaurid skulls to this taxon, including the well-preserved and prepared specimen CGS M 796 (van den Heever 1994). This specimen was later the subject of a study arguing for the presence of maxillary turbinates in therocephalians (thus inferring endothermy; Hillenius 1994), which received extensive popular coverage (e.g. Zimmer 1994), making *Glanosuchus* the first scylacosaurid many people (scientists and laypersons alike) had ever heard of. Subsequent studies on scylacosaurid anatomy and palaeobiology have also tended to focus on *Glanosuchus* (e.g. Jenkins *et al*. 2002; Maier & van den Heever 2002; Fourie & Rubidge 2009), likely also as an artefact of being the most abundant scylacosaurid in collections.
However, among the extensive sample of scylacosaurids with six incisors and no precanines (van den Heever's [1987] diagnosis for *Glanosuchus macrops*), there is a striking amount of variability in dental and overall cranial morphology. Although a large degree of ontogenetic and taphonomic variation is expected in any Karoo fossil with substantial sample size, several of the variable characters in the '*Glanosuchus*' sample are not readily explained by such factors. As discussed in the section on *Alopecognathus* above, even among skulls of comparable size and mode of distortion, there is a divide between robust and gracile '*Glanosuchus*' skulls, which also differ in characters not related to general skull shape (e.g. postcanine crown morphology, pterygoid boss morphology). The holotype of *G. macrops* (SAM-PK-637) is a typical robust morph skull: the upper canine is massive, and the area of the snout around it is relatively tall and broad compared to that of other scylacosaurids. The pterygoid bosses are angled anterolaterally and bear a single, curved tooth row, and the postcanines are recurved and thickened mesially. Here, these characters are considered diagnostic for separating *Glanosuchus* from *Alopecognathus*, and a large portion of '*Glanosuchus*' specimens *sensu* van den Heever (1987) are here transferred to the latter genus, including the subjects of the studies of Hillenius (1994) and Fourie & Rubidge (2009) (the skull studied by Maier & van den Heever [2002], SAM-PK-K238, also probably represents *Alopecognathus* based on their Fig. 1, but as it was destroyed by serial sectioning this cannot be confirmed).

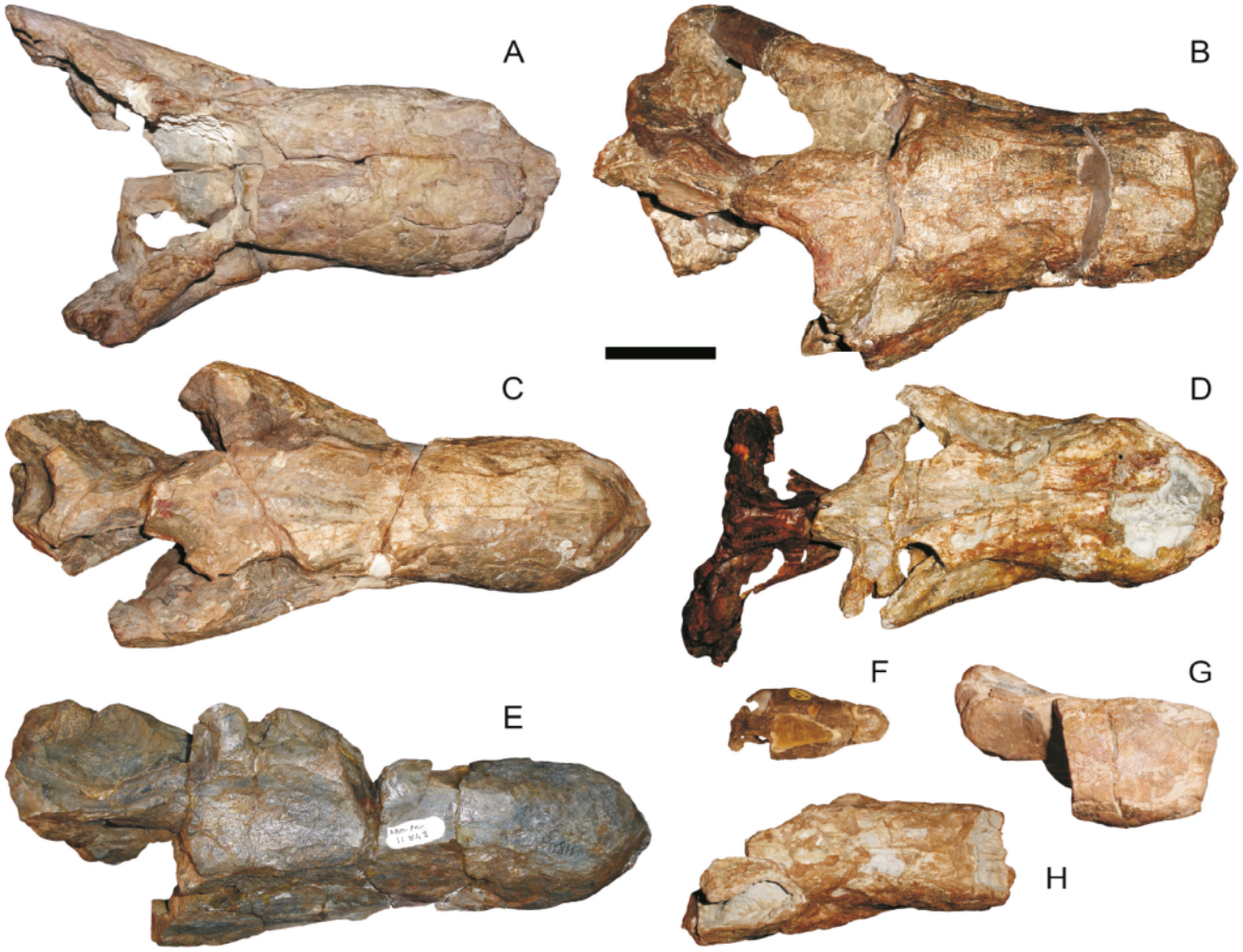



**Figure 10**. Specimens of *Glanosuchus macrops* Broom, 1904 in dorsal view. **A**, BP/1/1100, holotype of *Karroowalteria skinneri*. **B**, UCMP 42395. **C**, SAM-PK-637, holotype of *Glanosuchus macrops*. **D**, SAM-PK-11942, holotype of *Ptomalestes avidus*. **E**, SAM-PK-11843. **F**, NHMUK PV R 4096, holotype of *Crapartinella croucheri*. **G**, AMNH FARB 5502, holotype of *Pristerognathus platyrhinus*. **H**, SAM-PK-11560a, holotype of *Cynariognathus paucioridens*. All specimens to scale; scale bar equals 5 cm.

Despite the substantial reduction in abundance incurred by its split from *Alopecognathus*, *Glanosuchus* remains a reasonably well-represented taxon in collections, and several nominal scylacosaurid taxa can be regarded as its junior synonyms. Broom (1912) named *Pristerognathus platyrhinus* based on a partial snout and jaws (AMNH FARB 5502) that he distinguished from other species of the genus on the basis of its remarkably broad snout. Later he separated this species from *Pristerognathus* as a new genus, *Cynariognathus* Broom, 1931, based on postcanine count (which he regarded as eight in *Cynariognathus vs* six in *Pristerognathus*, despite the lack of a complete tooth row in the holotype of *P. polyodon*). AMNH FARB 5502 is a very poor specimen, and it would not be unreasonable to regard *C. platyrhinus* as a *nomen dubium* (as was done by van den Heever [1987]). However, the snout proportions and relatively large incisors and canines of this specimen are only observed in *Glanosuchus* among scylacosaurids, indicating that it should be referred to that taxon.

Brink & Kitching (1951) described the snout and partial jaws (BP/1/1100) of a very large scylacosaurid as a new taxon, *Walteria skinneri*. They considered it most similar to *Pristerognathus* and *Scymnosaurus*, but distinguished by its larger size and broader snout. Absolute skull size is a questionable character, but the proportional breadth of the snout around the canine in BP/1/1100 does occupy an extreme among scylacosaurids. Kuhn (1958) noted that the genus name *Walteria* was preoccupied by a sponge and replaced it with *Karroowalteria*. Boonstra (1969) stated that he considered BP/1/1100 to fall within the range of variation of *Pristerognathoides*, but then contradicted this by including it in the new combination *Alopecognathus skinneri* in his taxon list for the *Tapinocephalus* Zone. Based on the presence of six incisors and no precanines, van den Heever (1987) considered *K. skinneri* to be a synonym of *Glanosuchus macrops*, and this is upheld here. In addition to tooth count, BP/1/1100 accords with *Glanosuchus* in snout and pterygoid boss morphology.

Boonstra (1954) named two scylacosaurid species here considered synonymous with *Glanosuchus macrops*. *Cynariognathus paucioridens* is based on a very poor specimen (SAM-PK-11560a) preserving a similar portion of the skull (and with a similar quality of preservation) as the holotype of *Cynariognathus platyrhinus* (AMNH FARB 5502). Van den Heever (1987) considered *C. paucioridens* a *nomen dubium*, but the broad snout and anterolaterally angled pterygoid boss indicate that it should be synonymized with *G. macrops*. In contrast to the former specimen,




**Figure 11**. Specimens of *Glanosuchus macrops* Broom, 1904 in lateral view. SAM-PK-637, holotype of *Glanosuchus macrops*, in (**A**) right and (**B**) left lateral views. **C**, BP/1/1100, holotype of *Karroowalteria skinneri*, in right lateral view. **D**, UCMP 42395 in left lateral view. **E**, SAM-PK-11843 in right lateral view. **F**, CGS GM 74 in right lateral view. **G**, SAM-PK-11942, holotype of *Ptomalestes avidus*, in right lateral view. **H**, SAM-PK-11560a, holotype of *Cynariognathus paucioridens*, in right lateral view. **I**, AMNH FARB 5502, holotype of *Pristerognathus platyrhinus*, in left lateral view. **J**, NHMUK PV R 4096, holotype of *Crapartinella croucheri*, in left lateral view. All specimens to scale; scale bar equals 5 cm.

*Ptomalestes avidus* is represented by one of the better holotypes among scylacosaurids (SAM-PK-11942), a somewhat dorsoventrally crushed but, importantly, fully prepared cranium (missing the temporal arches) and lower jaws. Unfortunately, the same acid preparation that revealed many details of the skull rarely exposed in other scylacosaurids also damaged the bone surface of this specimen, obscuring previously visible sutural detail and dissolving the anterior snout surface and palate. (Further deterioration of this important specimen was apparently only prevented by the intervention of archaeologist Ione Rudner, who performed emergency conservation and was successful in stabilizing it, *per* van den Heever [1987].) One suture that remains clearly visible, however, is the mid-premaxillary suture on the palate. As discussed in the Introduction, there is variation in incisor count across the two premaxillae (five on the left and seven on the right). Boonstra (1954) considered *Ptomalestes* to have five incisors (and, in combination with other characters, believed it to be a distinct genus), whereas van den Heever (1987) considered *Ptomalestes* to have seven incisors (and accordingly synonymized it with *Pristerognathus*). Given that the conflicting counts of both researchers are actually correct, incisor count alone cannot be relied on to determine the identity of SAM-PK-11942. Here, the combination of a relatively broad snout, recurved postcanines, and anterolaterally angled pterygoid boss are taken as evidence for referral to *Glanosuchus*. It should be noted that if you take the average of the upper incisors across both sides, you get the count considered diagnostic for *Glanosuchus* by van den Heever (1987), and it is possible that the unusual condition in this specimen represents a developmental abnormality in which the tooth bud for the left I1 formed in the right premaxilla.

Mendrez (1975) placed a *Tapinocephalus* AZ specimen (NHMUK PV R 4096; originally referred by Broom [1915b] to the later Permian eutherocephalian taxon *Icticephalus polycynodon*) in a new family, genus, and species (Crapartinellidae: *Crapartinella croucheri*). She considered this specimen unique among therocephalians in having a dentigerous vomer. Van den Heever (1987) did not

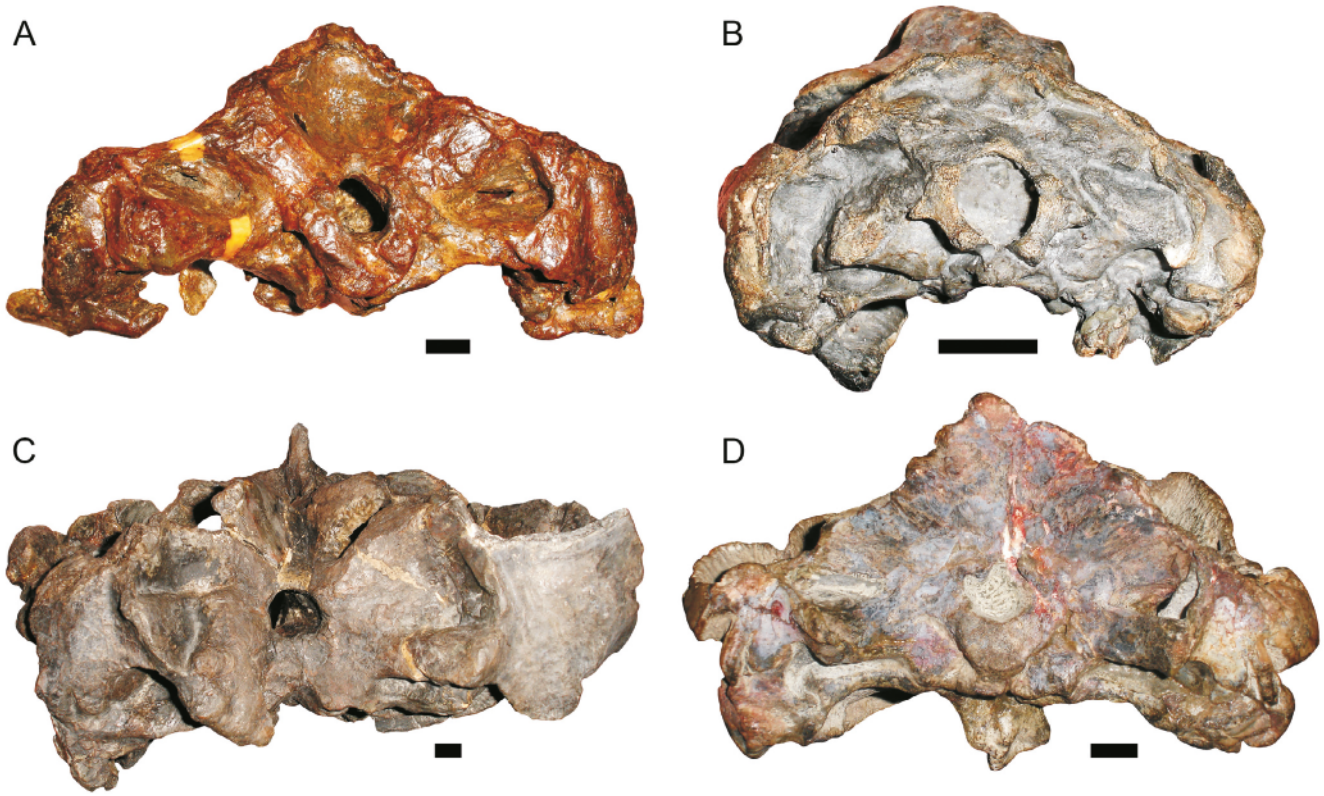



**Figure 12**. Scylacosaurid occipital morphology. **A**, SAM-PK-11942, holotype of *Ptomalestes avidus* (=*Glanosuchus macrops*). **B**, UCMP 42659, an indeterminate juvenile scylacosaurid. **C**, UCMP 42699, referred specimen of *Scylacosaurus sclateri*. **D**, MMK 4499, holotype of *Lycedops scholtzi* (=*Pardosuchus whaitsi*). Scale bars equal 1 cm.

address this specimen in detail, but noted that it could be juvenile. The large orbits relative to temporal fenestra size, broad intertemporal region, and very large, open interpterygoid vacuity all suggest that this is indeed the case. Examination of the specimen indicates that the supposed vomerine teeth instead represent bone damage, probably artefacts of acid preparation. The combination of paired vomers (a basal therocephalian feature) with an edentulous transverse process of the pterygoid (a scylacosaurian feature) indicate that this specimen is probably a juvenile scylacosaurid. Too little is currently known about scylacosaurid ontogeny for a definite referral, but available evidence suggests that NHMUK PV R 4096 represents a juvenile of *Glanosuchus macrops*. Although it does have a proportionally short, broad snout, this is likely taxonomically irrelevant at such an early ontogenetic stage. Of potential greater importance is the presence of anterolaterally angled pterygoid bosses, which at present appears to be unique to *G. macrops* among *Tapinocephalus* AZ scylacosaurids. These bosses are more densely dentigerous in NHMUK PV R 4096 than in adult *Glanosuchus* specimens, but this may be

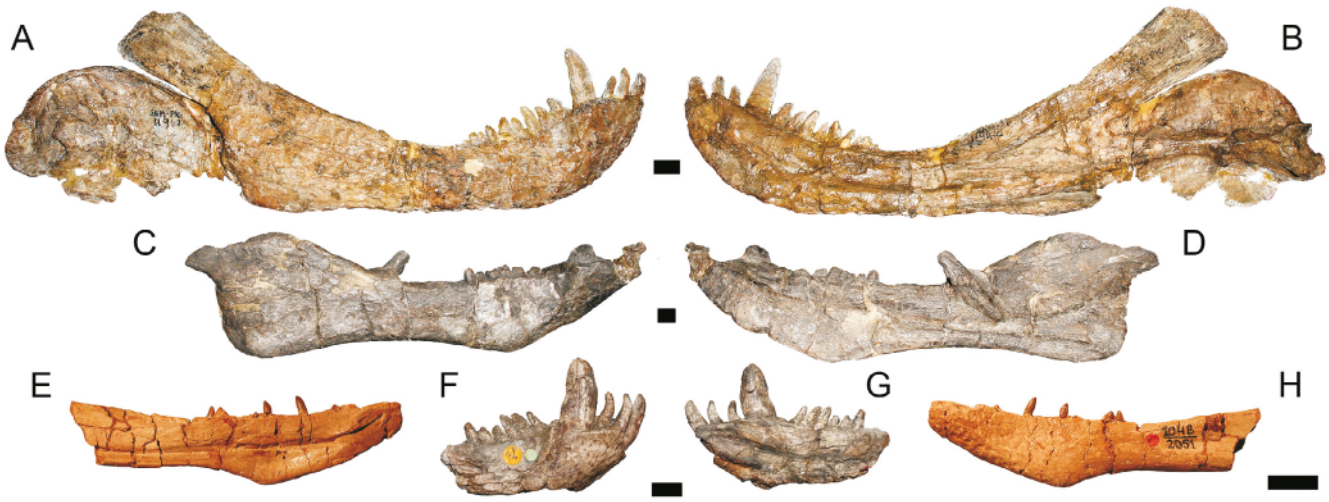



**Figure 13**. Mandibular morphology in scylacosaurids and a supposed biarmosuchian. Right mandibular ramus of SAM-PK-11942, the holotype of *Ptomalestes avidus* (=*Glanosuchus macrops*), in (**A**) lateral and (**B**) medial views. Right dentary of UCMP 42699, referred specimen of *Scylacosaurus sclateri*, in (**C**) lateral and (**D**) medial views. SGU 104B/2051, holotype of *Biarmosuchoides romanovi*, the anterior portion of a left dentary, in (**E**) medial and (**H**) lateral views. Anterior portion of the right dentary of NHMUK PV R 2581, holotype of *Pristerognathus polyodon*, in (**F**) lateral and (**G**) medial views. Scale bars equal 1 cm.

due to immaturity. With this noted, additional specimens of juvenile scylacosaurids and better prepared specimens of rare taxa such as *Alopecodon* will be needed before this referral can be confirmed.

Huttenlocker (2009) listed UCMP 42395, a poor partial skull and jaws from Lammerskraal, among his representative materials of Lycosuchidae. Several actual lycosuchid specimens are present in the Berkeley collections (e.g. UCMP 42581 and UCMP 42667, the latter representing a complete skeleton described by Cys [1967] as '*Cynariognathus platyrhinus*'), but UCMP 42395 is not among them; several features instead indicate its identification as a scylacosaurid. Lycosuchids have low tooth counts: always only five upper incisors, which are relatively large compared to the postcanines, and maximally five postcanines in the upper and lower jaws (Abdala *et al.* 2014b). The anterior dentition of UCMP 42395 is too poorly preserved to get a definite count, but the visible incisors are smaller than they would be in a lycosuchid. More importantly, it is clear that the postcanine count in this specimen exceeds that of any lycosuchid: at least seven postcanines are visible in both the left maxilla and dentary, which is within the typical range for scylacosaurids. The general cranial morphology of UCMP 42395 also accords more closely with a scylacosaurid than a lycosuchid identification, showing the elevation of the temporal region relative to the snout characteristic of the former group. Finally, UCMP 42395 bears a large, dentigerous pterygoid palatal boss (the one on the right side of the skull is damaged, but the one on the left is essentially intact), which is present in scylacosaurids but absent in lycosuchids (van den Heever 1994). Identification as *Glanosuchus macrops* among scylacosaurids is supported by the broad, deep snout and anterolaterally expanded palatal boss of this specimen.

***Hyorhynchus*** Seeley, 1889

*Type species*. *Hyorhynchus platyceps* Seeley, 1889.

*Etymology*. 'Pig snout', from the ancient Greek ὗς ('wild pig', Latinized *hyus*) and ῥύγχος ('snout', Latinized *rhynchus*).

*Diagnosis*. As for type and only species.

***Hyorhynchus platyceps*** Seeley, 1889

Figure 14

*Holotype*. NHMUK PV R 872, a partial skull (consisting only of the orbital region and posterior end of the snout) from the Gouph Tract in the vicinity of Beaufort West (Fig. 14E–G).

*Referred material*. CGS RMS 1058, a largely complete but worn and poorly prepared skull and lower jaws from Rietfontein, Prince Albert (Fig. 14A–D).

*Etymology*. 'Flat-headed', from the ancient Greek πλατύς ('flat', Latinized *platys*) and Latin *ceps* ('headed').

*Diagnosis*. Small (maximum basal skull length 21.19 cm, based on CGS RMS 1058) scylacosaurid characterized by a relatively short, strongly sloping snout, large orbits, and relatively broad interorbital region.

*Remarks*. Seeley (1889, p. 242) diagnosed *Hyorhynchus*

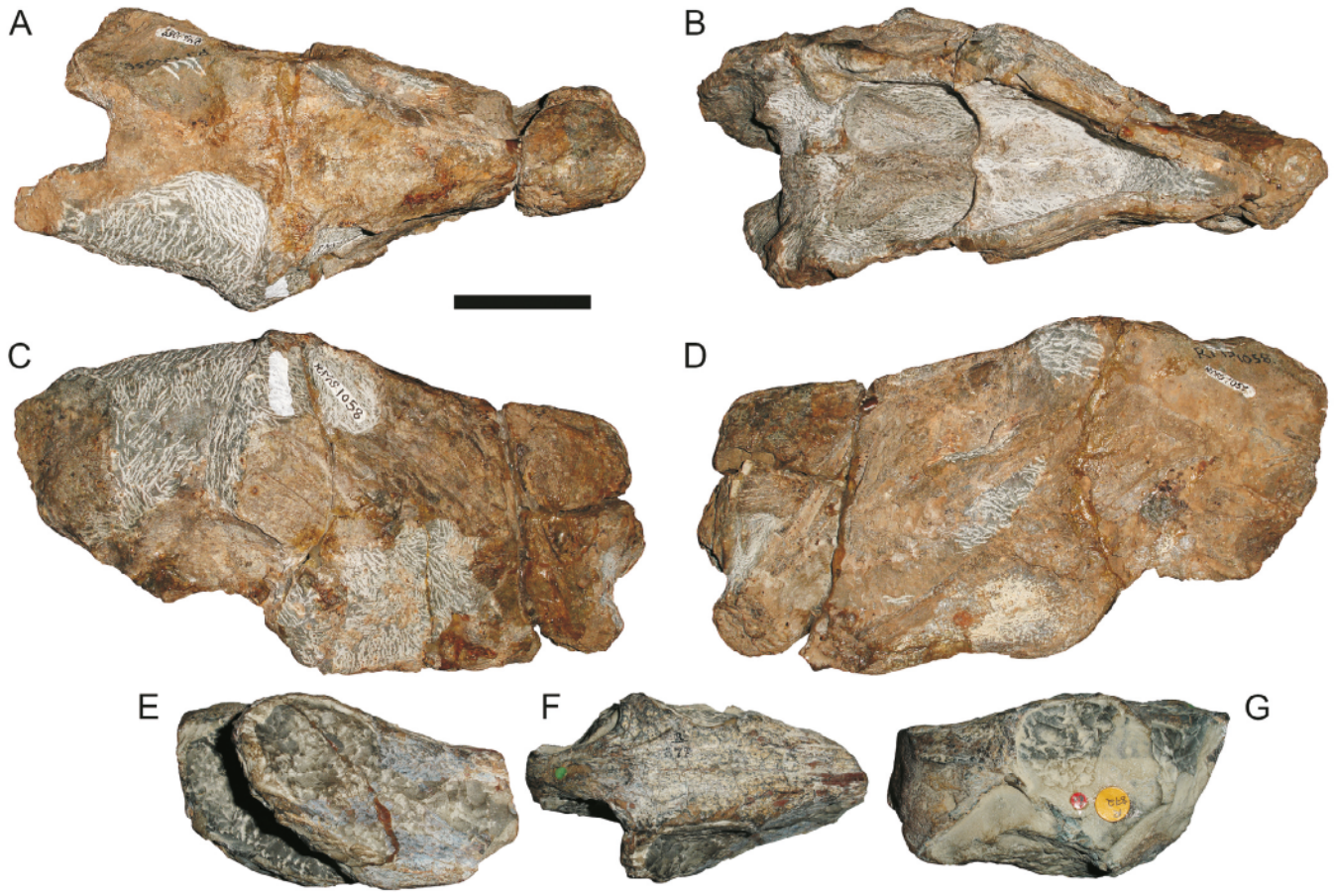



**Figure 14**. Specimens of *Hyorhynchus platyceps* Seeley, 1889. CGS RMS 1058 in (**A**) dorsal, (**B**) ventral, (**C**) right and (**D**) left lateral views. NHMUK PV R 872, holotype of *Hyorhynchus platyceps*, in (**E**) right lateral, (**F**) dorsal, and (**G**) left lateral views. All specimens to scale; scale bar equals 5 cm.

*platyceps* on the basis of its 'slender angular Pig-like snout, relatively large orbits, and a narrow parietal region' and considered it (p. 243) to belong to the 'Gennetotherioid division of the Anomodont order' (i.e. what would now be considered a gorgonopsian – Seeley's [1889] Gennetotheria was established to house *Lycosaurus*, and he stated that *Hyorhynchus* was most closely related to *Aelurosaurus* within the group). Broom (1932) and Boonstra (1934) both recognized that this specimen represents a therocephalian (although it is worth reiterating that the distinction between gorgonopsians and therocephalians had not yet been established in Seeley's time). Subsequent authors generally considered *H. platyceps* to be a dubious taxon (e.g. Romer 1956; Watson & Romer 1956; Boonstra 1969; van den Heever 1987).

Although NHMUK PV R 872 is highly incomplete, it does show some intriguing features. The interorbital region is proportionally broad, resulting in more laterally-directed orbits than are typical for scylacosaurids (Fig. 14F). This morphology is also present in *Maraisaurus parvus* (Fig. 15A,B), but *H. platyceps* appears to differ from that taxon in lacking an interorbital ridge and having the snout slope sharply anterior to the orbits (whereas in *M. parvus* the snout slopes very gradually anterior to the orbits, appearing nearly horizontal in lateral view). This peculiarity could be written off as taphonomic variation, were there not a second specimen (CGS RMS 1058) showing this same combination of features. CGS RMS 1058 demonstrates that *H. platyceps* was a remarkably short-snouted scylacosaurid, similar to *Pardosuchus whaitsi* in snout length (although transversely narrower in width and with a more sharply sloping dorsal profile). Unfortunately, the poor preparation of CGS RMS 1058 limits what can be said about the dentition of *H. platyceps*. At least five incisors and five postcanines are visible, but it is likely that more were present. Additional preparation of this specimen is needed to provide a fuller understanding of the anatomy of this rare and enigmatic therocephalian and confirm its distinction from *M. parvus*.

***Maraisaurus*** Boonstra, 1953

1954 *Pristerosaurus* Boonstra, p. 82

*Type species*. *Maraisaurus parvus* Boonstra, 1954.

*Etymology*. 'Marais's lizard', named after Johannes Marais, who collected the holotype, and the ancient Greek σαῦρος ('lizard', Latinized *saurus*).

*Diagnosis*. As for type and only species.

***Maraisaurus parvus*** Boonstra, 1953

Figure 15

1954 *Pristerosaurus microdon* Boonstra, p. 82

*Holotype*. SAM-PK-11944 (holotype of *Maraisaurus parvus*), a partial skull (missing the anterior snout and right temporal arch) and lower jaws from Buffelsvlei, Beaufort West (Fig. 15B–E).

*Referred material*. SAM-PK-9083 (holotype of *Pristerosaurus microdon*), a partial skull (missing the anterior snout) and lower jaws from Rietkuil, Beaufort West (Fig. 15A,F).

*Etymology*. Latin *parvus* ('small'), in reference to the small size of the holotype.

*Diagnosis*. Large (31 cm estimated maximum basal skull length, based on SAM-PK-9083; estimation based on the proportions of *Glanosuchus*) scylacosaurid characterized by a broad interorbital region, laterally-oriented orbits, weakly sloping snout, weak dorsoventral curvature of the

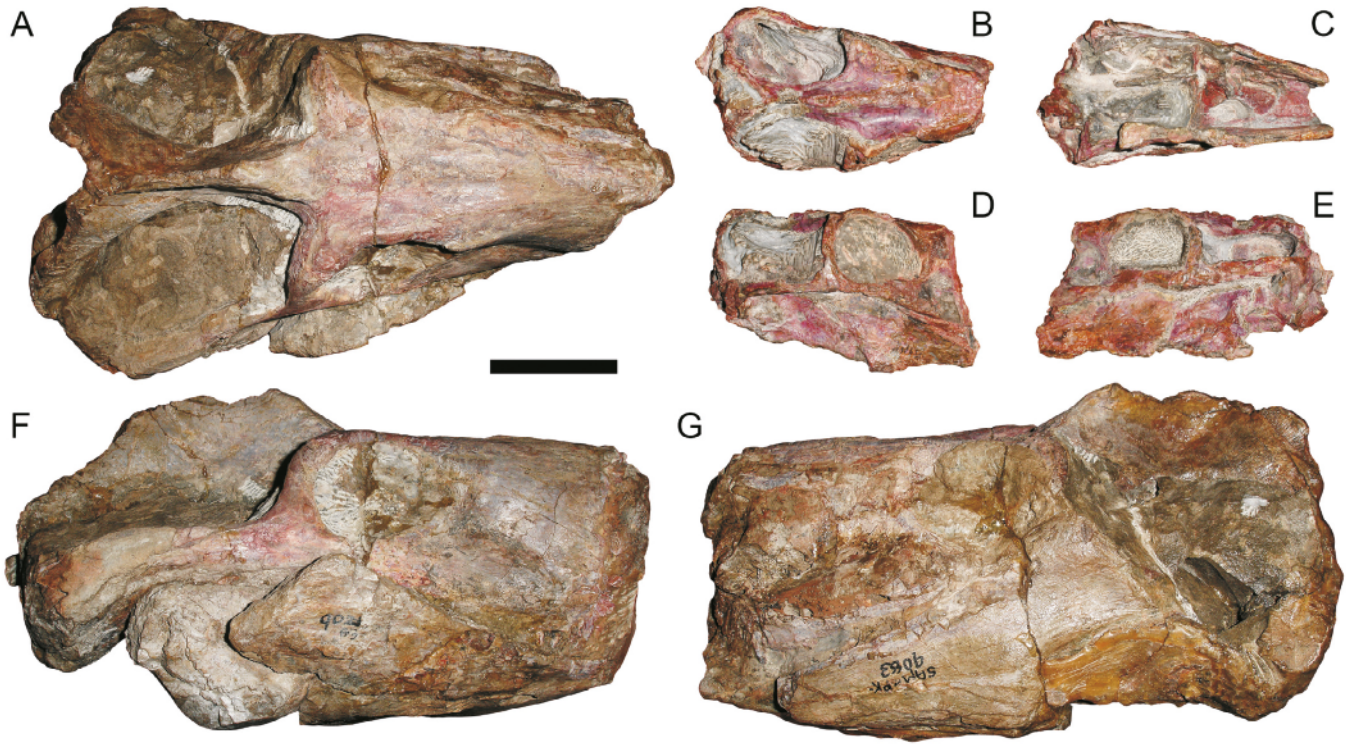



**Figure 15**. Specimens of *Maraisaurus parvus* Boonstra, 1953. SAM-PK-9083, holotype of *Pristerosaurus microdon*, in (**A**) dorsal, (**F**) right lateral, and (**G**) left lateral views. SAM-PK-11944, holotype of *Maraisaurus parvus*, in (**B**) dorsal, (**C**) ventral, (**D**) right lateral, and (**E**) left lateral views. All specimens to scale; scale bar equals 5 cm.

zygomatic arch, and a well-developed interorbital ridge extending between the pineal foramen and the anterior margins of the orbits. Dental formula unknown, upper postcanine count minimally six.

*Remarks*. Boonstra (1953) diagnosed *Maraisaurus parvus* on the basis of small size, proportionally large orbits, narrow, squarish snout, and relatively anterior position of the dentary. None of these characters allows the holotype of *M. parvus* to be uniquely distinguished from other scylacosaurids: small absolute size and relatively large orbits could be attributable to juvenile status; most scylacosaurids have a narrow snout, and the dentary is in a similar position as in other scylacosaurids (with the dentary angle located below the posterior part of the orbit). Later, Boonstra (1969) recognized that some of these features were likely due to the juvenile nature of SAM-PK-11944 and synonymized *Maraisaurus* with *Pristerognathoides*. Confusingly, however, he did not provide a synonymy for the species *M. parvus*. Although he listed *'Pristerognathoides parvus'* as a valid species in his faunal list for the *Tapinocephalus* Zone, he did not note whether this corresponded to *Pristerognathoides* (formerly *Maraiasaurus*) *parvus* (Boonstra, 1953) or *Pristerognathoides parvus* Boonstra, 1954 (see entry on *Pristerognathus* below for further information on the latter species). Van den Heever (1987) considered *Maraisaurus parvus* a *nomen dubium* due to lack of preservation of the anterior dentition.

Boonstra (1954) established *Pristerosaurus microdon* primarily on the basis of what he regarded as an aberrantly small canine (hence the species name). However, as previously noted by van den Heever (1987), the anterior snout and associated dentition is missing in SAM-PK-9083, and Boonstra's (1954) canine dimensions were based on a developing replacement canine rather than a fully erupted one. Boonstra (1954) also claimed that SAM-PK-9083 had small, weakly developed postcanines, but additional preparation of this specimen detailed by van den Heever (1987) revealed that the postcanines in this specimen are comparable in size and number (at least six, but probably more) to those of other scylacosaurids. Other than these dental features, Boonstra (1954, p. 82) provided only a few vague proportional characters diagnosing *P. microdon* (e.g. 'skull fairly large', 'snout broader than high', 'sagittal crest of parietals high and sharp'), all of which are either ontogenetically variable in or generally typical of scylacosaurids. Accordingly, van den Heever (1987) also regarded *Pristerosaurus microdon* as a *nomen dubium*.

Despite the inadequacy of Boonstra's (1953, 1954) original diagnoses and the absence of the anterior snout (with associated incisor/precanine/canine dentition) in the holotypes of both *M. parvus* and *P. microdon*, SAM-PK-9083 and SAM-PK-11944 exhibit several unusual, shared characters indicating that they represent a distinct scylacosaurid morphotype. These skulls have proportionally broad interorbital regions and laterally-directed orbits, such that very little of the orbit is visible in dorsal view (Fig. 15A,B). In all other scylacosaurids (with the exception of *Hyorhynchus*; see above), the orbits are angled dorsolaterally, with relatively broad exposure in dorsal view. This is true even when factoring in taphonomic distortion: even in highly laterally compressed skulls of other scylacosaurid taxa (e.g. the *Alopecognathus* specimens AMNH FARB 5559 [Fig. 4A] and SAM-PK-6533 [Fig. 4D] or the *Glanosuchus* specimen CGS GM 74), there is broader dorsal exposure of the orbits than is the case in the relatively weakly distorted SAM-PK-9083 and SAM-PK-11944 (based on the apparent natural curvature of the temporal arches in dorsal view in these specimens, although some lateral compression of SAM-PK-11944 is likely based on dislocation of the palatal elements). Only in the most extreme cases ('pancaked' skulls like the *Alopecognathus* specimen CGS MJF 211 [Fig. 4E]) does lateral compression yield comparably dorsally-obscured orbits, and those sorts of specimens can readily be distinguished from the likes of SAM-PK-9083 and SAM-PK-11944 by their relatively narrow interorbital regions. SAM-PK-9083 and SAM-PK-11944 are also distinguished by their possession of a well-developed interorbital ridge. This structure is somewhat overprepared in SAM-PK-9083, but is well preserved in SAM-PK-11944, where it clearly extends anteriorly from the pineal foramen, terminating between the anterior edges of the orbits. Although a raised mid-frontal suture is typical, particularly in large specimens, for all scylacosaurid taxa (as is also seen in gorgonopsians, and is probably related to strengthening the skull against stresses incurred while feeding; see Kammerer 2016, 2017), a large, well-developed ridge extending to the pineal foramen is unusual (as is the development of this structure in a relatively small, presumed juvenile specimen such as SAM-PK-11944). Finally, both SAM-PK-9083 and SAM-PK-11944 have temporal arches that are nearly horizontal in lateral view, in-plane throughout their length with the ventral margins of the orbits. This is in contrast with the highly curved temporal arches of most scylacosaurids. *Scylacosaurus* also appears to have relatively weakly curved temporal arches (based on UCMP 42669), but that taxon can be distinguished from SAM-PK-9083 and SAM-PK-11944 by its proportionally lower, longer snout (or at least, the portion of the snout between the orbits and canine) and more dorsally directed orbits. Based on the aforementioned characters, SAM-PK-9083 and SAM-PK-11944 are here considered to represent a distinct taxon, for which the name *Maraisaurus parvus* has priority.

*Maraisaurus* is one of the rarest and most poorly understood scylacosaurids. The palate is only prepared (poorly) in SAM-PK-11944, showing that this specimen had a relatively large interpterygoid vacuity (expected in a juvenile therocephalian) and an anterolaterally-curved, dentigerous pterygoid boss (similar to that of *Scylacosaurus* [Fig. 8C]). Little other detail is available from the palate of this specimen as currently prepared. Mandibles are preserved in both *Maraisaurus* specimens (including a large, well-preserved reflected lamina on the left lower jaw of SAM-PK-11944), but do not show features distinguishing them from e.g. *Alopecognathus* or *Glanosuchus*, and are not well-prepared enough to expose the lower dentition. Sutures are incompletely preserved in both

*Maraisaurus* specimens, although what can be observed is generally consistent with the reconstructions of Boonstra (1953, 1954).

In addition to the potential synonymy with *Hyorhynchus* noted above, there remains the possibility that *Maraisaurus*, a taxon diagnosed mainly on orbitotemporal characters for which the anterior snout is unknown, could be synonymous with *Alopecodon*, a taxon diagnosed mainly on snout and dental characters. Of the four known specimens of *Alopecodon*, one lacks the orbitotemporal region completely (AMNH FARB 5569), two preserve part of the orbital but none of the temporal region (SAM-PK-920 and NHMUK PV R 5750), and one preserves almost the entire skull but is missing the temporal arches (NHMUK PV R 4055) (Fig. 2). SAM-PK-920 does appear to have relatively laterally-directed orbits, but this is probably attributable to extreme lateral compression (with this said, the interorbital region of this specimen is still relatively broad, unlike CGS MJF 211 and other 'pancaked' skulls). More typical dorsally-visible orbits appear to be present in NHMUK PV R 4055, although that region does require additional preparation for confirmation. However, that specimen also shows no indication of an interorbital ridge, despite representing a slightly larger individual than SAM-PK-11944. In the absence of any definite, unique characters shared between the known *Alopecodon* and *Maraisaurus* specimens, these taxa are here considered distinct, with the caveat that additional, better-preserved fossils are required to test this distinction.

***Pardosuchus*** Broom, 1908

*Lycedops* Broom, 1935: 1

*Type species*. ***Pardosuchus whaitsi*** Broom, 1908.

*Etymology*. 'Leopard crocodile', from the ancient Greek **πάρδος** ('leopard' or 'panther', Latinized *pardus*) and **Σοῦχος** (Greek name for the Egyptian crocodile god Sobek, Latinized *suchus*).

*Diagnosis*. As for type and only species.

***Pardosuchus whaitsi*** Broom, 1908

Figures 12D, 16

1908 *Alopecodon rugosus* Broom, p. 363

1935 *Lycedops scholtzi* Broom, p. 1

*Holotype*. SAM-PK-1077, a very poorly prepared snout and partial lower jaws from near Fraserburg Road Station (=Leeu-Gamka), Prince Albert (Fig. 16C–E).

*Referred material*. CGS RMS 1287, a nearly complete skull and partial lower jaws from Klipfontein, Prince Albert (Fig. 16F,I); MMK 4499 (holotype of *Lycedops scholtzi*), a partial skull (missing parts of the temporal arches and a section of snout) and lower jaws from Abrahamskraal, Prince Albert (Figs 12D, 16A,B,J); SAM-PK-921 (holotype of *Alopecodon rugosus*), a partial skull (missing the temporal region and snout tip) and lower jaws from near Zeekoegat, Prince Albert (Fig. 16G,H); SAM-PK-K223, a fragmentary partial skull and lower jaws from Palmietfontein, Beaufort West; SAM-PK-K11360, a partial skull (missing much of the temporal and right orbital region) and fragments of the lower jaws from Putfontein, Beaufort West.

*Etymology*. Named after the Rev. John Henry Whaits (1870–1947), Anglican rector of Prince Albert, who collected the holotype.

*Diagnosis*. Small (estimated maximum basal skull length 17 cm, based on SAM-PK-1077; estimation based on the proportions of CGS RMS 1287) scylacosaurid with the dental formula I6/PrC1–2/C1/PC5–6, relatively short snout, and temporal fenestra narrower anteroposteriorly than transversely.

*Remarks*. In describing *Pardosuchus whaitsi*, Broom (1908) recognized a close similarity between the new taxon, *Glanosuchus macrops*, and *Scylacosaurus sclateri*, even going so far as to suggest that *Pardosuchus* and *Glanosuchus* could belong to the same genus (on the basis of shared incisor count). However, he decided to keep *Pardosuchus* and *Glanosuchus* separate based on differences in snout shape and the absence of a precanine in *Glanosuchus*. The holotype of *P. whaitsi* has suffered taphonomic distortion (left–right shear; Fig. 16C), but the difference in snout shape observed by Broom cannot be discounted as entirely deformational: the snout in SAM-PK-1077 is both proportionally shorter and narrower than that of *Glanosuchus*. Anteroposterior compression could shorten the snout but would make it broader as a result, whereas lateral compression could make the snout narrower but not any shorter.

Although the holotype of *P. whaitsi* is very incomplete and poorly prepared, there are additional, better-preserved specimens matching its preserved morphology. Broom (1935) established the taxon *Lycedops scholtzi* based on a largely complete skull (MMK 4499) broken into three sections, with the canine region missing between the two snout fragments (Fig. 16J). He distinguished this taxon from *Pristerognathus* by its possession of only four postcanine teeth, a blunter snout, and shorter, broader temporal fenestrae. The postcanine count in MMK 4499 is questionable, as the anterior portion of the maxilla is missing on both sides in this specimen. The first preserved postcanine in the right maxilla is located 5 mm behind the root of what Broom (1935) interpreted as an old canine being replaced. However, it is not certain in this specimen whether this was an old or a new replacement canine, and in either case, the canine root in scylacosaurids typically extends posterodorsally up into the maxilla, so the presence of exposed canine root high up on the maxilla above the first preserved postcanine does not necessarily mean additional postcanines could not have been present anteriorly. It is unlikely that many postcanines could have fit into this space, though, and MMK 4499 probably had a postcanine count near that of SAM-PK-1077 (five). MMK 4499 also preserves six incisors and has snout morphology very similar to SAM-PK-1077. Van den Heever (1987) considered *L. scholtzi* to be a *nomen dubium* (as no precanine count is available for the holotype), but similarity in snout shape and concordance in incisor and postcanine counts indicate that it should be considered a junior synonym of *P. whaitsi*.

Broom (1935) was correct in noting that the temporal fenestra was unusually shaped in MMK 4499, being small relative to skull size and wider than long. In all other

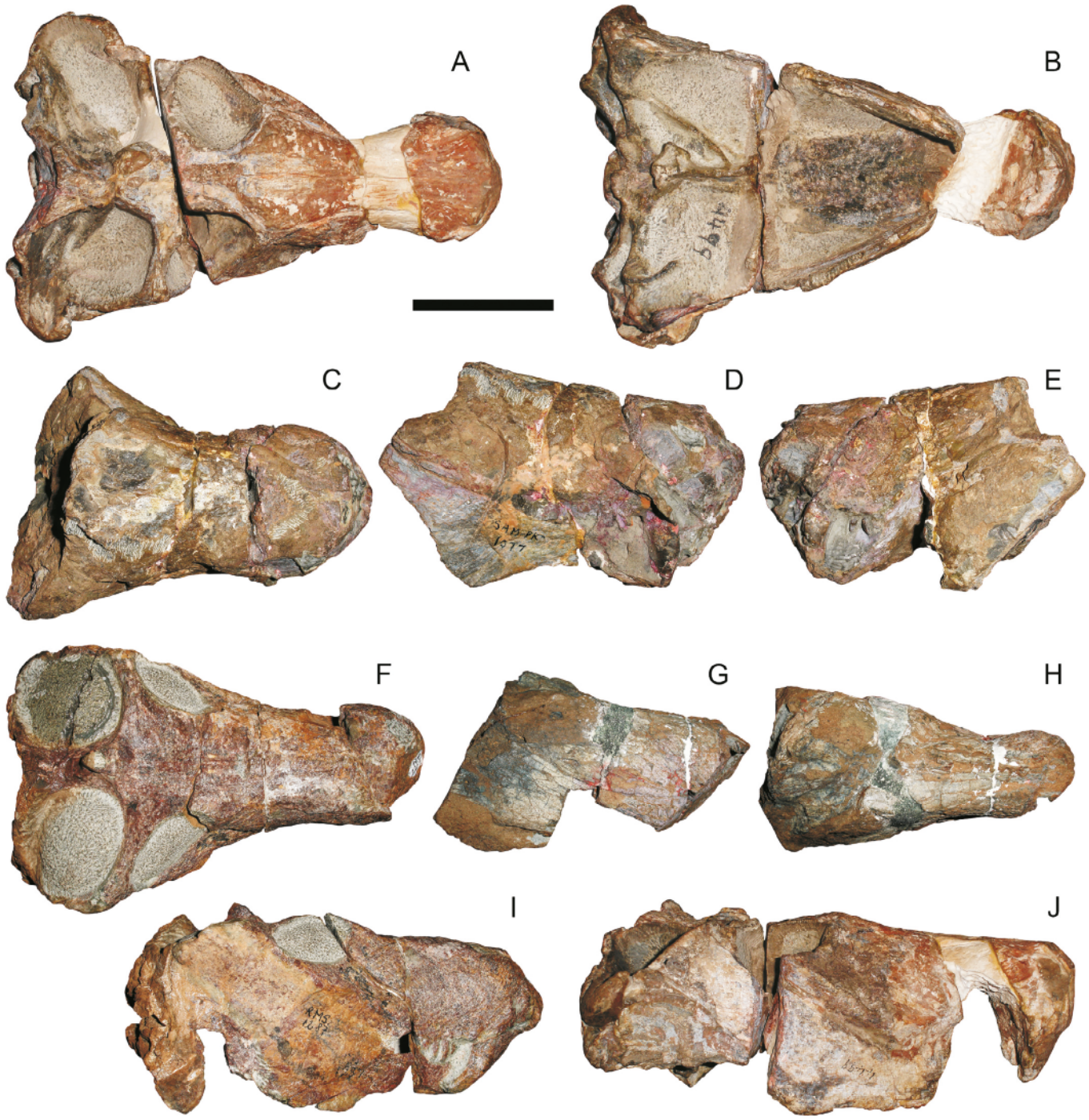



**Figure 16**. Specimens of *Pardosuchus whaitsi* Broom, 1908. MMK 4499, holotype of *Lycedops scholtzi*, in (**A**) dorsal, (**B**) ventral, and (**J**) right lateral views. SAM-PK-1077, holotype of *Pardosuchus whaitsi*, in (**C**) dorsal, (**D**) right lateral, and (**E**) left lateral views. CGS RMS 1287 in (**F**) dorsal and (**I**) right lateral views. SAM-PK-921, holotype of *Alopecodon rugosus*, in (**G**) right lateral and (**H**) dorsal views. All specimens to scale; scale bar equals 5 cm.

scylacosaurids (including other taxa where the fenestra is relatively small, such as *Pristerognathus*, or where the snout is relatively short, such as *Hyorhynchus* and probably *Maraisaurus*), the temporal fenestra is longer than wide. Several additional specimens, representing largely complete but only partially prepared (CGS RMS 1287 [Fig. 16F], SAM-PK-K223) or well-prepared but incomplete (SAM-PK-K11360) skulls, show the same morphology and can also be referred to *P. whaitsi* (the back of the fenestra is not intact in SAM-PK-K11360 so its exact length is uncertain, but the preserved portion shows the same expanded transverse width as the other specimens). These specimens demonstrate that the combination of a short but narrow (relative to *Glanosuchus*) snout, wider than long temporal fenestra, and six upper incisors with at least one precanine constitutes a consistent morphotype. These specimens also all have a relatively low postcanine count for scylacosaurids (five in CGS RMS 1287 and SAM-PK-K11360; uncertain due to incomplete preparation in SAM-PK-K223 but either five or six), like MMK 4499 and SAM-PK-1077. Unfortunately, these additional specimens generally have poor sutural preservation and palates that are either unprepared or badly worn. As such, the palatal boss morphology in *P. whaitsi* is currently unknown.

An additional species, *Alopecodon rugosus*, is also tentatively synonymized with *P. whaitsi* here. Broom (1908) named *A. rugosus* in the same publication as *P. whaitsi*, but did not compare the two taxa (restricting comparisons of the former to the other species of *Alopecodon*, *A. priscus*). However, SAM-PK-921 has an unusually short but narrow snout, much like SAM-PK-1077. SAM-PK-921 does have a higher upper postcanine tooth count than the other specimens of *P. whaitsi*, though, with seven left and six right postcanines preserved (Broom 1932; van den Heever 1987). Here, it is suggested that this could be attributable to the small size and probable juvenile status of SAM-PK-921. Alternatively, it is possible this specimen represents an anteroposteriorly distorted specimen of *Alopecognathus angusticeps*. Additional preparation or CT-scanning of SAM-PK-921 and definite *Pardosuchus* specimens is required to confirm this identification.

***Pristerognathus*** Seeley, 1894

1954 *Pristerognathoides* Boonstra, p. 94

*Type species*. *Pristerognathus polyodon* Seeley, 1894.

*Etymology*. 'Saw jaw', from the ancient Greek πριστήρ ('saw', Latinized *prister*) and γνάθος ('jaw', Latinized *gnathus*).

*Diagnosis*. As for type and only species.

***Pristerognathus polyodon*** Seeley, 1894

Figures 1D, 7G, 8D, 13F,G, 17, 18

1918 *Alopecognathus minor* Haughton, p. 180

1936b *Pristerognathus peyeri* Broili & Schröder, p. 299

1954 *Pristerognathoides minor* Boonstra, p. 94

1954 *Pristerognathoides parvus* Boonstra, p. 102

*Holotype*. NHMUK PV R 2581, a partial snout tip and anterior fragments of lower jaws from Tamboersfontein, De Cypher, Beaufort West (Figs 1D, 17F, 18B).

*Referred material*. BP/1/276, a partial skull (dorsal surface badly eroded) and lower jaws from Antjiesfontein, Prince Albert (Fig. 18A); BP/1/1768, a dorsoventrally crushed but nearly complete skull and lower jaws from Leeu-Gamka, Prince Albert; BSPG 1936-II-9 (holotype of *Pristerognathus peyeri*), a nearly complete skull and lower jaws from Kleinwaterval, Prince Albert (destroyed in WWII) (Figs 7G, 8D, 17C, 18E); CGS RS 330, a nearly complete skull and lower jaws from Brandewyns Gat, Beaufort West (Figs 17A, 18C); SAM-PK-3415 (holotype of *Alopecognathus minor*), a dorsoventrally crushed, nearly complete skull and lower jaws from Klipbank, Beaufort West (Figs 17B, 18F); SAM-PK-3611 (holotype of *Pristerognathoides parvus*), a partial skull (missing the occiput) and lower jaws from Blaauwkranse, Prince Albert (Figs 17E, 18G); SAM-PK-11689, a poorly prepared but largely complete skull from Prince Albert Road, Prince Albert (Figs 17D, 18D); SAM-PK-K312, a snout and lower jaws from Boontjiesakker, Beaufort West; SAM-PK-K10540, an eroded partial skull (missing much of the temporal region) and lower jaws from Putfontein, Beaufort West.

*Etymology*. 'Many teeth', from the ancient Greek πολύς ('many', Latinized *polys*) and ὀδών ('tooth', Latinized *odon*).

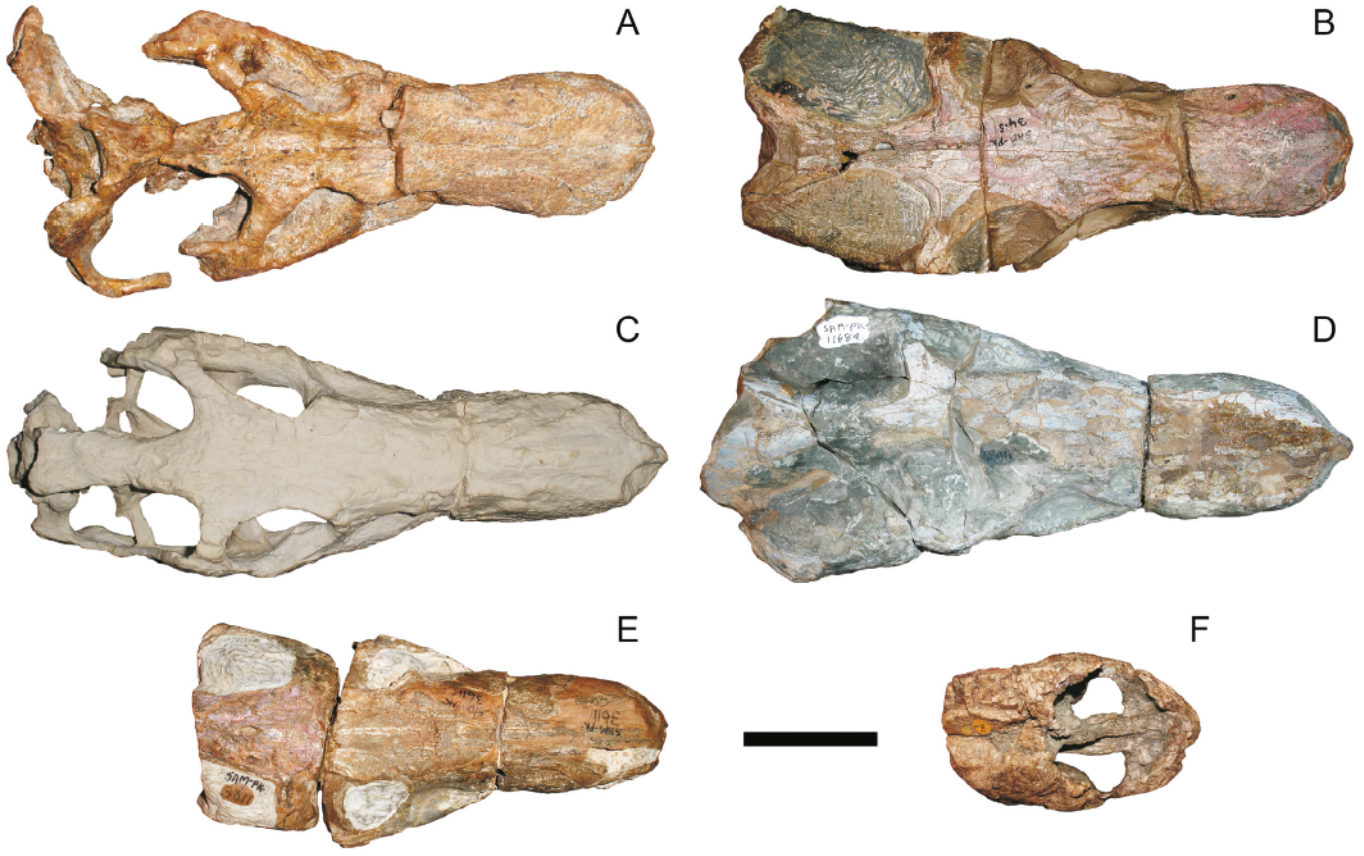



**Figure 17**. Specimens of *Pristerognathus polyodon* Seeley, 1894 in dorsal view. **A**, CGS RS 330. **B**, SAM-PK-3415, holotype of *Alopecognathus minor*. **C**, USNM 187095, cast of BSPG 1936-II-9, the destroyed holotype of *Pristerognathus peyeri*. **D**, SAM-PK-11689. **E**, SAM-PK-3611, holotype of *Pristerognathoides parvus*. **F**, NHMUK PV R 2581, holotype of *Pristerognathus polyodon*. All specimens to scale; scale bar equals 5 cm.

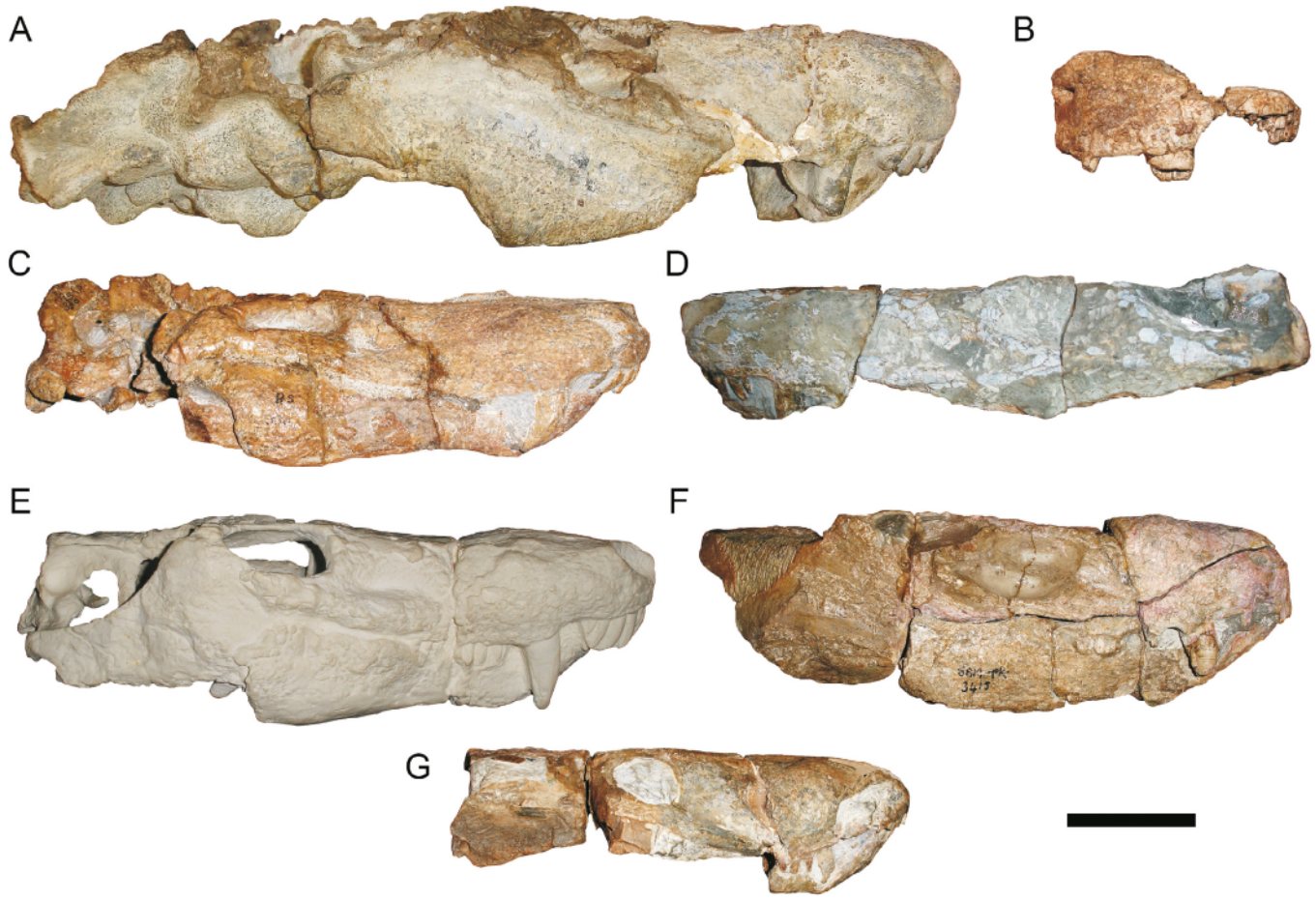



**Figure 18.** Specimens of *Pristerognathus polyodon* Seeley, 1894 in lateral view. **A**, BP/1/276 in right lateral view. **B**, NHMUK PV R 2581, holotype of *Pristerognathus polyodon*, in right lateral view. **C**, CGS RS 330 in right lateral view. **D**, SAM-PK-11689 in left lateral view. **E**, USNM 187095, cast of BSPG 1936-II-9, the destroyed holotype of *Pristerognathus peyeri*, in right lateral view. **F**, SAM-PK-3415, holotype of *Alopecognathus minor*, in right lateral view. **G**, SAM-PK-3611, holotype of *Pristerognathoides parvus*, in right lateral view. All specimens to scale; scale bar equals 5 cm.

*Diagnosis*. Large (maximum basal skull length 30.16 cm, based on BP/1/276) scylacosaurid characterized by the dental formula I6–7/PrC0–2/C1/PC7, relatively large, recurved upper incisors, narrow, densely dentigerous pterygoid bosses oriented perpendicular to the long axis of the skull, and constriction of the snout behind the canine in dorsal view.

*Remarks*. Although a venerable taxon (being the second scylacosaurid named), *Pristerognathus* has long been a problematic genus for therapsid systematists, a status largely attributable to the highly inadequate nature of the holotype. NHMUK PV R 2581 consists only of the anterior palate (dorsal surface of the snout eroded off) and anterior dentary fragments. At the time Seeley (1894) described this specimen, it was unlike any therapsid previously known (the only prior-named scylacosaurid, *Hyorhynchus*, being represented solely by a non-overlapping part of the skull). However, with the discovery of many additional scylacosaurid specimens in the early 20th century, the characters originally diagnosing *P. polyodon* ceased being unique, and the genus became something of a 'wastebasket'. Broom (1904) named a second species of *Pristerognathus*, *P. baini*, on the basis of an even worse specimen than NHMUK PV R 2581 (it preserves a similar part of the anatomy, but less of it, and the palatal surface is not visible). Broom (1912) later described a more complete, but also extremely poorly preserved, snout as a third species, *P. platyrhinus*. The first specimens referred to *Pristerognathus* that consist of more than a snout tip were a pair of largely complete skulls (MMK 5139 and SAM-PK-6533), which Broom (1925) described as two new species, *P. vanderbyli* and *P. vanwyki* (respectively). Based on these, he established *Pristerognathus* as the typical longirostrine Karoo scylacosaurid (shortly thereafter [Broom 1931] removing the brevirostrine *P. platyrhinus* from the genus and placing it in the new genus *Cynariognathus*). Subsequent referrals to *Pristerognathus* were largely based on these more complete skulls (rather than the holotype of *P. polyodon*), including two additional nominal species: *P. peyeri* Broili & Schröder, 1936b and *P. roggeveldensis* Boonstra, 1953.

Even in naming *P. roggeveldensis*, however, Boonstra (1953, p. 60) recognized the problematic nature of relying on the referred species (instead of the type species) to diagnose *Pristerognathus*, noting 'Seeley's genotype is of such a nature that identification with it as norm is hazardous'. Taking this idea to its logical conclusion, he later (Boonstra 1954) established a new genus (*Pristerognathoides*) for all the longirostrine scylacosaurid specimens he regarded as diagnosable (taking *Alopecognathus minor* as the type species, and also including as distinct *Pristerognathus roggeveldensis*, *P. vanwyki*, and a new

species, *Pristerognathoides parvus*). In a move with problematic downstream effects, however, he retained the genus *Pristerognathus* for use 'as a suitable label for all Pristerognathid Therocephalian specimens in which no other diagnostic characters are shown' (Boonstra, 1954, p. 87). Thus, in addition to the holotype, he included 27 additional 'fragmentary and weathered snouts' with six upper incisors in *Pristerognathus*, establishing the precedent for referring any otherwise unidentifiable scylacosaurid specimens to this genus, and filling the collections of the South African Museum with specimens labelled '*Pristerognathus*' rather than the more sensible 'Pristerognathidae indet.' (with other institutions adopting the same approach, as witness the profusion of '*Pristerognathus*' specimens appearing subsequently in the catalogues of the Bernard Price Institute and Council for Geoscience). The apparent abundance of this genus doubtless influenced the choice of *Pristerognathus* as the index fossil for what was long considered part of the *Endothiodon* Zone, first as the *Pristerognathus/Diictodon* Assemblage Zone (Keyser & Smith 1978) and later formalized as the *Pristerognathus* Assemblage Zone (Smith & Keyser 1995). Only recently (Day & Smith 2020) has the problematic nature of the latter (as a biozone characterized by the presence of early therocephalians generally in the absence of dinocephalians, with no link to the genus *Pristerognathus* particularly) been addressed, with most of the former *Pristerognathus* Assemblage Zone becoming the *Lycosuchus-Eunotosaurus* Subzone of the re-established *Endothiodon* Assemblage Zone.

Considering the above information, one might assume that *Pristerognathus* would have become a *nomen dubium*, but, despite its inadequacy in almost all other regards, NHMUK PV R 2581 does preserve the anterior dentition, so van den Heever (1987) retained *P. polyodon* as valid based on the possession of seven incisors and no precanines (Fig. 1D). As discussed in the Introduction, however, a seventh incisor is only present on the left premaxilla; six are present on the right, so the incisor count cannot be treated as fixed in this taxon. So where does this leave *Pristerognathus*? Although the poor nature of the holotype is troublesome for the referral of additional material, as discussed in the section on *Alopecognathus* above, there do seem to be two distinct longirostrine, non-*Scylacosaurus* scylacosaurid morphotypes in the sample from the Karoo Basin. Although few of the characters separating these morphotypes are preserved in NHMUK PV R 2581, it does differ from known *Alopecognathus* material in having a very narrow connection between the vomerine body and the palatal plate (this region is broad in *Alopecognathus*; Fig. 7D) and in having sharply posteriorly-canted lower postcanines (Fig. 13F,G), similar to many gorgonopsians (see e.g. Kammerer 2014) but unlike the weakly recurved lower postcanines of most scylacosaurids (e.g. Fig. 13A). As such, the name *Pristerognathus polyodon* is retained here for the non-*Alopecognathus* longirostrine morphotype, although it may eventually prove necessary to establish a neotype for this species, should additional longirostrine morphotypes be recognized in the fauna.

Although the majority of nominal longirostrine scylacosaurid species can be referred to *Alopecognathus angusticeps* (including *P. vanderbyli* and *P. vanwyki*, the species most responsible for establishing the 'image' of *Pristerognathus*), there are a few that can be considered synonymous with *Pristerognathus polyodon*. The destroyed holotype of *P. peyeri* exhibits less constriction of the snout behind the canine than in most *Pristerognathus* specimens (Fig. 17), but has a pterygoid boss morphology (mediolaterally expanded and densely dentigerous; Fig. 8D) that distinguishes it from *Alopecognathus* (Fig. 8A) and is similar to other *Pristerognathus*-morph specimens (e.g. BP/1/1678, CGS RS 330). SAM-PK-3415 (Figs 17B, 18F), the holotype of *Alopecognathus minor*, represents a comparable specimen, albeit more clearly showing the postcanine constriction of the snout. More problematic is SAM-PK-3611 (Figs 17E, 18G), the holotype of *Pristerognathoides parvus*. Van den Heever (1987) argued, citing communications with M.A. Cluver, that SAM-PK-3611 is chimaerical, with the temporal region representing a partial dicynodont skull incorrectly glued onto a therocephalian snout. As additional evidence in support of this conclusion, it can be added that the temporal block is narrower than the orbital region, such that the temporal arches do not articulate with the suborbital zygoma. There also appears to be an extra postorbital bar on the right side of the skull when the temporal and snout portions are united. Van den Heever (1987) considered this species to be a *nomen dubium*, and as currently prepared it is difficult to identify. Here, referral to *Pristerognathus polyodon* is preferred over *Alopecognathus angusticeps* based on snout shape, but given distortion in this specimen this should be taken as extremely tentative – additional preparation of the palate in this specimen is needed.

***Scylacosaurus*** Broom, 1903b
1915a *Scylacorhinus* Broom, p. 120
1953 *Therioides* Boonstra, p. 58
*Type species*. *Scylacosaurus sclateri* Broom, 1903b.
*Etymology*. 'Puppy lizard', from the ancient Greek σκύλαξ ('young dog', Latinized *skylax*) and σαῦρος ('lizard', Latinized *saurus*).
*Diagnosis*. As for type and only species.

***Scylacosaurus sclateri*** Broom, 1903b
Figures 8C, 12C, 13C,D, 19
1915a *Scylacorhinus falkenbachi* Broom, p. 120
1953 *Therioides cyniscus* Boonstra, p. 58
*Holotype*. SAM-PK-634, a partial skull (consisting of the snout and orbital region) from an unknown Karoo locality (stated to be Colesberg by Broom [1903b], but see remarks in Discussion) (Fig. 19C,G,H,K).
*Referred material*. AMNH FARB 5560 (holotype of *Scylacorhinus falkenbachi*), a partial skull (anterior half of snout) and lower jaws from Beaufort West (Fig. 19D,J); SAM-PK-11888 (holotype of *Therioides cyniscus*), a partial skull (missing much of the temporal region and right orbital region), lower jaws, and forelimb from Vindragersfontein, Beaufort West (Fig. 19E,I); UCMP 42669, a nearly complete skull (missing the sagittal crest) and lower jaws

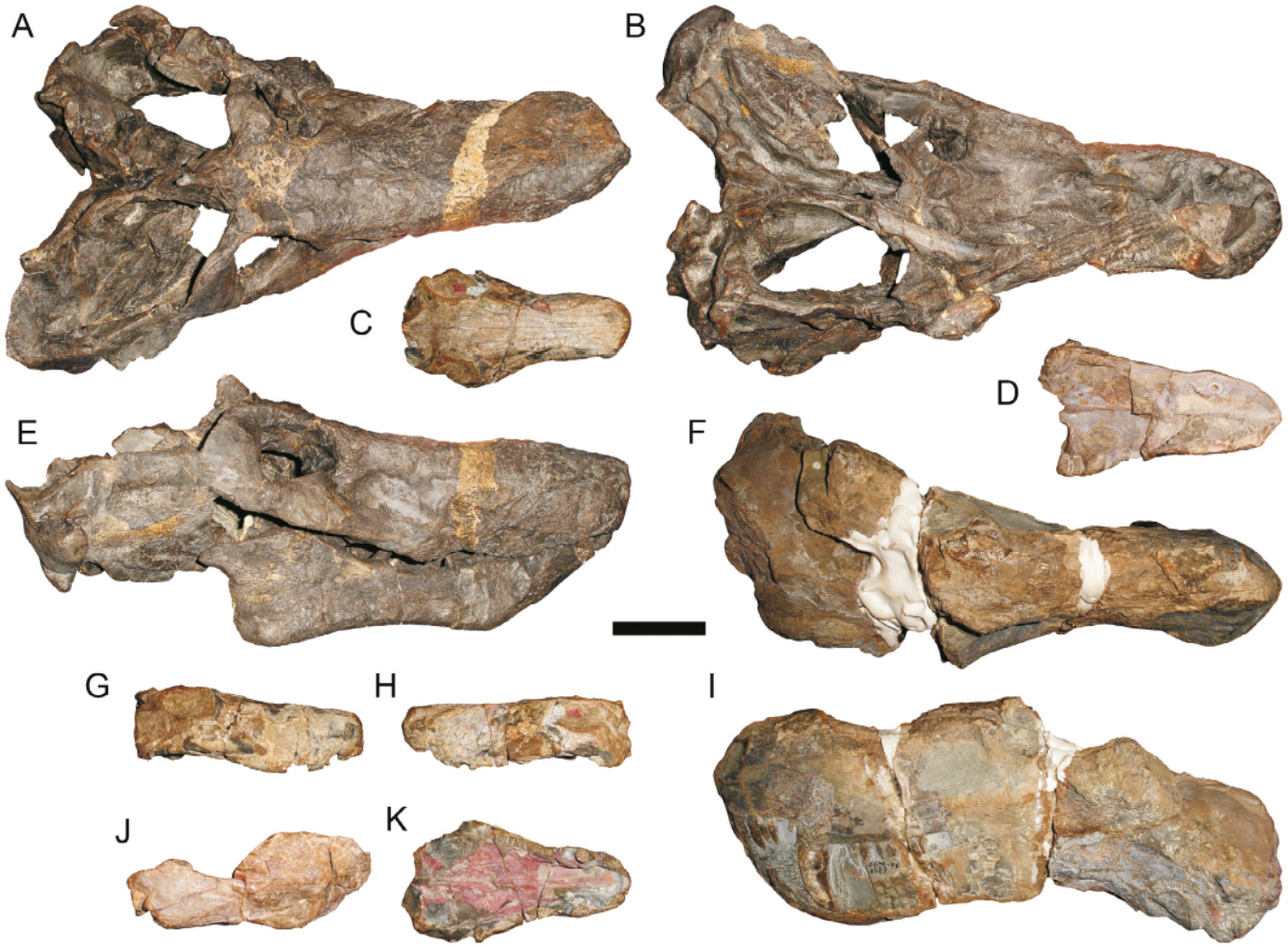



**Figure 19**. Specimens of *Scylacosaurus sclateri* Broom, 1903b. UCMP 42699 in (**A**) dorsal, (**B**), ventral, and (**E**) right lateral views. SAM-PK-634, holotype of *Scylacosaurus sclateri*, in (**C**) dorsal, (**G**) right lateral, (**H**) left lateral, and (**K**) ventral views. AMNH FARB 5560, holotype of *Scylacorhinus falkenbachi*, in (**D**) dorsal and (**J**) right lateral views. SAM-PK-11888, holotype of *Therioides cyniscus*, in (**F**) dorsal and (**I**) left lateral views. All specimens to scale; scale bar equals 5 cm.

from Jacobskraal, Prince Albert (Figs 8C, 12C, 13C,D, 19A,B,E).

*Etymology*. Named after William Lutley Sclater (1863–1944), director of the South African Museum from 1896 to 1906.

*Diagnosis*. A large (maximum basal skull length 34.4 cm, based on UCMP 42669) scylacosaurid characterized by the dental formula I7/prC1/C1/PC7, a relatively long, narrow snout, arcuate pterygoid bosses with a single tooth row, curving posteromedially to anterolaterally, quadrate processes of pterygoid diverging near the posterior end of the basicranial girder, and a dentary with an elongate symphysial region, concave ventral margin, and a constricted portion between the postcanine tooth row and coronoid process, giving it an 'hourglass' shape.

*Remarks*. Despite its status as the namesake of the family and one of the first scylacosaurids to be described, little has been published on *Scylacosaurus*. Broom's (1903b) description of this taxon featured minimal comparison with other taxa, noting only that the parietal of *Scylacosaurus* appears broader than that of *Lycosuchus* or *Ictidosuchus*, and that, unlike cynodonts, *Scylacosaurus* lacks a secondary palate. The main diagnostic feature of the new taxon was its tooth count, which Broom (1903b, p. 150) listed as 'incisors 6, canines 3, molars 7'. Broom (1915a) later described a new taxon (*Scylacorhinus falkenbachi*) that he regarded as similar to *Scylacosaurus* but differing from it and *Alopecodon* in having seven incisors and one precanine. However, Boonstra (1935) noted that the distinction between the incisors and precanines in *Scylacosaurus* was uncertain, and that the holotype of *S. falkenbachi* (AMNH FARB 5560) otherwise accorded closely with the morphology of *Scylacosaurus*. Accordingly, he synonymized *S. falkenbachi* with *S. sclateri*. On the basis of additional preparation, van den Heever (1987) revised the anterior tooth count for the holotype of *S. sclateri* (SAM-PK-634), identifying seven incisors and one precanine (the same as AMNH FARB 5560) and thus upholding Boonstra's (1935) synonymization of *Scylacorhinus* with *Scylacosaurus*.

Unremarked upon by previous workers, AMNH FARB 5560 differs from all other scylacosaurids in the extreme length of its dentary symphysis. Usually in this group, the dentary symphysis terminates below the lower canine (Fig. 13B). However, in AMNH FARB 5560, the symphysis is very long and weakly sloping, terminating well posterior to even the upper canine (which generally occupies a posterior position relative to the lower canine). This same

morphology is observed in a much larger skull (UCMP 42669) in which the right dentary has been prepared off the cranium. This specimen was collected by Charles Camp in 1936 but never described, though it has been mentioned in the literature as an 'unidentified scylacosaurid (cf. *Glanosuchus macrops*)' (Huttenlocker 2009, p. 879). The dentary of this specimen is unique among scylacosaurids not only in the length of the symphysis, but also in the morphology of the constriction between the postcanine tooth row and the coronoid process, giving the element as a whole an 'hourglass' shape (Fig. 13C). In other scylacosaurids (including *Glanosuchus*), the least tall portion of the dentary is in the same place (Fig. 13A), but in those taxa the ventral margin of the dentary is straight or convex, whereas in UCMP 42669 (and AMNH FARB 5560) this margin is concave, producing the 'hourglass' appearance. This shape is highly distinctive and permits ready differentiation of *Scylacosaurus* from other scylacosaurid specimens.

Although the bone surface of UCMP 42669 is poorly preserved, for the most part lacking visible sutures, the specimen is nearly complete, and greatly improves our understanding of the anatomy of *Scylacosaurus sclateri*. Although the intertemporal region is damaged, the sharply-angled anterior portion of the parietals indicates that a large, well-developed sagittal crest was present (Fig. 19E) (this may be usual for large individuals of multiple scylacosaurid taxa; see discussion of *Scymnosaurus watsoni* below). Deep, fairly discrete preorbital depressions are present; these depressions are typical for scylacosaurids (indeed, found to be a synapomorphy of the clade by Huttenlocker [2009]), but are exceptionally well-developed in UCMP 42669. The transverse processes of the pterygoid are strongly arcing and relatively small (compared to those of *Alopecognathus*, *Glanosuchus*, and *Pristerognathus*; Fig. 7). The pterygoid bosses are also arcuate (curving from their posteromedial origin to an anterolateral terminus) and appear to bear a single row of teeth (Fig. 8C), although surface preservation is poor. The braincase and basicranial girder of UCMP 42669 (Figs 12C, 19B) are generally similar to those of other scylacosaurids, but the quadrate processes of the pterygoid diverge from the midline in a more posterior position, so that there is a larger gap between these elements and the basal tubera (compare Fig. 19B with e.g. Fig. 7D,G).

Little additional *Scylacosaurus* material is present in collections, although it is hoped that the more robust diagnosis presented here will permit more ready recognition of this taxon in the future. SAM-PK-11888 is a poorly preserved partial skull that Boonstra (1953) described as a new taxon (*Therioides cyniscus*), distinguishing it from other early therocephalians on the basis of a tooth count of I6/C1/PC6–7 and an unusually robust, 'squarish' dentary symphysis. As noted by van den Heever (1987), this tooth count is incorrect: seven incisors are present in at least the left premaxilla, and a single precanine is present in each maxilla. Furthermore, the symphysis is, like the rest of the skull, strongly distorted, but does not appear any more robust than in other scylacosaurids. Based on anterior tooth count, van den Heever (1987) considered SAM-PK-11888 referable to *Scylacosaurus sclateri*. This is tentatively followed here; the symphysial morphology of SAM-PK-11888 does not perfectly match that of AMNH FARB 5560 and UCMP 42669, but the dentary is constricted near its midpoint, with a ventral concavity to the margin of this bone (Fig. 19I). As with many scylacosaurid specimens, however, additional preparation will be needed to test this identification; the possibility that SAM-PK-11888 represents a distorted specimen of *Alopecodon* or *Pristerognathus* cannot be excluded at present.

**Nomina dubia**

***Arnognathus parvidens*** Broom, 1907
Figure 20G

*Holotype*. SAM-PK-1069, an isolated right dentary from Victoria West.

*Remarks*. Broom (1907) based *Arnognathus parvidens* on a single right dentary exposed in lateral view, which he considered most similar to *Ictidosuchus primaevus*, but distinguished from it by the more prominent dentary angle. *Ictidosuchus* is a eutherocephalian (Huttenlocker 2009), and all subsequent coverage of *Arnognathus* treated it as a member of what would today be called Eutherocephalia, and specifically Baurioidea (see e.g. Haughton 1924; Haughton & Brink 1955; Romer 1956). However, van den Heever (1987) noted that SAM-PK-1069 has serrated postcanines, a typical feature of early therocephalians that is not present in eutherocephalians. The age of this specimen is somewhat uncertain: the geology of the area surrounding Victoria West is extremely complex, with the *Tapinocephalus* through *Daptocephalus* AZs all represented (Day & Rubidge 2019). Broom (1907) states that the holotype of *A. parvidens* was found at the same locality as that of the basal anomodont *Galechirus scholtzi*, a taxon restricted to the *Tapinocephalus* AZ (Day & Rubidge 2020), suggesting that SAM-PK-1069 originated in the Abrahamskraal Formation. This would be in keeping with the scylacosaurid identification for this specimen proposed by van den Heever (1987). The dentary of *Arnognathus* clearly differs from the 'hourglass' shape of *Scylacosaurus* and lacks the strong posterior cant to the postcanines of *Pristerognathus*, but otherwise could belong to any scylacosaurid, and here is considered a *nomen dubium* (Scylacosauridae indet.)

***Blattoidealestes gracilis*** Boonstra, 1954a
Figure 20A–C

*Holotype*. SAM-PK-4321, a crushed complete skull, lower jaws, and the majority of the postcranial skeleton from Prince Albert Road, Prince Albert.

*Remarks*. Boonstra (1954a) described *Blattoidealestes gracilis* as a new 'scaloposaurid' from the *Tapinocephalus* Zone. At the time, Scaloposauridae encompassed a broad array of small-bodied therocephalian taxa spanning the middle Permian through Early Triassic. More recent work, however, has shown that these 'scaloposaurids' *sensu lato* represent a heterogeneous assemblage of juvenile therocephalians, rather than any kind of coherent evolutionary unit (Kemp 1982, 1986; Hopson & Barghusen 1986;

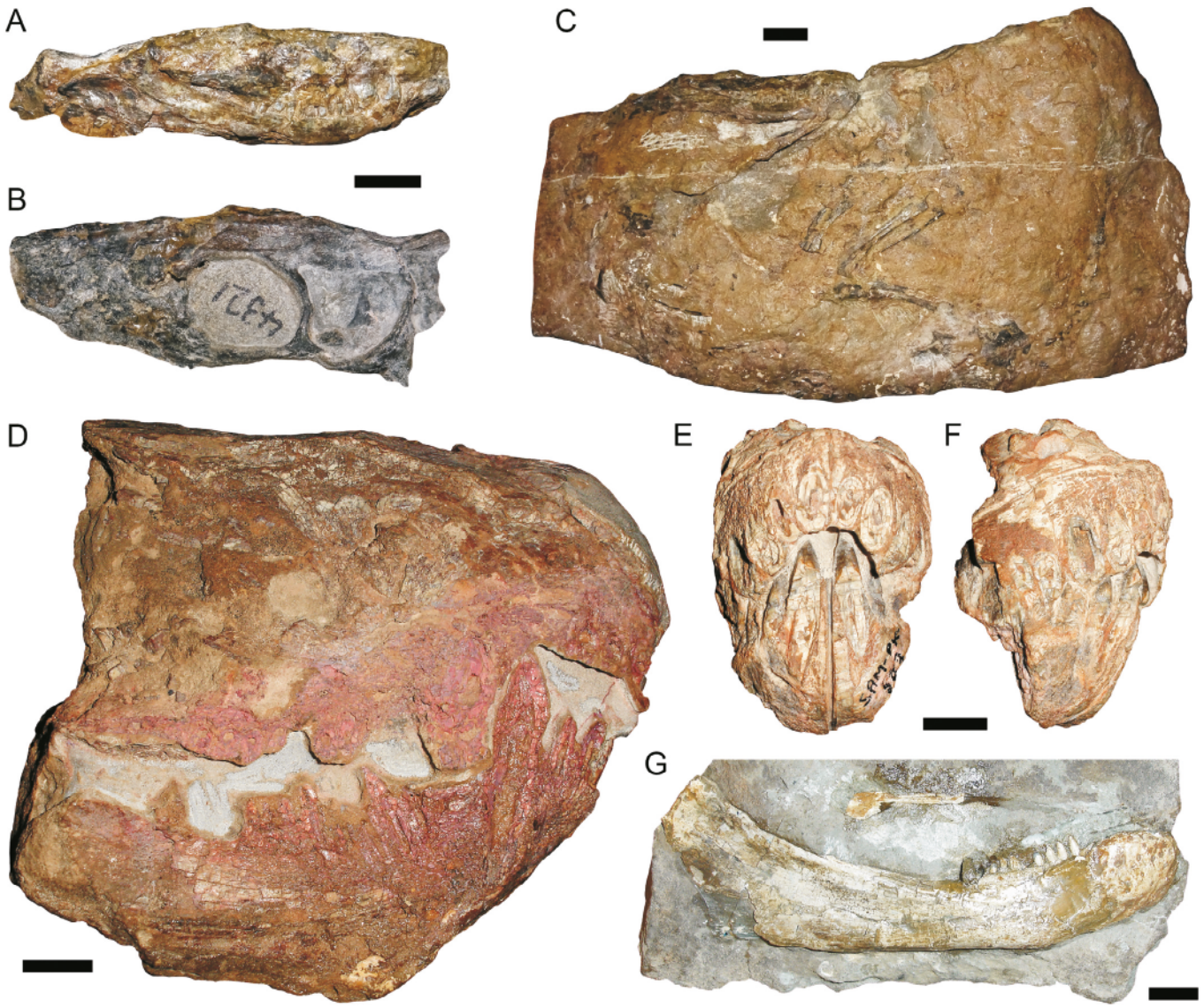



**Figure 20**. Dubious therocephalian taxa. SAM-PK-4321, holotype of *Blattoidealestes gracilis*, in (**A**) right lateral and (**B**) left lateral cranial views with (**C**) whole skeletal block. **D**, SAM-PK-630, holotype of *Ictidosaurus angusticeps*, in right lateral view. SAM-PK-583, holotype of *Pristerognathus baini*, in (**E**) anterior and (**F**) right lateral views. **G**, SAM-PK-1069, holotype of *Arnognathus parvidens*, in right lateral view. Scale bars equal 1 cm.

Huttenlocker & Sidor 2012). Among the supposed 'scaloposaurids' of the *Tapinocephalus* AZ, the holotype of *Simorhinella baini* has been shown to represent a juvenile lycosuchid (Abdala *et al*. 2014b) and *Crapartinella croucheri* represents a juvenile scylacosaurid (possibly *Glanosuchus macrops*; see above). Based on its proportionally enormous orbits and poorly ossified skeleton, SAM-PK-4321 is also best interpreted as a juvenile. The presence of serrated canines indicates that SAM-PK-4321 is an early therocephalian, and its combination of a high tooth count (probably I6/C1/PC8) and relatively elongate snout indicates that it is a scylacosaurid rather than a lycosuchid. Based on available data, however, this specimen is specifically indeterminate (as previously noted by Huttenlocker & Smith [2017]), and should be considered a *nomen dubium* (Scylacosauridae indet.) The block containing this specimen does appear to preserve most of the skeleton of this individual, and given how little is known about scylacosaurid postcranial anatomy (and particularly ontogenetic variation thereof), this specimen represents a prime candidate for further study through CT-scanning.

***Ictidoparia brevirostris*** Broom, 1925

*Holotype*. An unnumbered skull from Lammerskraal, Prince Albert, now lost.

*Remarks*. Next to nothing is known about this taxon – Broom (1925) described it briefly, but did not figure the holotype, which was then lost (Broom, 1932). Broom's description includes no comparisons with other therocephalians and little in the way of distinguishing features, so *Ictidoparia* must be considered a *nomen dubium*. Based on size (Broom estimated the skull would be 6.2 cm long), possession of a narrow snout, and origin in the *Tapinocephalus* AZ, this specimen was probably a juvenile scylacosaurid. However, in the absence of any further information it should be treated only as Therocephalia indet.

***Ictidosaurus angusticeps*** Broom, 1903b

Figure 20D

*Holotype*. SAM-PK-630, the anterior end of a snout and occluded lower jaws from near Beaufort West.

*Remarks*. Broom (1903b) described *Scylacosaurus sclateri*

and *Ictidosaurus angusticeps* in the same publication and noted that they were very similar, but differentiated the latter taxon by its dorsoventrally deeper snout and lower incisor count (originally stated to be five). Subsequent authors have generally considered *I. angusticeps* to represent a valid taxon, but have differed in its familial attribution, variously placing it in Scylacosauridae (Williston 1925; Vjuschkov 1964), Pristerognathidae (Haughton 1924; Romer 1956; Watson & Romer 1956), Akidnognathidae (Haughton & Brink 1954), Ictidosuchidae (Huene 1956), Scaloposauridae (Romer 1945), or in its own family Ictidosauridae (Broom 1932; although confusingly Broom also included *Scylacosaurus* in this family, seemingly forgetting that he had already established the family Scylacosauridae for that genus). Most recently, van den Heever (1987) considered *I. angusticeps* to be a valid scylacosaurid taxon diagnosed by the presence of six incisors and one precanine in the upper dentition.

SAM-PK-630 consists of a laterally compressed, very poorly preserved and prepared partial snout and jaws. The left side of the snout and ventral surface of this specimen are largely unprepared and the palate is still totally embedded in rock. The right side of the snout was eroded at the surface and has received preparation around the teeth. Erosion of the lower jaw has revealed the entire lower dentition (including the tooth roots) in section, showing a dental formula of i3/c1/pc8. The number of upper teeth is less certain. Broom (1903b) originally stated that there are five incisors, but later (Broom, 1932) revised this number to six (plus one precanine). This is correct in terms of the preserved teeth, but there is a substantial diastema between the sixth incisor and the precanine and this region is very badly eroded; it is not impossible that a second precanine or seventh incisor could have been present in the intact skull. Even if this specimen does have six incisors and one precanine, this does not permit distinction between the various scylacosaurid taxa with 6–7 incisors (see Introduction). The relatively narrow snout is suggestive of *Alopecognathus*, but given the compression of this specimen, that is uncertain, and not enough of the skull is preserved to show other distinguishing features of the scylacosaurid species herein considered valid. At present, *I. angusticeps* must be considered a *nomen dubium* (Scylacosauridae indet.)

Multiple specimens have been referred to *I. angusticeps* over the years, none of which show any uniquely shared features with the holotype beyond also being isolated snouts with an occluded mandibular symphysis. AMNH FARB 5527 was referred to this species by Broom (1915a); although also found near Beaufort West, it was found in stratigraphically higher rocks of the '*Endothiodon* Zone' (likely representing the *Tropidostoma-Gorgonops* Subzone of the modern *Endothiodon* AZ). This specimen represents a gorgonopsian; as noted by Boonstra (1935) and van den Heever (1987), it has a tall, robust mandibular symphysis with a clear mentum and a combination of five upper and four lower incisors. The same characters indicate that NHMUK PV OR 49419, a supposed *I. angusticeps* specimen from the Gouph, is also a gorgonopsian (Kammerer 2014). Unfortunately, both of these specimens are still largely unprepared; new preparation or CT-scanning will be required to identify them beyond Gorgonopsia *incertae sedis*.

***Pristerognathus baini*** Broom, 1904
Figure 20E,F

*Holotype*. SAM-PK-583, the anterior tips of a snout and occluded lower jaws, shoulder girdle, and pelvis from Letjesbosch, Beaufort West.

*Remarks*. Broom (1904) described *Pristerognathus baini* based on a badly eroded snout tip collected many years prior by Thomas Bain (stated to be from an unknown locality by Broom; Kitching [1977] identified the locality as Letjesbosch). He provided no distinguishing features for *P. baini*, although van den Heever (1987) indicated it had been differentiated from *P. polyodon* on the basis of its smaller size. Because of the extreme incompleteness of SAM-PK-583, most workers have considered *P. baini* to be dubious (e.g. Haughton 1924; Boonstra 1969). However, van den Heever (1987) considered it synonymous with *Glanosuchus macrops*, based on the presence of six upper incisors and no precanines. In this work, that tooth count occurs in several taxa considered valid (*Alopecognathus* and *Glanosuchus*), so *P. baini* once again becomes a *nomen dubium* (Scylacosauridae indet.)

***Scymnosaurus watsoni*** Broom, 1915b
Figure 21

1954 *Pristerosaurus watsoni* Boonstra, p. 84

*Holotype*. NHMUK PV R 4100, a partial skull (missing the anterior snout and left temporal arch) from Uitkyk, Beaufort West.

*Remarks*. Broom (1915b) described NHMUK PV R 4100, a skull missing the anterior portion of the snout, as a new species of *Scymnosaurus* (*S. watsoni*), a genus founded on a specimen (SAM-PK-632, holotype of the type species *S. ferox*) consisting only of the anterior portion of the snout. Watson (1914) had earlier questionably referred this specimen to *Lycosuchus vanderrieti*, but the absence of teeth on the transverse process of the pterygoid and general skull shape indicate that it is a scylacosaurid rather than lycosuchid (thus also separating it from *Scymnosaurus*, which is currently considered an indeterminate lycosuchid; Abdala *et al*. 2014b). Boonstra (1934) recognized *Scymnosaurus watsoni* as a valid taxon, but later (Boonstra 1954) transferred this species to *Pristerosaurus* (as *P. watsoni*), before finally reverting to including it in *Scymnosaurus* (Boonstra 1969). Van den Heever (1987) recognized this specimen as scylacosaurid, but considered it a *nomen dubium*.

Although reasonably well-prepared, the poor preservation of the palate in this specimen complicates identification. The most notable feature of this specimen is the very tall, well-developed sagittal crest. However, this feature seems to become exaggerated in all scylacosaurids at large size (probably related to expansion of the jaw musculature), as seen in e.g. *Alopecognathus* (GPIT-PV-116189) and *Scylacosaurus* (UCMP 42669). Pterygoid morphology in NHMUK PV R 4100 (relatively large transverse processes and quadrate processes diverging well anterior to the




**Figure 21**. NHMUK PV R 4100, holotype of *Scymnosaurus watsoni* (Scylacosauridae indet.), in (**A**) right lateral, (**B**) ventral, and (**C**) dorsal views. Scale bar equals 5 cm.

basal tubera) indicate that it is not *Scylacosaurus*, but it is difficult to eliminate other scylacosaurid taxa as possibilities. The proportions of the preserved skull are very similar to those of SAM-PK-9083 (holotype of *Pristerosaurus microdon*), so Boonstra's (1954) referral is worth considering (although the orbits show greater exposure dorsally in NHMUK PV R 4100 than expected for *Maraisaurus*). Until more information on the anatomy of *Maraisaurus* (and other rare scylacosaurids such as *Alopecodon* and *Hyorhynchus*) is available, however, this is speculative, and at present *Scymnosaurus watsoni* must be considered a *nomen dubium* (Scylacosauridae indet.)

## DISCUSSION

### Karoo scylacosaurid biostratigraphy

Day (2013) and Day & Rubidge (2020) provided updated stratigraphic range data for scylacosaurids, following the taxonomy of van den Heever (1987). They identified the bulk of scylacosaurid diversity occurring in the upper *Tapinocephalus* AZ (i.e. the *Diictodon-Styracocephalus* Subzone), with *Alopecodon priscus*, *Pardosuchus whaitsi*, and *Scylacosaurus sclateri* restricted to this subzone and *Pristerognathus polyodon* predominantly found in this subzone, but possibly extending into the overlying *Lycosuchus-Eunotosaurus* Subzone of the *Endothiodon* AZ. In contrast to these relatively short-ranging taxa, they considered *Glanosuchus macrops* and *Ictidosaurus angusticeps* to range from the *Eodicynodon* AZ to the *Endothiodon* AZ (with *Glanosuchus* extending to the upper boundary of the *Lycosuchus-Eunotosaurus* Subzone).

The taxonomic revisions proposed in the current work necessitate a reconsideration of biostratigraphy in the Scylacosauridae, however. Although the list of specimens referred to them has changed somewhat since van den Heever's (1987) revision, the relatively rare scylacosaurids *Alopecodon*, *Pardosuchus*, and *Scylacosaurus* are still restricted to the *Diictodon-Styracocephalus* Subzone of the *Tapinocephalus* AZ (and to this list can be added the newly revalidated *Maraisaurus*). All known specimens of these taxa appear to originate in exposures of the upper Abrahamskraal Formation, most in the Moordenaars Member (Day, 2013). The one possible exception is SAM-PK-634, the holotype of *Scylacosaurus sclateri*. Broom (1903b) stated that this specimen was obtained in Colesberg, but Kitching (1977) considered this locality problematic. Van den Heever (1987) noted that only late Permian strata (of the *Cistecephalus* and *Daptocephalus* AZs) are exposed at Colesberg, and suggested that this specimen was originally collected in *Tapinocephalus* AZ strata elsewhere, an argument that is accepted here in the absence of any other post-*Endothiodon* AZ records of Scylacosauridae.

As concerns the formerly long-ranging taxa *Glanosuchus* and *Ictidosaurus*, recognition of the *Eodicynodon* AZ scylacosaurid records as a distinct new taxon (*Eutheriodon*) removes their first appearance data, and *Ictidosaurus* is here considered invalid. Furthermore, *Glanosuchus* records from the *Endothiodon* AZ (e.g. CGS M 796) have been transferred to *Alopecognathus*, leaving the former genus restricted to the *Tapinocephalus* AZ (indeed, possibly also restricted to the *Diictodon-Styracocephalus* Subzone). This leaves *Alopecognathus* and *Pristerognathus* as the only boundary-crossing scylacosaurid taxa, extending from the *Diictodon-Styracocephalus* Subzone of the *Tapinocephalus* AZ to the *Lycosuchus-Eunotosaurus* Subzone of the *Endothiodon* AZ. Although published, historical records of these taxa from the *Endothiodon* AZ are few, there are a

number of (mostly undescribed) specimens from the *Lycosuchus-Eunotosaurus* Subzone in the collections of the Council for Geoscience (Pretoria) (see lists of referred materials in the Systematic Palaeontology section above). As with most aspects of this enigmatic taxon, the stratigraphic range of *Hyorhynchus* is uncertain – the holotype has only a vague locality (Gouph Tract) and could be from the *Tapinocephalus* or *Endothiodon* AZ. However, the referred specimen (CGS RMS 1058) was collected in the Poortjie Member of the Teekloof Formation, indicating that this taxon is present in the *Lycosuchus-Eunotosaurus* Subzone of the *Endothiodon* AZ.

The large number of scylacosaurid taxa restricted to the *Diictodon-Styracocephalus* Subzone of the *Tapinocephalus* AZ makes sense both from a sampling perspective (this is the most densely sampled section of middle Permian rock in the basin; Day 2013) and from an evolutionary history perspective (as the top of this interval corresponds with the end-Guadalupian mass extinction; Day *et al.* 2015). Under the taxonomic scheme proposed herein, five out of seven scylacosaurid species went extinct by the end of the *Tapinocephalus* AZ, an unsurprising degree of intensity for large-bodied predators during a biotic crisis.

Recognition of NMQR 2908 and NMQR 2910 as a distinct taxon apparently restricted to the *Eodicynodon* AZ has important implications for a probable third record (NMQR 3488) from near Jansenville in the Eastern Cape. The Abrahamskraal Formation in this region has yielded an unusual fauna, consisting of taxa (the burnetiamorph *Pachydectes elsi* and the dicynodont *Lanthanostegus mohoii*) historically known only from this site, making correlation with middle Permian strata in the western part of the basin difficult. In reviewing this site, Day & Rubidge (2020) noted that it could represent either the lowermost *Tapinocephalus* AZ or the *Eodicynodon* AZ. More recently, Rubidge *et al.* (2021) reported a new record of *Lanthanostegus* from the southwestern part of the basin in the lowest local exposures of the Abrahamskraal Formation, which they considered equivalent to the strata at Jansenville, although uncertain whether these represent *Tapinocephalus* AZ or a previously unknown assemblage intermediate in age between the *Eodicynodon* and *Tapinocephalus* AZs. The presence of *Eutheriodon* in classic *Eodicynodon* AZ exposures in the Western Cape and at Jansenville in the Eastern Cape adds a further wrinkle to this issue, suggesting that the latter do indeed encompass the *Eodicynodon* AZ, or that the range of *Eutheriodon* extends from that assemblage zone to the lower *Tapinocephalus* AZ. Further collecting at these localities is needed to resolve this issue.

**Scylacosaurid records outside South Africa**

Although the vast majority of published scylacosaurid records are from the Main Karoo Basin of South Africa, several papers have argued for the presence of this group in other southern African basins. However, none of the relevant fossils have been described in detail. Drysdall & Kitching (1963, p. 17) noted the discovery of 'a single Therocephalian resembling *Pristerognathus*' in beds of the Madumabisa Mudstone Formation at their Locality 20 in the upper Luangwa Valley, Zambia. However, no additional information about this specimen was published, and it is probable that, like most of the fossils they collected, it remains unprepared. Therapsid-bearing rocks of middle Permian age are not known from the upper Luangwa Valley; at present, such records in the Madumabisa Mudstone Formation are known only from the Mid-Zambezi Valley in southern Zambia (Sidor *et al.* 2014; although these have not yet produced therocephalians). So, a scylacosaurid identification of Drysdall & Kitching's (1963) specimen appears unlikely. Boonstra (1969, p. 57) noted that a *Tapinocephalus* AZ-equivalent fauna is known from Zimbabwe, 'where a *Criocephalus* and a therocephalian, probably pristerognathid, have been found.' The former consists of fragmentary crania from Gunyankas Kraal (figured by Boonstra [1968] as '*Criocephalus gunyankaensis*'), but the latter has never been figured or described. Given its association with dinocephalians, it is very likely that the therocephalian from this locality is middle Permian in age and could well represent a scylacosaurid, but this must remain speculation until the specimen receives further study.

Extensive collections have been made of therapsid fossils from middle Permian strata in Russia, some of which have been referred to Scylacosauridae. The taxonomic history of Russian therocephalians is complex and often contradictory (see Ivakhnenko [2011] for review), but four taxa have frequently been classified as scylacosaurids: *Hexacynodon purlinensis* Tatarinov, 1974, *Kotelcephalon viatkensis* Tatarinov, 1999, *Porosteognathus efremovi* Vjuschkov, 1955, and *Scylacosuchus orenburgensis* Tatarinov, 1968 (see e.g. Battail & Surkov 2000; Tatarinov 2008). *Hexacynodon* comes from the late Permian Purly Locality, and Ivakhnenko (2011) has convincingly argued that the holotype maxilla (long confused with the more extensive material of a bizarre taxon now known as *Purlovia maxima*) is referable to the whaitsiid *Moschowhaitsia vjuschkovi*, so this taxon is not a scylacosaurid. *Scylacosuchus* is generally similar in overall morphology to scylacosaurids, but lacks several classic features of early therocephalians (e.g. serrations on the teeth), and in recent phylogenies is consistently recovered as an early-diverging eutherocephalian (e.g. Kammerer & Masyutin 2018; Liu & Abdala 2020). A skull fragment (PIN 4415/3) from the Klyuchevka locality, listed as Scylacosauridae gen. indet. by Ivakhnenko (2011) and noted as being most similar to *Scylacosuchus*, exhibits no diagnostic characters of the family, and indeed, can be excluded from it by the absence of canine serrations (and presence instead of canine facets). Eutherocephalian identity also makes more sense considering the association of this specimen with typical latest Permian taxa (the chroniosuchian *Chroniosuchus* and the dicynodontoid *Peramodon*). The only known specimen of *Kotelcephalon* (PIN 2212/91) is a very poorly preserved skull, extremely dorsoventrally crushed with the bone surface badly eroded, complicating interpretation of its morphology. However, several of the teeth in this specimen are intact, preserved with their enamel, and clearly unserrated, suggesting that this specimen also represents a eutherocephalian rather than a scylacosaurid.

The above three taxa are all from well-supported late Permian localities (*Hexacynodon* and *Scylacosuchus*) or a locality of questionable late Permian age (a variety of age estimates have been proposed for the Kotelnich locality yielding *Kotelcephalon*, with correlation to the current *Endothiodon* AZ of the Karoo being most likely; see Kammerer & Masyutin 2018). However, a more robustly supported middle Permian age can be inferred for *Porosteognathus*, which is part of the Isheevo Fauna that also yields the dinocephalians *Syodon*, *Titanophoneus*, and *Ulemosaurus* (Ivakhnenko 2011). Although known only from fragmentary material, *Porosteognathus* does appear to represent a non-eutherocephalian therocephalian: the dentition is serrated and a median pterygoid ridge anterior to the interpterygoid vacuity is absent. However, it differs from both lycosuchids and scylacosaurids in having dentition on the palatal boss of the pterygoid (absent in Lycosuchidae) and on the transverse process of the pterygoid (absent in Scylacosauridae) (Fig. 8F). This morphology is also present in the recently described *Gorynychus masyutinae* from the Kotelnich locality, which has been recovered as a non-lycosuchid, non-scylacosaurid early therocephalian forming the sister-taxon of Eutherocephalia (Kammerer & Masyutin 2018). It is possible that these Russian early therocephalians form a clade intermediate between Scylacosauridae and Eutherocephalia, but additional material of *Porosteognathus* will likely be needed to test this idea.

The most recently described Russian taxon referred to Scylacosauridae is *Julognathus crudelis* from the Sundyr-1 locality (Suchkova & Golubev 2019). This taxon can be identified as an early therocephalian based on its serrated dentition, but because of the extremely fragmentary nature of the known material, no scylacosaurid synapomorphies are visible. However, its dentary morphology is remarkably similar to that described herein for *Scylacosaurus*; although the shape of the symphysis is different between the two genera (with an autapomorphic flange-like rounded edge to the base of the mentum in *Julognathus*), both display a distinct 'hourglass' shape with an elongate symphysial region and highly concave ventral margin. As such, *Julognathus* is the most likely contender currently known for an actual scylacosaurid record outside the Main Karoo Basin. Intriguingly, this mandibular morphology is also observed in a supposed biarmosuchian, *Biarmosuchoides romanovi* from the Dubovka-1 locality (Orenburg Region, Russia) (Fig. 13E,H). While this could be convergence (a roughly similar dentary shape is indeed present in *Biarmosuchus tener* itself, based on the holotype PIN 1758/2), the possibility that *Scylacosaurus*, *Julognathus*, and *Biarmosuchoides* form a scylacosaurid subclade with unusual jaw morphology cannot be discounted. Hopefully the discovery of more complete specimens of the latter taxa will permit further evaluation of this hypothesis.

## CONCLUSIONS

Karoo scylacosaurids were, for their time, a relatively diverse and successful clade. Although the current revision recognizes only a small percentage of nominal scylacosaurid species as valid, the presence of seven coeval large predators in the upper Abrahamskraal Formation is remarkable, especially in comparison with the diversity of anteosaurian dinocephalians in the same environments (with only a single species, *Anteosaurus magnificus*, currently considered valid; Kammerer 2011). Comparable standing diversity in Karoo ecosystems, however, is known in the group that in many ways replaced scylacosaurids in the late Permian: Gorgonopsia (Kammerer 2016). In both cases, peak diversity is observed prior to mass extinctions, when herbivore diversity was also at its apex (with dinocephalians, pareiasaurs, and dicynodonts at the end of the Guadalupian, and primarily dicynodonts with some lingering pareiasaurs at the end of the Lopingian), indicative of 'boom and bust' cycles in carnivorous theriodont evolution (which may well have continued into the Triassic, had archosauromorph reptiles not edged out cynodonts as they were beginning to evolve large predatory taxa in the Anisian).

The current work is necessarily restricted to lower-level systematic study of the Scylacosauridae. Incorporation of the taxa recognized herein in a phylogenetic analysis to test their relationships is desirable, but not possible at present. Huttenlocker (2009) included the scylacosaurid taxa known from well-prepared skulls in his analysis of therocephalian relationships (although his codings for '*Glanosuchus*' and '*Ictidosaurus*' are largely based on *Alopecognathus* and *Eutheriodon* under the herein-proposed taxonomy), and recovered them in a polytomy. The additional scylacosaurid taxa recognized here (particularly *Alopecodon*, *Hyorhynchus*, *Maraisaurus*, and *Pardosuchus*) are largely known from specimens so poorly prepared that their incorporation into a phylogenetic analysis would be useless. Repreparation and/or CT-scanning of these specimens is necessary to reveal data of phylogenetic import, and it is greatly hoped that the current work will prove a springboard for renewed research on scylacosaurids, rather than the final word on the subject.

## POSTSCRIPT

Following resubmission of this manuscript, a paper describing a new possible scylacosaurid taxon from the Permian Kotelnich locality of Russia was published (Suchkova *et al.* 2023). The new taxon, *Koksharovia grechovi*, is represented by a block of skeletal elements (KPM 456) including a left dentary fragment (KPM 456-1) and right maxillary fragment (KPM 456-2). Importantly, Suchkova *et al.* (2023) noted close similarities between the dentary of the new therocephalian and that of *Biarmosuchoides romanovi*, independently concluding that the latter represents a scylacosaurid rather than a biarmosuchian.

I am pleased to dedicate this work to professor emeritus Bruce Rubidge. No other scientist in recent memory has contributed so much to our understanding of those rocks yielding the majority of the world's early therocephalian specimens (those of the Abrahamskraal Formation). Comprehensive revision of the alpha taxonomy and biostratigraphy of the *Tapinocephalus* AZ fauna was long one of Bruce's major research goals, and with recent theses by his students resolving the Tap Zone Pareiasauria (van den Brandt 2020) and Tapinocephalidae (Neumann 2019), Scylacosauridae was the last major holdout. For many years he advertised 'PhD in therocephalian systematics' on the ESI website to address this problem, with no takers (perhaps wisely on the part of students; even for someone who has made a

career of tackling the thorniest issues in therapsid taxonomy, I did not find this work to be an easy task). It is my hope that the next generation of researchers will be more willing to work on early therocephalians, and can begin to address the palaeobiology, palaeoecology, and evolutionary history of these animals in greater detail.

Immense gratitude is due the many curators and collections managers who facilitated my examination of therocephalian fossils in their care over the years: Carl Mehling (AMNH), Sifelani Jirah and Bernhard Zipfel (BP/ESI), Oliver Rauhut (BSPG), Nonhlanhla Mchunu (CGS), Ingmar Werneburg (GPIT), Thomas Schossleitner (MB), David Morris (MMK), Paul Barrett, Michael Day, and the late Angela Milner (NHMUK), Jennifer Botha and Elize Butler (formerly of the NMQR), Valeriy Golubev and the late Mikhail Ivakhnenko (PIN), Claire Browning and Zaituna Skosan (SAM), Heidi Fourie (TM), Pat Holroyd (UCMP), Juri van den Heever (US), and Matt Carrano and Hans-Dieter Sues (USNM). Thanks also to the reviewers, Jun Liu and Adam Huttenlocker, for their comments on the initial manuscript, and Kimberley Chapelle for her editorial work.

## ABBREVIATIONS

**Institutional**

| | |
|---|---|
| AMNH | American Museum of Natural History, New York, U.S.A.; |
| BP | Evolutionary Studies Institute (formerly the Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; |
| BSPG | Bayerische Staatssammlung für Paleontologie und Geologie, Munich, Germany; |
| CGS | Council for Geoscience, Pretoria, South Africa; |
| GPIT | Paläontologische Sammlung, Eberhard Karls Universität Tübingen, Tübingen, Germany; |
| MB | Museum für Naturkunde, Berlin, Germany; |
| KPM | Vyatka Paleontological Museum, Kirov, Russia; |
| MMK | McGregor Museum, Kimberley, South Africa; |
| NHMUK | Natural History Museum, London, U.K.; |
| NMQR | National Museum, Bloemfontein, South Africa; |
| PIN | Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; |
| SAM | Iziko South African Museum, Cape Town, South Africa; |
| TM | Ditsong National Museum of Natural History (formerly the Transvaal Museum), Pretoria, South Africa; |
| UCMP | University of California Museum of Paleontology, Berkeley, U.S.A.; |
| US | University of Stellenbosch, Stellenbosch, South Africa; |
| USNM | National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. |

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## REFERENCES

ABDALA, F. 2007. Redescription of *Platycraniellus elegans* (Therapsida, Cynodontia) from the Lower Triassic of South Africa, and the cladistic relationships of eutheriodonts. *Palaeontology* **50**, 591–618.

ABDALA, F., RUBIDGE, B.S. & VAN DEN HEEVER, J. 2008. The oldest therocephalians (Therapsida, Eutheriodontia) and the early diversification of Therapsida. *Palaeontology* **51**, 1011–1024.

ABDALA, F., JASHASHVILI, T., RUBIDGE, B.S. & VAN DEN HEEVER, J. 2014a. New material of *Microgomphodon oligocynus* (Eutherapsida, Therocephalia) and the taxonomy of southern African Bauriidae. **In**: Kammerer, C.F., Angielczyk. K.D. & Fröbisch, J. (eds), *Early Evolutionary History of the Synapsida*, 209–231. Dordrecht, Springer.

ABDALA, F., KAMMERER, C.F., DAY, M.O., JIRAH, S. & RUBIDGE, B.S. 2014b. Adult morphology of the therocephalian *Simorhinella baini* from the middle Permian of South Africa and the taxonomy, paleobiogeography, and temporal distribution of the Lycosuchidae. *Journal of Paleontology* **88**, 1139–1153.

ANDERSON, J.M. 1968. The confused state of classification of the family Procynosuchidae. *Palaeontologia africana* **11**, 77–84.

ANGIELCZYK, K.D. & KAMMERER, C.F. 2018. Non-mammalian synapsids: the deep roots of the mammalian family tree. **In**: Asher, R. & Zachos, F. (eds), *Handbook of Zoology: Mammalia*, 117–198. Berlin, DeGruyter.

BATTAIL, B. & SURKOV, M.V. 2000. Mammal-like reptiles from Russia. **In**: Benton, M.J., Shishkin, M.A., Unwin, D.M. & Kurochkin, E.N. (eds), *The Age of Dinosaurs in Russia and Mongolia*, 86–119. Cambridge, Cambridge University Press.

BOONSTRA, L.D. 1934. A contribution to the morphology of the mammal-like reptiles of the suborder Therocephalia. *Annals of the South African Museum* **31**, 215–267.

BOONSTRA, L.D. 1935. On some South African reptiles of the suborder Therocephalia preserved in the American Museum of Natural History. *American Museum Novitates* **771**, 1–12.

BOONSTRA, L.D. 1953. The lower jaw articulatory region in some pristerognathid therocephalians. *Annals of the South African Museum* **42**, 54–63.

BOONSTRA, L.D. 1954a. A scaloposaurid from the *Tapinocephalus*-zone. *Annals and Magazine of Natural History* (12)**7**, 153–157.

BOONSTRA, L.D. 1954b. The pristerognathid therocephalians from the *Tapinocephalus*-zone in the South African Museum. *Annals of the South African Museum* **42**, 65–107.

BOONSTRA, L.D. 1964. The girdles and limbs of the pristerognathid Therocephalia. *Annals of the South African Museum* **48**, 121–165.

BOONSTRA, L.D. 1968. The braincase, basicranial axis and median septum in the Dinocephalia. *Annals of the South African Museum* **50**, 195–273.

BOONSTRA, L.D. 1969. The fauna of the *Tapinocephalus* Zone (Beaufort beds of the Karoo). *Annals of the South African Museum* **56**, 1–73.

BRINK, A.S. & KITCHING, J.W. 1951. Some theriodonts in the collection of the Bernard Price Institute. *Annals and Magazine of Natural History* (12)**4**, 1218–1236.

BROCKLEHURST, N. 2019. Morphological evolution in therocephalians breaks the hypercarnivore ratchet. *Proceedings of the Royal Society B* **286**, 20190590.

BROILI, F. & SCHRÖDER, J. 1936a. Beobachtungen an Wirbeltieren der Karrooformation. XV. Ein Therocephalier aus den unteren Beaufort-Schichten. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Abteilung der Bayerischen Akademie der Wissenschaften zu München* **1936**, 1–20.

BROILI, F. & SCHRÖDER, J. 1936b. Beobachtungen an Wirbeltieren der Karrooformation. XXIII. Ein weiterer Therocephalier aus den unteren Beaufort-Schichten. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Abteilung der Bayerischen Akademie der Wissenschaften zu München* **1936**, 283–310.

BROOM, R. 1903a. On an almost perfect skull of a new primitive theriodont (*Lycosuchus vanderrieti*). *Transactions of the South African Philosophical Society* **14**, 197–205.

BROOM, R. 1903b. On some new primitive theriodonts in the South African Museum. *Annals of the South African Museum* **4**, 147–158.

BROOM, R. 1903c. On the classification of the theriodonts and their allies. *Report of the South African Association for the Advancement of Science* **1**, 286–294.

BROOM, R. 1904. On two new therocephalian reptiles (*Glanosuchus macrops* and *Pristerognathus baini*). *Transactions of the South African Philosophical Society* **15**, 85–88.

BROOM, R. 1905. On the use of the term Anomodontia. *Records of the Albany Museum* **1**, 266–269.

BROOM, R. 1908. On some new therocephalian reptiles. *Annals of the South African Museum* **4**, 361–367.

BROOM, R. 1912. On some new fossil reptiles from the Permian and Triassic beds of South Africa. *Proceedings of the Zoological Society of London* **1912**, 859–876.

BROOM, R. 1914. Croonian Lecture: On the origin of mammals. *Philosophical Transactions of the Royal Society of London* **206**, 1–48.

BROOM, R. 1915a. Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History. II.— Permian, Triassic and Jurassic reptiles of South Africa. *Bulletin of the American Museum of Natural History* **25**, 105–164.

BROOM, R. 1915b. On some new carnivorous therapsids in the collection of the British Museum. *Proceedings of the Zoological Society of London* **1915**, 163–173.

BROOM, R. 1925. On some carnivorous therapsids. *Records of the Albany Museum* **3**, 309–326.

BROOM, R. 1931. Notices of some new genera and species of Karroo fossil reptiles. *Records of the Albany Museum* **4**, 161–166.

BROOM, R. 1932. *The Mammal-like Reptiles of South Africa and the Origin of Mammals*. London, H.F. & G. Witherby, 376 pp.

BROOM, R. 1935a. A new genus and some new species of mammal-like reptiles. *Annals of the Transvaal Museum* **18**, 1–12.

BROOM, R. 1935b. On some new genera and species of Karroo fossil reptiles. *Annals of the Transvaal Museum* **18**, 55–72.

BROOM, R. 1936. On some new genera and species of Karroo fossil reptiles, with notes on some others. *Annals of the Transvaal Museum* **18**, 349–386.

BROOM, R. 1937. A few more new fossil reptiles from the Karroo. *Annals of the Transvaal Museum* **19**, 141–146.

CLUVER, M.A. & HOTTON, N., III. 1981. The genera *Dicynodon* and *Diictodon* and their bearing on the classification of the Dicynodontia (Reptilia, Therapsida). *Annals of the South African Museum* **83**, 99–146.

CLUVER, M.A. & KING, M.A. 1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. *Annals of the South African Museum* **91**, 195–273.
CYS, J.M. 1967. Osteology of the pristerognathid *Cynariognathus platyrhinus* (Reptilia: Theriodontia). *Journal of Paleontology* **41**, 776–790.
DAY, M.O. 2013. *Middle Permian continental biodiversity changes as reflected in the Beaufort Group of South Africa: a bio- and lithostratigraphic review of the* Eodicynodon, Tapinocephalus *and* Pristerognathus *Assemblage Zones*. Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.
DAY, M.O. & RUBIDGE, B.S. 2019. Biesiespoort revisited: a case study on the relationship between tetrapod assemblage zones and Beaufort lithostratigraphy south of Victoria West. *Palaeontologia africana* **53**, 51–65.
DAY, M.O. & RUBIDGE, B.S. 2020. Biostratigraphy of the *Tapinocephalus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**, 149–164.
DAY, M.O. & SMITH, R.M.H. 2020. Biostratigraphy of the *Endothiodon* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**, 165–180.
DAY, M.O., RAMEZANI, J., BOWRING, S.A., SADLER, P.M., ERWIN, D.H., ABDALA, F. & RUBIDGE, B.S. 2015. When and how did the terrestrial mid-Permian mass extinction occur? Evidence from the tetrapod record of the Karoo Basin, South Africa. *Proceedings of the Royal Society of London B* **282**, 20150834.
DRYSDALL, A.R. & KITCHING, J.W. 1963. A re-examination of the Karroo succession and fossil localities of part of the Upper Luangwa Valley. *Memoir of the Geological Survey of Northern Rhodesia* **1**, 1–62.
FOURIE, H. & RUBIDGE, B.S. 2009. The postcranial skeleton of the basal therocephalian *Glanosuchus macrops* (Scylacosauridae) and comparison of morphological and phylogenetic trends amongst the Theriodontia. *Palaeontologia africana* **44**, 27–39.
GRINE, F.E., HAHN, B.D. & GOW, C. 1978. Aspects of relative growth and variability in *Diademodon* (Reptilia: Therapsida). *South African Journal of Science* **74**, 50–58.
GRUNERT, H.R., BROCKLEHURST, N. & FRÖBISCH, J. 2019. Diversity and disparity of Therocephalia: macroevolutionary patterns through two mass extinctions. *Scientific Reports* **9**, 5063.
HAUGHTON, S.H. 1918. Investigations in South African fossil reptiles and Amphibia. 11. Some new carnivorous Therapsida, with notes upon the brain-case in certain species. *Annals of the South African Museum* **12**, 175–215.
HAUGHTON, S.H. 1924. A bibliographic list of pre-Stormberg Karroo Reptilia, with a table of horizons. *Transactions of the Royal Society of South Africa* **12**, 51–104.
HAUGHTON, S.H. & BRINK, A.S. 1954. A bibliographical list of Reptilia from the Karroo beds of Africa. *Palaeontologia africana* **2**, 1–187.
HILLENIUS, W.J. 1994. Turbinates in therapsids: evidence for late Permian origins of mammalian endothermy. *Evolution* **48**, 207–229.
HOPSON, J.A. & BARGHUSEN, H.R. 1986. An analysis of therapsid relationships. **In**: Hotton, N., III, Maclean, P.D., Roth, J.J. & Roth, E.C. (eds), *The Ecology and Biology of the Mammal-like Reptiles*, 83–106. Washington, D.C., Smithsonian Institution Press.
HOPSON, J.A. & KITCHING, J.W. 1972. A revised classification of cynodonts (Reptilia; Therapsida). *Palaeontologia africana* **14**, 71–85.
HUENE, F. VON. 1956. *Paläontologie und Phylogenie der Niederen Tetrapoden*. Jena, Gustav Fischer Verlag, 716 pp.
HUTTENLOCKER, A.K. 2009. An investigation into the cladistic relationships and monophyly of therocephalian therapsids (Amniota: Synapsida). *Zoological Journal of the Linnean Society* **157**, 865–891.
HUTTENLOCKER, A.K. 2014. Body size reductions in nonmammalian eutheriodont therapsida (Synapsida) during the end-Permian mass extinction. *PLOS ONE* **9(2)**, e87553.
HUTTENLOCKER, A.K. & ABDALA, F. 2015. Revision of the first therocephalian, *Theriognathus* Owen (Therapsida: Whaitsiidae), and implications for cranial ontogeny and allometry in nonmammaliaform eutheriodonts. *Journal of Paleontology* **89**, 645–664.
HUTTENLOCKER, A.K. & SIDOR, C.A. 2012. Taxonomic revision of therocephalians (Therapsida, Theriodontia) from the Lower Triassic of Antarctica. *American Museum Novitates* **3738**, 1–19.
HUTTENLOCKER, A.K. & SIDOR, C.A. 2016. The first karenitid (Therapsida, Therocephalia) from the upper Permian of Gondwana and the biogeography of Permo-Triassic therocephalians. *Journal of Vertebrate Paleontology* **36**, e1111897.
HUTTENLOCKER, A.K. & SMITH, R.M.H. 2017. New whaitsioids (Therapsida: Therocephalia) from the Teekloof Formation of South Africa and therocephalian diversity during the end-Guadalupian extinction. *PeerJ* **5**, e3868.
HUTTENLOCKER, A.K., SIDOR, C.A. & ANGIELCZYK, K.D. 2015. A new eutherocephalian (Therapsida, Therocephalia) from the upper Permian Madumabisa Mudstone Formation (Luangwa Basin) of Zambia. *Journal of Vertebrate Paleontology* **35**, e969400.
HUTTENLOCKER, A.K., SIDOR, C.A. & SMITH, R.M.H. 2011. A new specimen of *Promoschorhynchus* (Therapsida: Therocephalia: Akidnognathidae) from the Lower Triassic of South Africa and its implications for theriodont survivorship across the Permo-Triassic boundary. *Journal of Vertebrate Paleontology* **31**, 405–421.
IVAKHNENKO, M.F. 2011. Permian and Triassic therocephals (Eutherapsida) of Eastern Europe. *Paleontological Journal* **49**, 981–1144.
JENKINS, I., THOMASON, J.J. & NORMAN, D.B. 2002. Primates and engineering principles: applications to craniodental mechanisms in ancient terrestrial predators. *Senckenbergiana lethaea* **82**, 223–240.
KAMMERER, C.F. 2011. Systematics of the Anteosauria (Therapsida: Dinocephalia). *Journal of Systematic Palaeontology* **9**, 261–304.
KAMMERER, C.F. 2014. A redescription of *Eriphostoma microdon* Broom, 1911 (Therapsida, Gorgonopsia) from the *Tapinocephalus* Assemblage Zone of South Africa and a review of Middle Permian gorgonopsians. **In**: Kammerer, C. F., Angielczyk, K. D. & Fröbisch, J. (eds), *Early Evolutionary History of the Synapsida*, 171–184. Dordrecht, Springer.
KAMMERER, C.F. 2016. Systematics of the Rubidgeinae (Therapsida: Gorgonopsia). *PeerJ* **4**, e1608.
KAMMERER, C.F. 2017. Anatomy and relationships of the South African gorgonopsian *Arctops* (Therapsida, Theriodontia). *Papers in Palaeontology* **3**, 583–611.
KAMMERER, C.F. & MASYUTIN, V. 2018. A new therocephalian (*Gorynychus masyutinae* gen. et sp. nov.) from the Permian Kotelnich locality, Kirov Region, Russia. *PeerJ* **6**, e4933.
KAMMERER, C.F. & RUBIDGE, B.S. 2022. The earliest gorgonopsians from the Karoo Basin of South Africa. *Journal of African Earth Sciences* **194**, 104631.
KEMP, T.S. 1972. Whaitsiid Therocephalia and the origin of cynodonts. *Philosophical Transactions of the Royal Society of London, Series B* **264**, 1–54.
KEMP, T.S. 1982. *Mammal-like Reptiles and the Origin of Mammals*. London, Academic Press, xiv + 363 pp.
KEMP, T.S. 1986. The skeleton of a baurioid therocephalian therapsid from the Lower Triassic (*Lystrosaurus* Zone) of South Africa. *Journal of Vertebrate Paleontology* **6**, 215–232.
KEYSER, A.W. 1973. A preliminary study of the type area of the *Cistecephalus* Zone of the Beaufort Series, and a revision of the anomodont family Cistecephalidae. *Memoirs of the Geological Survey of South Africa* **62**, 1–71.
KEYSER, A.W. 1975. A re-evaluation of the cranial morphology and systematics of some tuskless Anomodontia. *Memoirs of the Geological Survey of South Africa* **67**, 1–110.
KEYSER, A.W. & SMITH, R.M.H. 1978. Vertebrate biozonation of the Beaufort Group with special reference to the Western Karoo Basin. *Annals of the Geological Survey of South Africa* **12**, 1–36.
KING, G.M. 1988. *Anomodontia. Handbuch der Paläoherpetologie. 17 C*. Stuttgart, Gustav Fischer Verlag, 174 pp.
KITCHING, J.W. 1977. The distribution of the Karroo vertebrate fauna. *Bernard Price Institute for Palaeontological Research Memoir* **1**, 1–131.
KUHN, O. 1958. Ein neuer Lacertilier aus dem fränkischen Lithographieschiefer. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1958**, 380–382.
LIU, J. & ABDALA, F. 2017. The tetrapod fauna of the upper Permian Naobaogou Formation of China: 1. *Shiguaignathus wangi* gen. et sp. nov., the first akidnognathid therocephalian from China. *PeerJ* **5**, e4150.
LIU, J. & ABDALA, F. 2019. The tetrapod fauna of the upper Permian Naobaogou Formation of China: 3. *Jiufengia jiai* gen. et sp. nov., a large akidnognathid therocephalian. *PeerJ* **7**, e6463.
LIU, J. & ABDALA, F. 2020. The tetrapod fauna of the upper Permian Naobaogou Formation of China: 5. *Caodeyao liuyufengi* gen. et sp. nov., a new peculiar therocephalian. *PeerJ* **8**, e9160.
MAIER, W. & VAN DEN HEEVER, J. 2002. Middle ear structures in the Permian *Glanosuchus* sp. (Therocephalia, Therapsida), based on thin sections. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe* **5**, 309–318.
MAISCH, M.W. 2017. Re-assessment of *Silphoictidoides ruhuhuensis* von Huene, 1950 (Therapsida, Therocephalia) from the Late Permian of Tanzania: one of the most basal baurioids known. *Palaeodiversity* **10**, 25–39.
MENDREZ, C.H. 1972. On the skull of *Regisaurus jacobi*, a new genus of Bauriamorpha Watson and Romer 1956 (=Scaloposauria Boonstra 1953), from the *Lystrosaurus*-Zone of South Africa. **In**: Joysey, K.A. & Kemp, T.S. (eds), *Studies in Vertebrate Evolution*, 191–212. New York, Winchester Press.
MENDREZ, C.H. 1974. Etude du crane d'un jeune specimen de

*Moschorhinus kitchingi* Broom, 1920 (?*Tigrisuchus simus* Owen, 1876), Therocephalia, Pristerosauria, Moschorhinidae d'Afrique Australe (Remarques sur les Moschorhinidae el les Whaitsiidae). *Annals of the South African Museum* **64**, 71–115.

MENDREZ, C.H. 1975. Principales variations du palais chez les Thérocéphales sud-africains (Pristerosauria et Scaloposauria) au cours du Permien supérieur et du Trias inférieur. *Colloques international du Centre national de la recherche scientifique* **218**, 379–408.

MODESTO, S.P., RUBIDGE, B.S., DE KLERK, W.J. & WELMAN, J. 2001. A dinocephalian therapsid fauna on the Ecca-Beaufort contact in Eastern Cape Province, South Africa. *South African Journal of Science* **97**, 161–163.

NEUMANN, S. 2019. *Taxonomic revision of the short-snouted tapinocephalid Dinocephalia (Amniota–Therapsida) – the key to understanding middle Permian tetrapod biodiversity*. Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.

OSBORN, H.F. 1903. On the primary division of the Reptilia into two sub-classes, *Synapsida* and *Diapsida*. *Science* **17**, 275–276.

OWEN, R. 1859. On some reptilian remains from South Africa. *The Edinburgh New Philosophical Journal* **10**, 289–291.

OWEN, R. 1876. *Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum*. London, Taylor and Francis, xii + 88 pp., 70 pls.

PUSCH, L.C., PONSTEIN, J., KAMMERER, C.F. & FRÖBISCH, J. 2020. Novel endocranial data on the early therocephalian *Lycosuchus vanderrieti* underpin high character variability in early theriodont evolution. *Frontiers in Ecology and Evolution* **7**(464), 1–27.

ROMER, A.S. 1945. *Vertebrate Paleontology*. Chicago, University of Chicago Press, 687 pp.

ROMER, A.S. 1956. *Osteology of the Reptiles*. Chicago, University of Chicago Press, 772 pp.

SCHULZE, F.E. 1886. Über den Bau und das System der Hexactinelliden. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin (Physikalisch-Mathematische Classe)* **1886**, 1–97.

SEELEY, H.G. 1889. Researches on the structure, organization, and classification of the fossil Reptilia.— VI. On the anomodont Reptilia and their allies. *Philosophical Transactions of the Royal Society of London B* **180**, 215–296.

SEELEY, H.G. 1894. Researches on the structure, organisation, and classification of the fossil Reptilia.— Part IX., Section 1. On the Therosuchia. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* **185**, 987–1018.

SIGOGNEAU, D. 1970. Révision systématique des Gorgonopsiens sud-africains. *Cahiers de Paléontologie*. Paris, Centre National de la Recherche Scientifique, 417 pp.

SIGOGNEAU-RUSSELL, D. 1989. *Theriodontia I. Handbuch der Paläoherpetologie. 17 B/I*. Stuttgart, Gustav Fischer Verlag, 127 pp.

SIGURDSEN, T., HUTTENLOCKER, A.K., MODESTO, S.P., ROWE, T.B. & DAMIANI, R. 2012. Reassessment of the morphology and paleobiology of the therocephalian *Tetracynodon darti* (Therapsida), and the phylogenetic relationships of Baurioidea. *Journal of Vertebrate Paleontology* **32**, 1113–1134.

SMITH, R.M.H. & KEYSER, A.W. 1995. Biostratigraphy of the *Pristerognathus* Assemblage Zone. *South African Committee for Stratigraphy Biostratigraphic Series* **1**, 13–17.

SMITH, R.M.H., RUBIDGE, B.S. & VAN DER WALT, M. 2012. Therapsid biodiversity patterns and paleoenvironments of the Karoo Basin, South Africa. **In**: Chinsamy-Turan, A. (ed.), *Forerunners of Mammals: Radiation, Histology, Biology*, 31–62. Bloomington, Indiana University Press.

SUCHKOVA, Y.A. & GOLUBEV, V.K. 2019. A new primitive therocephalian (Theromorpha) from the middle Permian of Eastern Europe. *Paleontological Journal* **53**, 305–314.

SUCHKOVA, Y.A., GOLUBEV, V.K. & SHUMOV, I.S. 2023. New primitive therocephalians from the Permian of Eastern Europe. *Paleontological Journal* **56**, 1419–1427.

TATARINOV, L.P. 1968. [New Theriodonts from the Upper Permian of the USSR]. **In**: Tatarinov, L.P. (ed.), *Verkhnepaleozoiskie i mezozoiskie zemnovodnye i presmykaiushchiesia SSSR*, 32–46. Moscow, Nauka. [In Russian].

TATARINOV, L.P. 1974. [Theriodonts of the USSR]. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* **143**, 1–226. [In Russian].

TATARINOV, L.P. 1999. New theriodonts (Reptilia) from the Late Permian fauna of the Kotelnich Locality, Kirov Region. *Paleontological Journal* **33**, 550–556.

TATARINOV, L.P. 2008. [Infraclassis Therosauria]. **In**: Ivakhnenko, M.F. & Kurochkin, E.N. (eds), *Fossil vertebrates of Russia and Adjacent Countries. Fossil Reptiles and Birds. Part 1*, 184–223. Moscow, GEOS. [In Russian].

VAN DEN BRANDT, M. 2020. *Morphology, taxonomy, phylogeny and stratigraphic ranges of South African middle Permian pareiasaurs*. Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg.

VAN DEN HEEVER, J.A. 1980. On the validity of the therocephalian family Lycosuchidae (Reptilia, Therapsida). *Annals of the South African Museum* **81**, 111–125.

VAN DEN HEEVER, J.A. 1987. *The comparative and functional cranial morphology of the early Therocephalia (Amniota: Therapsida)*. Unpublished Ph.D. thesis, University of Stellenbosch, Stellenbosch.

VAN DEN HEEVER, J.A. 1994. The cranial anatomy of the early Therocephalia (Amniota: Therapsida). *Universiteit van Stellenbosch Annale* **1994**, 1–59.

VJUSCHKOV, B.P. 1955. [Theriodonts of the Soviet Union]. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* **49**, 128–175. [In Russian].

VJUSCHKOV, B.P. 1964. [Suborder Theriodontia (Theriodonts): the Superfamily Scaloposauroidea (=Therocephalia).] **In**: Rozhdestvensky, A.K. & Tatarinov, L.P. (eds), *Osnovy paleontologii: zemnovodnye, premykayushchiesya i ptitsy*, 275–280. Moscow, Nauka. [In Russian].

WATSON, D.M.S. 1914. Notes on some carnivorous therapsids. *Proceedings of the Zoological Society of London* **1914**, 1021–1038.

WATSON, D.M.S. & ROMER, A.S. 1956. A classification of therapsid reptiles. *Bulletin of the Museum of Comparative Zoology* **114**, 35–89.

WILLISTON, S.W. 1925. *The Osteology of the Reptiles*. Cambridge, Harvard University Press, 300 pp.

ZIMMER, C. 1994. The importance of noses. *Discover* **15**, 24–25.