

Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

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

Adam K. Huttenlocker ^a, Christian A. Sidor ^b & Roger M. H. Smith ^c

^a Department of Biology, University of Washington, Seattle, Washington, 98195, U.S.A.

^b Department of Biology and Burke Museum, University of Washington, Seattle, Washington, 98195, U.S.A.

^c Department of Karoo Palaeontology, Iziko South African Museum, PO Box 61, Cape Town, 8000, South Africa

Version of record first published: 21 Mar 2011.

To cite this article: Adam K. Huttenlocker , Christian A. Sidor & Roger M. H. Smith (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*, 31:2, 405-421

To link to this article: <http://dx.doi.org/10.1080/02724634.2011.546720>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

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

ADAM K. HUTTENLOCKER,^{*1} CHRISTIAN A. SIDOR,² and ROGER M. H. SMITH³

¹Department of Biology, University of Washington, Seattle, Washington 98195, U.S.A., huttenla@u.washington.edu;

²Department of Biology and Burke Museum, University of Washington, Seattle, Washington 98195, U.S.A., casidor@u.washington.edu;

³Department of Karoo Palaeontology, Iziko South African Museum, PO Box 61, Cape Town, 8000 South Africa, rsmith@iziko.org.za

ABSTRACT—The anatomy of a new subadult specimen of eutheriocephalian therapsid, attributed to *Promoschorhynchus* cf. *P. platyrhinus*, is described from lowermost Triassic *Lystrosaurus* Assemblage Zone strata in the main Karoo Basin of South Africa. The specimen preserves information previously unknown in the genus, including details of the posterior region of the skull and intertemporal region, and a partial (though disarticulated) postcranial skeleton. A cladistic analysis of 32 therapsid taxa, including 24 Permo-Triassic theriocephalian genera, and 121 craniodental and postcranial characters supports the specimen's placement within the Permian akidnognathid genus *Promoschorhynchus* (making it the youngest documented occurrence of this taxon) within a monophyletic Theriocephalia. Inclusion of new postcranial characters strengthens support of the theriocephalian clade. The new record of *Promoschorhynchus* offers insights into the diversity of eutheriodonts across the Permo-Triassic boundary (PTB) in the Karoo Basin. In contrast to cynodonts, theriocephalians exhibited decreased rates of cladogenesis across the PTB, with several Triassic lineages having roots in the Late Permian rather than representing earliest Triassic radiations.

INTRODUCTION

The origins of classic mammalian characteristics such as an enlarged coronoid process of the dentary, a broadened epitygoid (= alisphenoid), expansion of the temporal musculature to form a parietal (= sagittal) crest, and possibly respiratory turbinates among other features, can be traced as far back as the Middle Permian (± 270 Ma) where they first appeared in theriodont therapsids (Rubidge and Sidor, 2001). Among these early theriodonts, the best resolved relationship is the sister-group relationship shared by theriocephalians and cynodonts (Hopson and Barghusen, 1986; Hopson, 1991; Sidor and Hopson, 1998; Rubidge and Sidor, 2001; Kemp, 2009; but see Botha et al., 2007, and Abdala et al., 2007), which together form the clade Eutheriodontia (“Therosauria” of Kemp, 1982).

Although many representatives of the Permian radiation of eutheriodonts became extinct prior to or within the Early Triassic, eutheriodonts were diverse during the Permo-Triassic transition. Theriocephalians were particularly diverse during the Permian and can be divided into six widely recognized clades: the basal Lycosuchidae and Scylacosauridae, and the eutheriocephalian clades Akidnognathidae (= Euchambersiidae), Hofmeyriidae, Whaitsiidae, and Baurioidea (Hopson and Barghusen, 1986; Hopson, 1991; van den Heever, 1994; Rubidge and Sidor, 2001; Huttnerlocker, 2009).

This paper reports on a recent, problematic eutheriocephalian record from the lowermost Triassic of South Africa and discusses its affinities to the known theriocephalian families that occur in the proximity of the Permo-Triassic boundary (herein termed ‘PTB’). The specimen was recovered from 2.5 m above the PTB in the lowermost *Lystrosaurus* Assemblage Zone of the Pal-

ingkloof Member, Balfour Formation (Smith and Botha, 2005; Botha and Smith, 2006). The Palingkloof Member has yielded remains of small temnospondyl amphibians, procolophonoids, archosauromorphs, dicynodont therapsids, and a diversity of eutheriodonts (Damiani et al., 2003). The latter include the eutheriocephalians *Moschorhinus kitchingi*, *Olivierosuchus parringtoni*, and *Tetracynodon darti*; immature specimens attributed to *Ericiolacerta parva* and *Regisaurus jacobi* (Damiani et al., 2003; Botha and Smith, 2006; Fourie and Rubidge, 2007); and the cynodonts *Galesaurus*, *Progalesaurus*, and *Thrinaxodon* (Sidor and Smith, 2004; Botha and Smith, 2006). The cynodont *Platycranellus* is known from coeval deposits of the Harrismith Member of the Normandien Formation (Abdala, 2007). The specimen described here adds to the current record of PTB eutheriodonts and offers insights into the diversification of eutheriodonts across the PTB.

Identification of the Specimen as *Promoschorhynchus* cf. *P. platyrhinus*

The specimen under study was originally reported as a new Triassic record of the baurioid genus *Ictidosuchoides* by Ward et al. (2005) as well as Botha and Smith (2006). The range of *Ictidosuchoides* appears to be restricted, however, to the Upper Permian *Tropidostoma* through *Dicynodon* Assemblage Zones (Kammerer, 2008).

Additional preparation and study of the specimen has revealed its akidnognathid affinities based on features of the anterior snout, dentition, and lower jaw (see below). The initial assignment to the baurioid *Ictidosuchoides* was likely the result of its generally gracile appearance and small size. In addition, it differs from more robust akidnognathids such as *Moschorhinus* and *Cerdops* in its greater marginal tooth count and the presence of facets and ridges on the precanines and incisors, the taxonomic significance of which is discussed here.

*Corresponding author.

Among small, South African akidognathids, the specimen exhibits features that are consistent with published diagnoses of the Permian *Cerdosuchus aulodon* (Broom, 1936; Brink, 1988), in particular the dental formula, broad prefrontal, and almost identical cranial measurements. Unfortunately, the type and only specimen of *Cerdosuchus*, which may have been recovered from older deposits near Graaff Reinet (*Cistecephalus* or *Dicynodon* Assemblage Zone), was lost prior to this investigation (H. Fourie and A. Abdala, pers. comm., 2009) and no photographs were published. Furthermore, because *Cerdosuchus* was a singleton taxon, no accompanying paratypic material was recovered from the type locality, thereby making impossible the designation of a neotype according to the provisions of ICZN Article 75.3.6. Broom (1936) reported on another small akidognathid specimen (i.e., the holotype of *Notaelurodon kitchingi*) from coeval deposits, but its state of preservation preserves little information beyond the dental formula.

Whereas the provenance and proper synonymies of the earlier Broom specimens remain dubious, more complete material referred to the Permian *Promoschorhynchus platyrhinus* Brink (1954) has been described and its provenance well documented. *Promoschorhynchus* may ultimately be considered a subjective junior synonym of *Cerdosuchus* Broom at a later date. However, this cannot be certain until the holotype of *Cerdosuchus* is found or more material is discovered from the type locality. The holotype of *Promoschorhynchus* and other specimens referred by Mendrez (1974b) exhibit an upper dental formula comprising five incisors, one precanine, one canine, and five to six postcanines. The incisors and caniniform dentition (precanines and canines) bear distinct facets, as in the specimen studied here. These shared characteristics suggest that the present specimen is likely allied to the genus *Promoschorhynchus*, although its geologically younger occurrence and slightly more gracile appearance, among other features, may separate it specifically from its predecessors. The specimen, herein referred to *Promoschorhynchus cf. P. platyrhinus*, reveals details of the dentition, dorsal skull roof, temporal region, and postcranial skeleton previously unknown in the genus and merits a more detailed description.

Anatomical Abbreviations—**art**, articular; **bo**, basioccipital; **bs**, basisphenoid process of pterygoid; **c vert**, caudal vertebra; **can**, canine tooth; **co**, coracoid; **cr v**, ventrointermediate crest of pterygoid; **d**, dentary; **d vert**, dorsal vertebra; **ec**, ectopterygoid; **eo**, exoccipital; **epi**, epipterygoid; **f**, frontal; **fi**, fibula; **fm**, foramen magnum; **hu**, humerus; **icd**, interclavicle; **ip**, interparietal; **j**, jugular foramen; **l**, lacrimal; **m**, maxilla; **mp**, metapodial; **n**, nasal; **p**, parietal; **pal**, palatine; **pbs**, parabasisphenoid complex; **pc**, procoracoid; **ph**, phalanx; **pm**, premaxilla; **po**, postorbital; **pop**, paroccipital process of opisthotic; **pr q**, quadrate ramus of pterygoid; **pr tr**, transverse process of pterygoid; **pra**, prearticular; **prf**, prefrontal; **pro**, prootic; **ptf**, posttemporal fenestra; **q-qj**, quadrate-quadratojugal; **ra**, radius; **sc**, scapula; **sm**, septomaxilla; **so**, supraoccipital; **sq**, squamosal; **st**, sternum; **sur**, surangular; **t**, tabular; **ti**, tibia; **to**, tooth; **u**, ulna; **un**, ungual.

Institutional Abbreviations—**BP**, Bernard Price Institute, Johannesburg; **CGP**, Council for Geosciences (formerly Geological Survey) Keyser Collection, Pretoria; **RC**, Rubidge Collection, Graaff Reinet; **SAM**, South African Museum, Cape Town.

STRATIGRAPHY AND GEOLOGICAL CONTEXT

Figure 1 shows the stratigraphic position of the new akidognathid specimen and its associated fauna in the upper Balfour Formation (Beaufort Group) some 10 m above the base of the Palingkloof Member and 2.5 m above the PTB. The specimen was found embedded in mudrocks exposed in an ephemeral stream bed next to a vertical dolerite dyke in the lower reaches of the

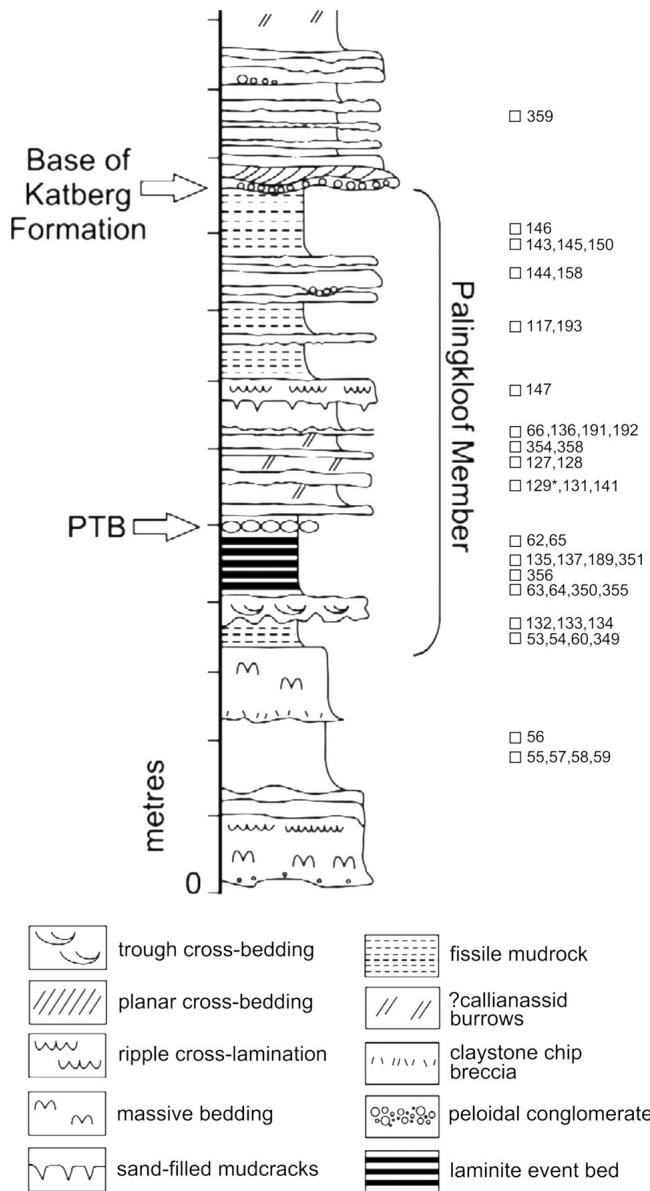


FIGURE 1. Stratigraphic section and relative positions of Permian and Triassic vertebrates at the Bethel 763 locality, Bethulie District (modified from Botha and Smith, 2006). Vertical units are represented in 5-m intervals. See online Supplementary Data, Appendix S1, for detailed occurrence data. Number 129 (asterisk) represents the new akidognathid record.

Bethel canyon. Thermal metamorphism during the intrusion of the dyke altered the color of the siltstone matrix from reddish brown to olive grey and the fossil bone from the characteristic dark grey to white. Detailed stratigraphic logs of the Bethel canyon show the fossil locality lies only 2.5 m above the PTB, which is positioned at the top of a 2.5-m-thick interval of laminated mudrocks ('event beds' of Smith and Ward, 2001; 'maroon laminites' of Ward et al., 2005). The positioning of the PTB in the Karoo Basin has in recent years come under intensive review since it was first demonstrated that the vertebrate fossils in the upper Balfour Formation record an extinction event that coincides with the mapped change in lithofacies at the base of the Palingkloof Member (Smith, 1995). The same faunal extinction

has since been demonstrated at a number of separate sections throughout the southern Karoo Basin where it has been shown to occur in the same roughly 40-m-thick stratigraphic interval towards the top of the Balfour Formation culminating at the top of the first significant maroon-colored laminated mudrocks (within the basal strata of the Palingkloof Member). Subsequent sampling of isotope geochemistry and paleomagnetics (Ward et al., 2005) confirmed that the extinction of the *Dicynodon* Assemblage Zone fauna in the Karoo Basin is indeed synchronous with the end-Permian mass extinction recorded in the marine sections of China. Thus, although no radiometric dates are available for the PTB sections within the Karoo Basin, the marine record date of 251 Ma (Bowring et al., 1998) has been adopted for the level at which the majority of the Late Permian vertebrate taxa disappear.

The facies sequence through the Karoo PTB is interpreted as evidence for climatic warming and drying that caused lowering of groundwater tables and die-off of vegetation along the river banks and on floodplains, which in turn led to a switch from high to low sinuosity rivers (Ward et al., 2000) and periods of extreme drought (Botha and Smith, 2006). The new akidnognathid lived in the Karoo Basin during this time and, like the other survivors, may have been in some way drought-adapted (Smith and Botha-Brink, 2009).

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905

EUTHERIODONTIA Hopson and Barghusen, 1986
THEROCEPHALIA Broom, 1903
AKIDNOGNATHIDAE Nopsca, 1928
PROMOSCHORHYNCHUS Brink, 1954

Type Species—*P. platyrhinus* Brink, 1954.

Definition—All akidnognathids sharing a more recent common ancestry with *P. platyrhinus* than *Oliverosuchus parringtoni* (see Huttenlocker, 2009).

Revised Diagnosis—Autapomorphic in its possession of upper incisors and precanines bearing external longitudinal ridges and facets (in contrast to contemporary *Cerdops*, *Moschorhinus*); dental formula I5-pC(1-2)-C1- PC(5-6) / i4-c1-pc6; prefrontal broad anterior to orbit; parietal exposed posteriorly on occiput (shared with *Regisaurus*); sternum with weakly developed midventral ridge and lacking anterior facet for interclavicle and posterior notch.

Shares with *Oliverosuchus*: anterior border of orbit positioned on transverse midline of skull (also shared with scylacosaurids and basal baurioids); nasals bearing marked constriction at mid-length; well-developed mastoid process of opisthotic and squamosal, separated from quadrate process by deep groove (shared with some baurioids); moderately well-developed crista choanalisis, extending posteriorly from the upper canines nearly to the level of the anterior border of the suborbital vacuity. Differs from *Akidnognathus* in possessing smooth postcanines, bearing no facets or striae.

PROMOSCHORHYNCHUS PLATYRHINUS Brink, 1954
(Figs. 2–5)

Holotype—BP/1/484, anterior skull roof and palate.

Referred Specimens—SAM-PK-K10014 (present specimen), nearly complete skull, mediolaterally compressed and lacking left zygomatic arch, left and right dentaries, right postdentary bones, associated postcranial material comprising much of the anterior skeleton (including pectoral girdles and forelimb), tibia, fibula, isolated podials; RC 116, nearly complete skull with articulated lower jaw, missing dorsal skull roof and intertemporal region (see Mendrez, 1974b); CGP R85, anterior skull roof (see Mendrez, 1974b).

Locality and Horizon—SAM-PK-K10014 was collected from the lowermost *Lystrosaurus* Assemblage Zone (Lower Triassic), Palingkloof Member, Balfour Formation, Beaufort Group, Karoo Supergroup; Bethel 763, Bethulie District, Free State Province, South Africa.

Diagnosis—As for genus.

DESCRIPTION

The specimen described here (Figs. 2–5) includes a nearly complete skull, lower jaws, and portions of the postcranial skeleton (including disarticulated vertebrae, ribs, sternum, interclavicle, both scapulocoracoids, and partial forelimb and hind limb elements including disarticulated podials). The cranium is slightly compressed mediolaterally, missing its left zygomatic arch, and is closely associated with and partially obscured by the right dentary and postcranial material on its right side. Loose articulation of the braincase and scapulocoracoid, as well as the presence of incompletely fused neurocentral sutures, suggests that the specimen represents a subadult (Kemp, 1986). The palatal region is largely obscured. A list of standard cranial measurements is provided in Table 1 and compared to those of some selected PTB therocephalians.

Anterior Skull Roof

The antorbital region of SAM-PK-K10014 is relatively long and narrow, with a straight dorsal margin in lateral view. The major bones of this region are well preserved and articulated in their natural positions (Fig. 4). Anteriorly, the premaxilla bears a tall dorsal process that bows anteriorly to extend slightly rostral to the incisors, forming a slightly recumbent rostrum, as in most eutherococephalians. Ventrally, the alveolar margin of the premaxilla lacks an anterior upturning and is relatively horizontal. The precise position of the premaxillary foramen could not be determined.

The septomaxilla is a large element and is highly visible within the external naris on both sides of the skull, although it is best preserved on the right (Figs. 2A, 3A). It has a well-developed internarial process and a large facial exposure, broadly contacting the premaxilla ventrally. Additionally, the external naris is relatively large, being greater than 50% of the diameter of the orbit. These features are similar to the condition reported in the akidnognathids *Oliverosuchus*, *Promoschorhynchus*, and *Moschorhinus* (Huttenlocker, 2009). Enlarged facial exposure of the septomaxilla, overlapping the premaxilla, accompanied by large, anteriorly facing external nares, are considered diagnostic of the Akidnognathidae clade (Huttenlocker, 2009).

The foramina of the narial region are well preserved in SAM-PK-K10014 and merit some attention. Among therocephalians, the premaxillary and septomaxillary foramina have been examined in detail in *Moschowhaisia* (Tatarinov, 1964), *Oliverosuchus* (Findlay, 1968), *Regisaurus* (Mendrez, 1972), and *Ictidostoma* (Hillenius, 2000). The terminology of Hillenius (2000) is followed here. A large septomaxillary foramen is present and is bordered laterally by the maxilla and medially by the septomaxilla. Within this foramen is the posterior orifice of the septomaxillary canal, which pierces through the septomaxilla and emerges at its anterior orifice located near the internarial process. The septomaxillary canal has been most recently suggested to have contained the nasolacrimal duct, which may have drained orbital fluids to the vomeronasal organ (Hillenius, 2000).

The maxilla shares a suture anteriorly with both the septomaxilla (contributing to the septomaxillary foramen) and the premaxilla (bordering an additional neurovascular foramen). It bears a moderately high, broad facial plate dorsal to the alveolar margin. The height of the maxilla in the present specimen is greater than 40% its length, which is consistent with non-baurioid eutherococephalians. By comparison, basal baurioids (e.g., *Ictidosuchoides*,

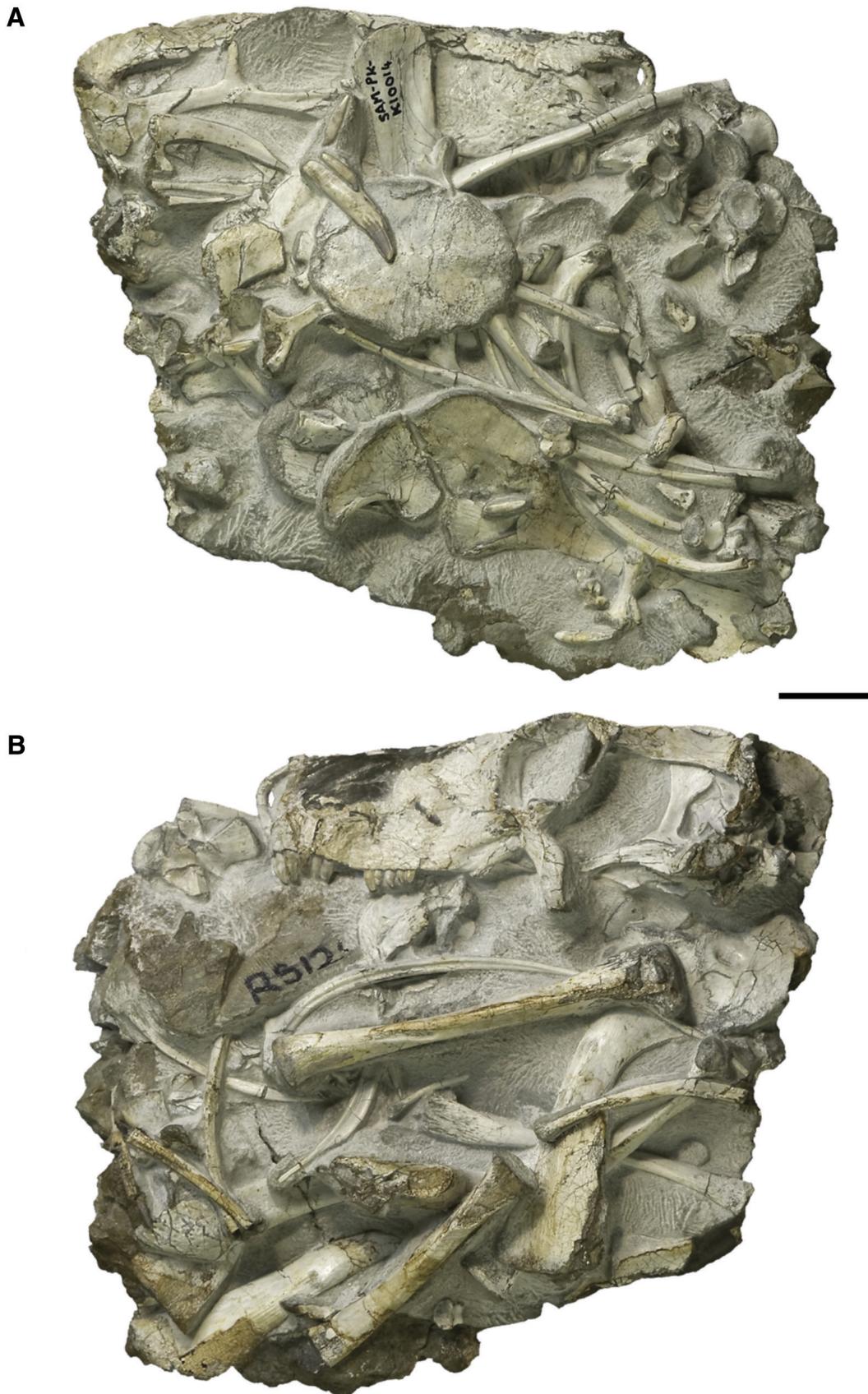


FIGURE 2. Photographs of *Promoschorhynchus* cf. *P. platyrhinus* (SAM-PK-K10014) in **A**, right and **B**, left lateral views. Scale bar equals 20 mm.

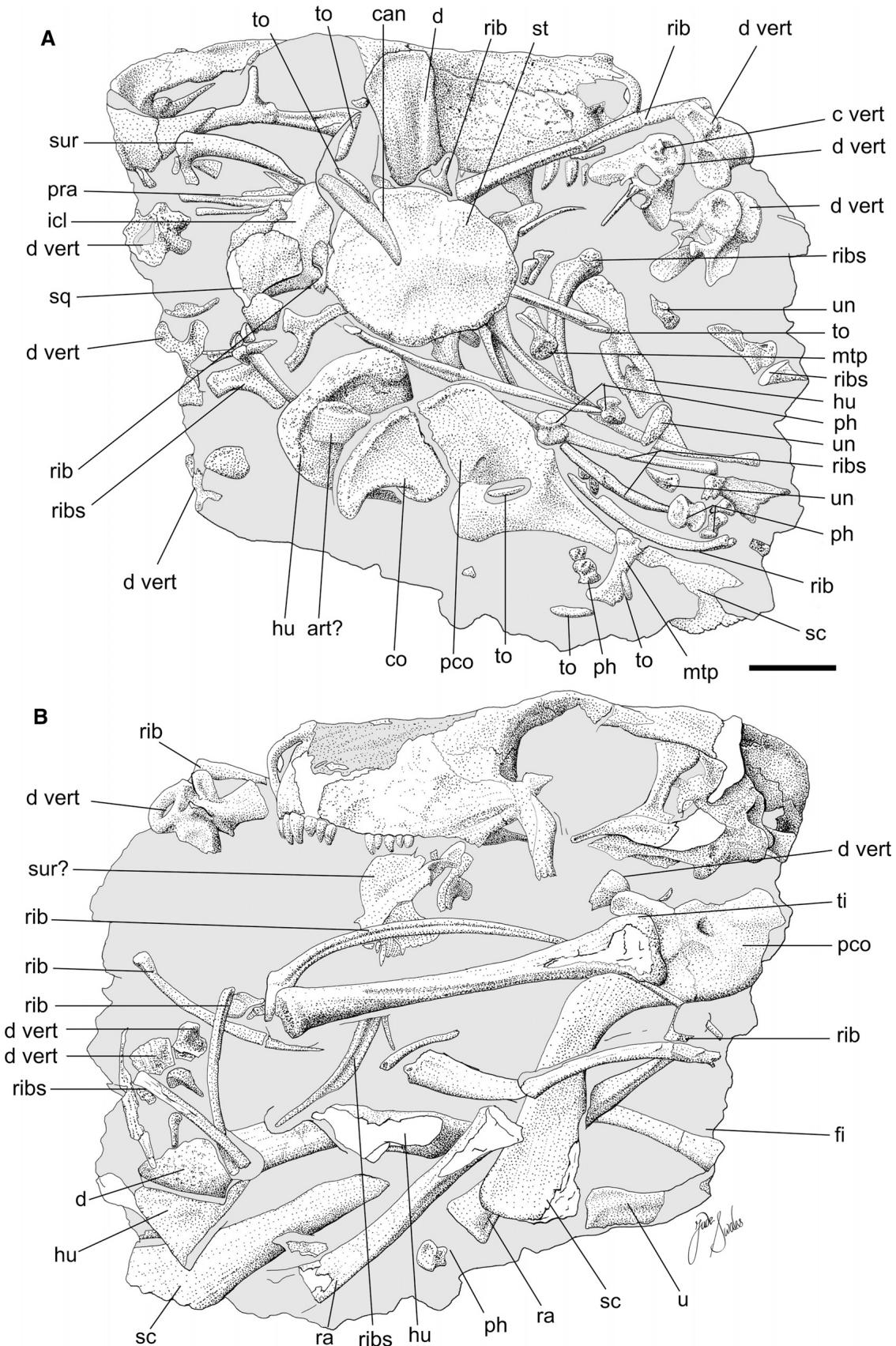


FIGURE 3. Interpretive drawings of *Promoschorhynchus* cf. *P. platyrhinus* (SAM-PK-K10014) in **A**, right and **B**, left lateral views with individual elements labeled (see text for abbreviations). Scale bar equals 20 mm.

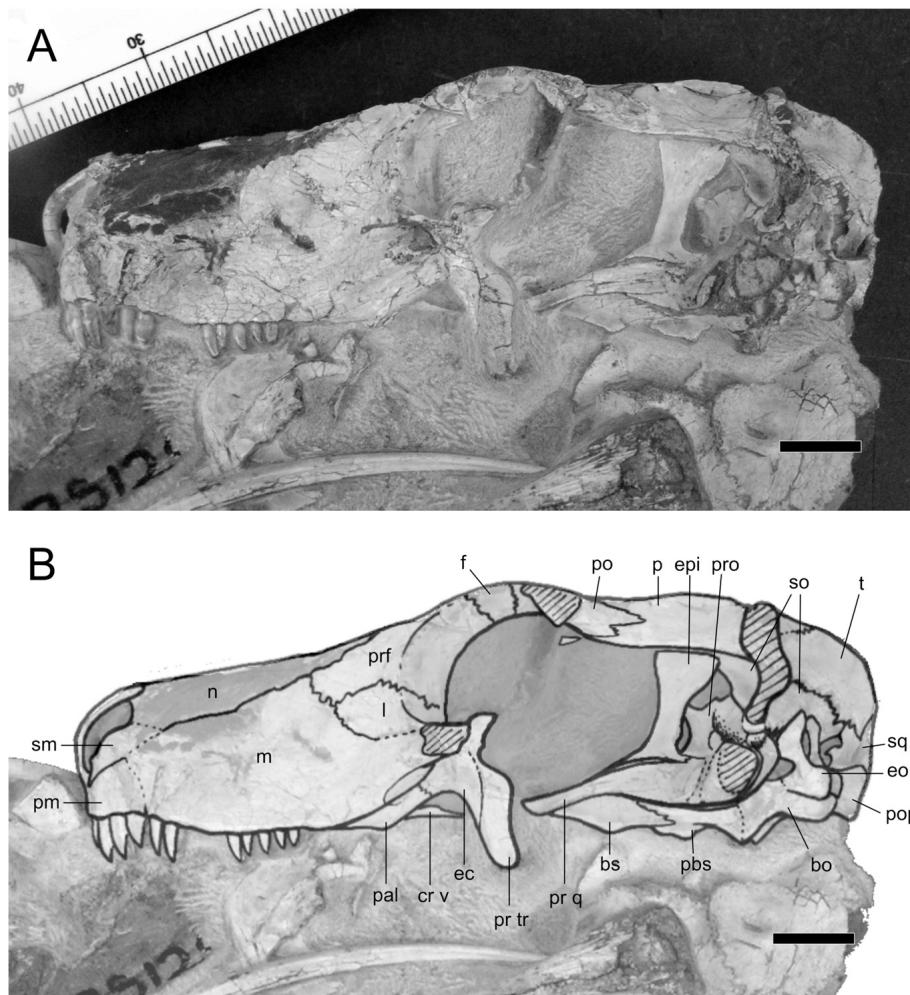


FIGURE 4. Skull of *Promoschorhynchus* cf. *P. platyrhinus* (SAM-PK-K10014). A, Photograph of skull in left lateral view; B, photograph with overlay of sutures and individual cranial elements (see text for abbreviations) in left lateral view. Scale bars equal 10 mm.

Ictidosuchops, *Regisaurus*) typically present a low maxilla having a height less than 40% its length (Huttenlocker, 2009). In dorsal view, the maxilla is slightly constricted behind the dominant canine, although the full extent of this constriction is uncertain due to transverse compression of the skull. The maxilla also bears numerous, radially oriented grooves and foramina on the external surface of the facial plate (Figs. 2A, 3A). Such foramina are common among eutheriodonts and can be found in both the maxilla and anterior portion of the dentary. Although the significance of the foramina is uncertain, it has been suggested that a maxillary plexus of the trigeminal nerve received signals from tactile vibrissae or ‘amplifying receptors’ via these foramina (Findlay, 1968:50–51). Recently, the presence of a maxillary canal communicating with a posterior and anterior sinus has been identified in an akidnognathid therocephalian (Sigurdsen, 2006). Sigurdsen (2006) suggested that this system in therocephalians and cynodonts, presumably housing the maxillary branch of the trigeminal nerve, may be homologous to the infraorbital canal of mammals.

Dorsally and medially, the maxilla contacts the nasal. The nasal is very long and narrow, comparable to the condition seen in the baurioid *Ictidosuchoides* (pers. observ.). It is bordered posteriorly by the prefrontal and frontal bones. There is no nasal-lacrimal contact, as in most therocephalians (a possible exception being *Tetracynodon darti*; personal observation). The dorsal surface bears a small midsagittal crest (‘frontonasal crest’ of

Huttenlocker, 2009), usually present in akidnognathids and whaitsiids. The frontal-nasal suture is broadly W-shaped. The anterior portion of the left nasal is broken, revealing an internal mold of the ventral surface of the nasal formed by a mudstone infilling of the nasal cavity. A longitudinal groove indicates the presence of a narrow ridge, located anterodorsally and extending slightly laterally from the ventral surface of the nasal bone. Among therocephalians this feature is significant, because a similar anteriorly located ridge has been identified only in *Akidnognathus* (Brink, 1960b), *Moschowhaitsia* (Tatarinov, 1963), and the scylacosaurid *Glanosuchus* (Hillenius, 1994). This configuration was distinguished from the olfactory turbinal ridges of earlier synapsids (Romer and Price, 1940) and interpreted as evidence of respiratory nasoturbinals in a nonmammalian synapsid by Hillenius (1994). The condition observed here is identical to other therocephalians, plus the gorgonopsian *Leontocephalus* and some cynodonts (Hillenius, 1994). An ossified ridge for the maxilloturbinals was also described and figured in a single specimen of *Glanosuchus* (Hillenius, 1994:fig. 11), although subsequent investigations have failed to locate maxilloturbinal ridges in other therocephalian taxa (Sigurdsen, 2006). Hillenius (1994) suggested that such structures arose independently in therocephalians and cynodonts during the Late Permian. However, the homology of these structures to mammalian respiratory turbinals is controversial and remains uncertain. The presence of maxilloturbinals in SAM-PK-K10014 cannot be confirmed at present.

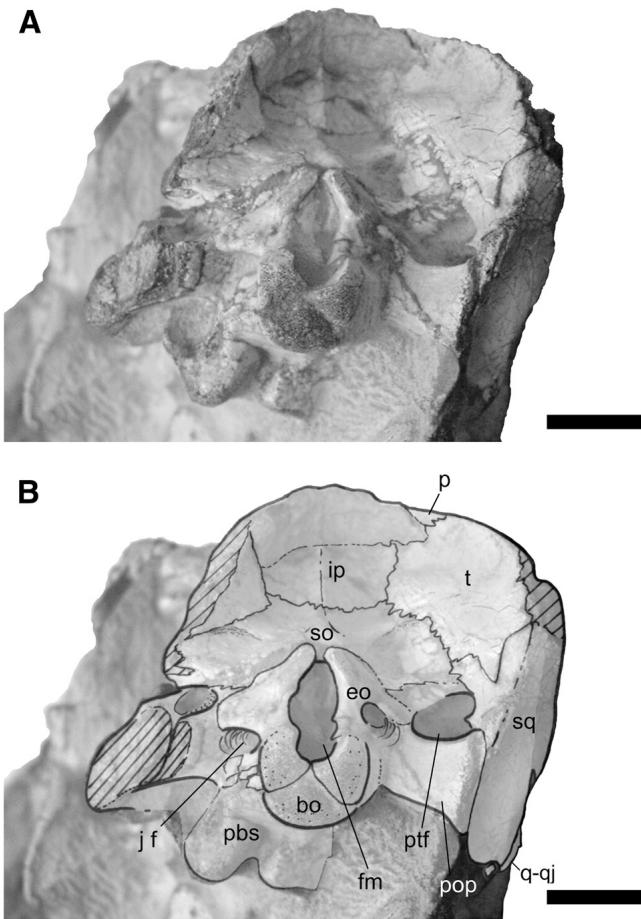


FIGURE 5. Skull of *Promoschorhynchus* cf. *P. platyrhinus* in occipital view. **A**, Photograph of occipital region; **B**, photograph of occiput with overlay of sutures and individual cranial elements (see text for abbreviations). Scale bars equal 10 mm.

Circumorbital Region

The orbits are relatively large in SAM-PK-K10014, being nearly the diameter of the temporal fenestrae (as in *Ictidosuchoides*, *Regisaurus* and other baurioids). However, this may be due to the immaturity of the individual. The anterior border of the orbit is positioned at the anteroposterior midline of the skull as in scylacosaurids and baurioids. The orbital border is formed by the lacrimal, prefrontal, frontal, postorbital, and jugal. A post-frontal bone is absent, as in all eutheriocephalians (Hopson and Barghusen, 1986; Huttenlocker, 2009; polymorphic in *Hofmeyravatus*). Dorsally, the prefrontal and postorbital do not contact each other, such that the frontal makes a moderate contribution to the dorsal orbital wall. A diminutive midsagittal crest is present on the frontal and narrowly continues anteriorly onto the nasal, as in akidnognathids and whaitsiids. Despite the large size of the orbits, the interorbital region is relatively broad when compared to other Permo-Triassic therocephalians (see Table 1). Whereas the interorbital distance is proportionately wide, the postorbital bar is extremely thin such that it is damaged on the left side of the skull. A narrow postorbital bar forms the posterior border of the orbit and has a contribution from the postorbital dorsally and the jugal ventrally. Such a delicate postorbital bar is uncommon in akidnognathid eutheriocephalians and may be a juvenile feature as it is similarly narrow in subadults of the

akidnognathid *Olivierosuchus* (e.g., BP/1/3849). Derived baurioids such as *Bauria*, *Ericiolacerta*, and *Tetracycynodon* apparently lack a complete postorbital bar (Huttenlocker, 2009).

The anteroventral border of the orbit is composed mainly of the lacrimal anteriorly and the jugal posteriorly. The suborbital bar is very shallow and formed almost entirely by the jugal, which extends rostrally just posterior to the anterior orbital margin where it meets the lacrimal. This condition appears to be common among eutheriocephalians, although the jugal extends beyond the anterior orbital margin in the derived baurioids *Ericiolacerta* and *Bauria* as in more primitive therocephalians and gorgonopsians (Huttenlocker, 2009).

Temporal Region

Just posterior to the orbit and suborbital bar, the jugal and squamosal form the zygomatic arch. The arch is intact on the right side of the skull. In dorsal view, it is widest toward its posterior extent, producing a somewhat triangular skull (a characteristic feature of Therocephalia). In lateral view, the zygomatic arch is shallow and slightly bowed, having a concave ventral margin throughout its length. The arch continues posteriorly toward the posteroventral process of the squamosal. Ventrolaterally, this process bears a notch housing the ventral portion of the quadrate, which has been figured in *Olivierosuchus* (Brink, 1965:fig. 49; Kemp, 1972:fig. 5b) and *Regisaurus* (Mendrez, 1972:figs. 4, 7), but has been most widely noted in the genus *Theriognathus* (Kemp, 1972). Contrary to Kemp (1972) and Botha et al. (2007), the ‘quadrate notch’ is not unique to *Theriognathus* and cynodonts, and is well preserved on the right side of the skull in articulation with the quadrate-quadratojugal complex in SAM-PK-K10014. The squamosal also appears to bear a medially directed prootic process, a ubiquitous feature in scylacosaurids and eutheriocephalians (absent in lycosuchids and cynodonts among eutheriodonts). The precise structure of the prootic process and pterygo-paroccipital foramen, however, cannot be appropriately characterized due to crushing. The stapes cannot be observed in the specimen.

The intertemporal region is very narrow and the parietal makes up its dorsal border, as in all eutheriodonts. The temporal fenestrae and parietal crest are somewhat expanded antero-posteriorly. The crest is nearly half the length of the temporal fenestra. A moderately large parietal foramen is present between the paired parietals and is bound posterolaterally by the parietal crest. In lateral view, the dorsal margin of the parietal crest is only moderately developed, as in most baurioids (e.g., *Regisaurus*). By contrast, the parietal crest of other adult eutheriocephalians is generally high with a steep posterodorsal inclination (Huttenlocker, 2009).

Braincase and Occiput

Much of the braincase, including the epitylgoid, is visible in left lateral view because the corresponding zygomatic arch is not preserved (Fig. 4). The occiput is well preserved and illustrated in Figure 5. The epitylgoid is a tall, blade-like element situated dorsal to the quadrate process of the pterygoid. The ascending process is only slightly expanded anteroposteriorly but widens toward its dorsal contact with the parietal. It is very similar to that of *Ictidosuchoides* and *Regisaurus* in its dimensions, but lacks an ossified posterior apophysis. The posterior apophysis appears to have a spotty distribution in therocephalian phylogeny, because it is present in taxa as disparate as the akidnognathids *Moschorhinus* and *Promoschorhynchus*, whaitsiids, and the baurioid *Regisaurus*. The absence of an ossified posterior apophysis in SAM-PK-K10014 is surprising given its presence in other specimens of *Promoschorhynchus* (i.e., RC 116). This may either represent retention of the plesiomorphic eutheriocephalian condition

TABLE 1. Cranial measurements of SAM-PK-K10014 compared with selected PTB eutherococephalians.

Reference	Akidognathidae						Bauinfoidea		
	SAM-PK-K10014 (present specimen)	<i>Promoschorhynchus</i> (BP1484) Brink, 1954)	<i>Promoschorhynchus</i> (RC 116) Mendrez, 1974b)	<i>Cerdops</i> (Broom, 1948)	<i>Oliverosuchus</i> (Brink, 1965)	<i>Ictidosuchops</i> (Brink, 1960, 1965)	<i>Tropidostoma-</i> <i>Dicynodon</i> AZ	<i>Tropidostoma-</i> <i>Dicynodon</i> AZ	<i>Regisaurus</i> (Mendrez, 1972)
Interval	<i>Lystrosaurus</i> AZ	<i>Dicynodon</i> AZ	<i>Dicynodon</i> AZ	<i>Dicynodon</i> AZ	<i>Dicynodon</i> AZ	<i>Lystrosaurus</i> AZ	<i>Lystrosaurus</i> AZ	<i>Lystrosaurus</i> AZ	<i>Lystrosaurus</i> AZ
Maximum skull length	123	—	~135	~135	102	103	139	119	
Maximum breadth	>34	—	~100	~80	66	64	79	73	
Minimum interorbital width	23.5	—	—	—	21	18	20	17	
Minimum intertemporal width	11	—	—	—	10	12	10	11	
Distance between anterior border of Pmx and anterior orbital border	~58	—	~66	—	49	52	70	59	
Distance between anterior border of Pmx and anterior orbital border	~84	—	—	—	~70	~70	—	85	
Breadth of rostrum at level of maximum constriction	>19	~40	~39	—	27	22	27	27	
Maximum length of parietal crest	~13	—	—	—	16	~10	—	—	10
Maximum length of maxillary dentition	~24	26	~27	—	~20	—	—	—	32
Total length of postcanine tooth row	11.5	16	~14	—	~8	~20	~25	24	
Interorbital width/max skull length	19%	—	—	—	20%	17%	14%	14%	
Antorbital length/max skull length	~47%	—	~48%	~40%	~48%	51%	50%	50%	
Dental formula	15-pC2-C1-PC5	15-pC1-C1-PC5	15-pC5/i4- cl-pc6	14-pC1(?)-C1- PC3	16-pC2-C1-PC3	16-pC2-C(1-2)- PC(8-9)	16-pC2-C(1-2)- PC9+	16-C1-PC10	

Measurements for *Oliverosuchus* and *Ictidosuchops* updated from Brink (1960, 1965). Measurements are in millimeters.

or a juvenile condition in which the posterior apophysis was not yet fully ossified. The weakly ossified nature of the braincase in the current specimen supports the latter hypothesis.

Posterior to the epitylgoid is the prootic, which is bound laterally by the squamosal, dorsally by the supraoccipital, and posteroventrally by the opisthotic and parabasisphenoid. The lateral processes of the prootic enclose the pterygo-paroccipital foramen as in all scylacosaurids and eutheriocephalians (“Scylacosaura” of van den Heever, 1994). A well-developed anterodorsal process extends anteriorly within the incisura prootica and only slightly overlaps with the ascending ramus of the epitylgoid in lateral view. Its contribution to the fenestra ovalis cannot be observed.

The prootic articulates dorsally with the supraoccipital. The supraoccipital extends anteriorly and dorsally where it shares a suture with the epitylgoid (previously reported in *Ictidosuchops*, *Promoschorhynchus*, and *Regisaurus*; Mendrez, 1972, 1974), but it is also well exposed posteriorly on the occipital surface. In occipital view, it is a very short, broad bone, bordered by the interparietal, tabular, squamosal, opisthotic, exoccipital, and foramen magnum. Dorsally, the extent of the interparietal (= postparietal) is uncertain because it is largely obscured by matrix (Fig. 5). However, a portion of the parietal can be seen making a contribution to the occipital surface. An occipital contribution from the parietal is also known in the baurioid *Regisaurus*. The tabular, located lateral to the supraoccipital and interparietal, appears as a tall bone making a significant contribution to the lambdoidal crest dorsolaterally. Ventrally, the tabular is somewhat restricted and does not extend below the posttemporal fenestra, nor does it contact the opisthotic. The tabular is bordered ventrolaterally by the squamosal.

Together, the squamosal and opisthotic border the posttemporal fenestra. In posterior view, the fenestra is bound dorsally by the posterodorsal process of the opisthotic and ventrally by the paroccipital process of the opisthotic. The paroccipital process is preserved on both sides of the skull (Fig. 5) and, in spite of slight crushing on the left side, maintains a predominantly horizontal transverse orientation. The process demonstrates a shallow groove on its dorsal surface, as in all eutheriocephalians. The paroccipital process articulates laterally with the squamosal, and forms a vertically oriented ridge just medial to the external auditory meatus. This arrangement resembles the ‘mastoid process’ of other specimens of *Promoschorhynchus* and *Oliverosuchus*, and is less prominent than that of *Ictidosuchops* (Crompton, 1955) and *Regisaurus* (Mendrez, 1972).

Medial to the paroccipital processes of the opisthotic, the exoccipitals, basioccipital, and supraoccipital form the margin of the foramen magnum. Lateral to the foramen magnum, the exoccipital is a triangular bone in posterior view, having a lateral process and medial proatlas tubercle in addition to its contribution to the occipital condyle. It is pierced by a small foramen just medial to the jugular foramen. Ventral to the foramen magnum, the occipital condyle is a tripartite structure, formed by the paired exoccipitals and unpaired basioccipital.

Palate

As preserved, the specimen does not permit a complete description of the palatal region. However, a few notable features of the palate can be addressed because they are observable in left ventrolateral view (see Fig. 4). Suborbital vacuities are present and bordered by the palatine, ectopterygoid, and pterygoid. The vacuities may have been somewhat small, although it is difficult to determine their size precisely because of the mediolateral compression of the skull. Suborbital vacuities are present in all Therocephalia, except adult *Theriognathus* and the akidnognathid *Euchambersia*.

The posterior portion of the left palatine is visible in lateral and ventrolateral views (Fig. 4). It preserves a portion of the

crista choanalis that spans from the lateral borders of the choana to the posterior extent of the palatine, where it meets the ectopterygoid and the anterior border of the suborbital vacuity. In akidnognathids, the crista often is well developed and may include a contribution from the ectopterygoid, but only extends as far posterior as the mid-palatine in a few taxa (e.g., *Moschorhinus*). The long crista choanalis of SAM-PK-K10014, which nearly contacts the anterior border of the suborbital vacuity, is consistent with that figured for *Promoschorhynchus platyrhinus* (Mendrez, 1974b, 1975; Sigurdsen, 2006).

The pterygoid transverse process (Fig. 4) is well exposed in left lateral view. It is positioned below the midpoint of the orbit and is expanded posterolaterally, with a strong ventral orientation as in most therocephalians. There are no teeth present on the transverse process. Posterior to the transverse process are the basisphenoid process and quadrate ramus, of which the latter supports the epitylgoid. Neither ramus bears denticles.

Lower Jaw

The lower jaw of SAM-PK-K10014 is disarticulated and only portions of the left and right dentary, right surangular, and fragmentary right prearticular could be identified. The anterior-most portion of the left dentary is visible in Figure 3. It has a slender ramus, but deepens very slightly toward the mental region. Instead of narrowing anteriorly, as it does in hofmeyriids, whaitsiids, and baurioids, the dentary bears a slight mental protuberance. There is also pronounced pitting on the surface of the dentary in this region, as on the maxilla. Individual teeth are not preserved within their dentary alveoli, making an accurate lower tooth count impossible to determine at present.

The posterior portion of the right dentary is visible (Fig. 2), where it has become disarticulated, rotated so that its medial side faces laterally, and overlies the anterior border of the right orbit. The coronoid process is very well developed and broad, with a straight terminal end consistent with that figured for *P. platyrhinus* by Mendrez (1974b). The medial surface reveals a broad fossa that is confluent with a narrow fissure for reception of the surangular, coronoid, and prearticular (Mendrez, 1974b:fig. 8). The surangular is very thin and highly curved, having a concave ventral margin. There appears to have been a lateral mandibular fenestra, as in all eutheriocephalians (see Fig. 6). The prearticular is a narrow, splint-like element and is very fragmentary in the specimen.

Dentition

The upper dentition of SAM-PK-K10014 consists of five premaxillary teeth, as well as two precanines, one canine, and five postcanines in the maxilla. All of the tooth crowns bear a single cusp. The formula for the lower dentition cannot be determined. However, Mendrez (1974b) previously identified four lower incisors, one canine, and six small postcanines in the dentary of *P. platyrhinus* (based on RC 116; Table 1).

The incisors are moderate in size and not as exaggerated as those in *Cerdops* or *Moschorhinus*. The number of upper incisors and caniniforms (precanines and canines) resembles conservative akidnognathids, such as *Oliverosuchus* (contra Findlay, 1968), and other specimens of *Promoschorhynchus*, although *Oliverosuchus* and more derived akidnognathids (e.g., *Cerdops* and *Moschorhinus*) drastically reduced the number of postcanines. The Upper Permian *Akidnognathus parvus* is unique in the combination of only one maxillary precanine, retention of a primitively high postcanine tooth count (as many as seven) in which all marginal teeth bear longitudinal striae, and highly procumbent, striated lower incisors (Brink, 1960b). The upper incisors of SAM-PK-K10014 are slightly spatulate, bearing smooth (i.e., non-serrated) mesial and distal cutting ridges and a series of longitudinal facets (inaccurately termed ‘longitudinal grooves’

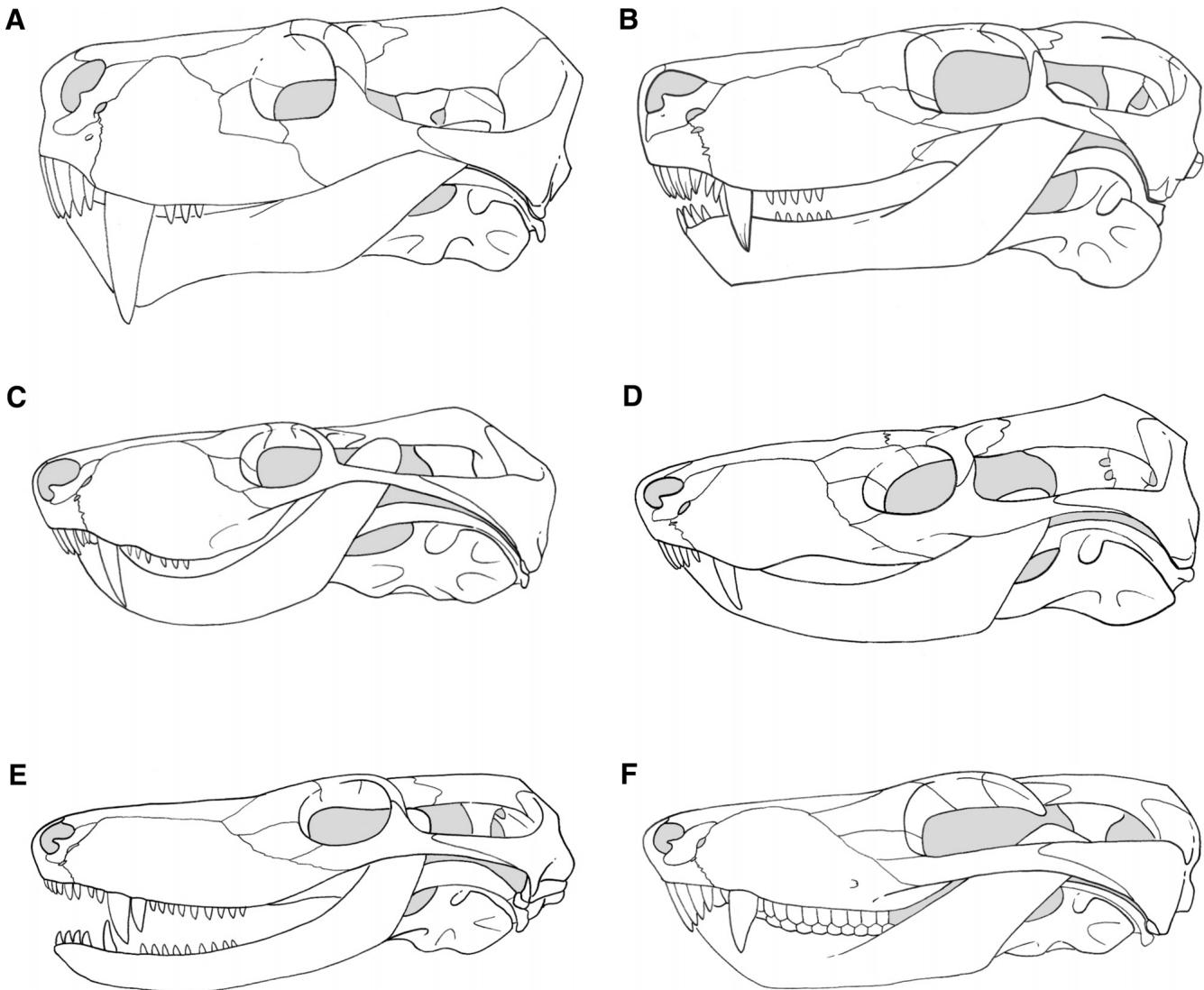


FIGURE 6. Cranial restorations of selected therocephalian taxa in left lateral aspect. **A**, The akidognathid eutheriocephalian *Moschorhinus kitchingi* (modified from Durand, 1991); **B**, akidognathid *Promoschorhynchus* (based on SAM-PK-K10014 and RC 116); **C**, hofmeyriid *Mirotenthes digitipes*; **D**, whaitsiid *Theriognathus microps*; **E**, basal ‘ictidosuchid’ baurioid *Ictidosuchoides longiceps* (modified from Hopson, 1994); **F**, derived baurioid *Bauria cynops* (modified from Brink, 1963). Skulls not to scale.

by Huttenlocker, 2009). The two maxillary precanines are also faceted, but these teeth are slightly smaller than the incisors and appear to lack cutting edges. A moderately well developed canine tooth, polygonal in cross-section, is disarticulated and associated with the right side of the skull. It also demonstrates longitudinal facets, but only bears a single, smooth cutting edge along its distal margin. The five postcanines are the smallest set of teeth within the maxilla, being subequal in size and about two-thirds the length of the incisors. They are simple, subcircular in cross-section, and lack facets as well as cutting edges.

Postcranial Skeleton

Due to the disarticulated state of the postcrania, it is not possible to provide an accurate vertebral count. However, there are at least seven anterior dorsal vertebrae preserved in the specimen. The amphicoelous dorsal vertebrae are lightly built, and the centrum and overlying neural arch appear to have been preserved in the process of fusing, indicating that the specimen represents

a subadult. The neural spine is tall and exhibits a square profile with a flat top when viewed laterally. The dorsoventrally deep transverse processes are predominantly situated on the lateral portions of the neural arch, only slightly extending ventrally onto the centrum, and are angled posterolaterally with a very strong dorsal inclination. The lateral portion of the transverse process extends dorsal to the zygapophyses. Likewise, the zygapophyses exhibit a strong dorsal inclination. At least two vertebrae show extreme inward rotation of the prezygapophyses, so that the orientation of the articular surfaces with their corresponding postzygapophyses was vertical (rather than horizontal). This pattern of articulation likely would have limited lateral flexion of the anterior trunk and promoted greater dorsoventral flexion. A single, small caudal vertebra is preserved overlying one of the anterior dorsals (Fig. 2).

Numerous disarticulated ribs are scattered on both sides of the specimen. The ribs are extremely long and slender with a flattened, subtriangular cross-section and a long costal groove along the posterior surface of the shaft. The tuberculum is tall

and broad, corresponding to the high-angled transverse process to which it articulates, whereas the capitulum is comparatively slender, as in *Regisaurus* (Fourie and Rubidge, 2007).

The sternum is a large, flat, oval element, only slightly longer than it is wide. In contrast to *Regisaurus* (Kemp, 1986; Fourie and Rubidge, 2007) and *Olivierosuchus* (Brink, 1965), the anterior border is straight with no indentation for the overlapping interclavicle. Likewise, there is no posterior notch, which is usually present in regisaurids (Kemp, 1986) and *Olivierosuchus* (Brink, 1965; J. Botha-Brink, pers. comm., 2010). The ventral surface of the sternum preserves a weakly developed midline ridge that becomes more prominent posteriorly.

Though largely disarticulated, much of the pectoral girdle is preserved in the specimen, including the interclavicle and both scapulocoracoids. Clavicles could not be identified. The interclavicle is associated with the sternum (Fig. 2) where it is seen as a broad, shield-shaped bone. The posteromedial ridge is well developed on the ventral surface, as in *Eriolacerta* (Watson, 1931) and *Regisaurus* (Fourie and Rubidge, 2007). The procoracoid, coracoid, and scapula are loosely sutured in the specimen and are slightly disarticulated (Fig. 2A). The procoracoid is flat and bears a strong convex margin anteriorly. The procoracoid foramen is located dorsally near the procoracoid-scapula suture, but still resides well within the procoracoid, as in most eutheriocephalians (except *Tetracynodon*, *Eriolacerta*, and *Bauria* where it lays on the suture). Posteriorly, the procoracoid shares a broad suture with the blade-like coracoid. The coracoid-scapula suture is very narrow and most of the dorsal portion of the coracoid contributes to the glenoid fossa. The glenoid is highly concave with a strong posterior orientation. Dorsally, the scapular blade is very tall and slender, with an anteroposteriorly expanded dorsal end as in most eutheriocephalians. The scapula lacks an acromion process and lacks any indication for the attachment of a cleithrum along its anterior border. The apparent lack of an ossified cleithrum is noteworthy, because its presence has been documented in basal theropcephalians attributed to ‘*Scymnosaurus major*’ and *Pristerognathus* (Broom, 1936; Boonstra, 1964), the baurioids *Eriolacerta* and *Bauria* (Watson, 1931), and has been observed in a juvenile akidognathid likely allied to *Cerdops* (MCZ 8960; A.K.H., pers. observ.). Its absence in *Promoschorhynchus* and other eutheriocephalians (e.g., *Regisaurus*; Fourie and Rubidge, 2007) may suggest a phylogenetically labile distribution among theropcephalians.

The forelimbs are represented by two partial humeri, partial and nearly complete radii, and a very fragmentary proximal ulna (Figs. 2, 3). The humerus is relatively robust with expanded proximal and distal ends and a strong deltopectoral crest. The proximal crest was oriented vertically in life along a parasagittal plane, whereas 90° torsion of the shaft facilitated a more horizontal orientation of the distal end. The shaft is long and bears a single large, oval foramen near the expanded entepicondyle. However, the accompanying ectepicondylar foramen is apparently lacking in SAM-PK-K10014, as in all theropcephalians in which this element is known, with the possible exception of lycosuchids. The distal-most articular condyles of the humerus are not preserved. The radius is a slender bone with laterally expanded proximal and distal ends. The proximal end is slightly less expanded and bears a shallow articular facet to receive the humeral capitulum. A narrow ridge extends proximodistally along the anterior side of the shaft.

Little of the hind limb is preserved except for a single tibia and fibula (Fig. 3). The left tibia is very long and straight with expanded proximal and distal ends. The slender shaft is somewhat compressed mediolaterally and bears a sharp ridge that extends distally along the anterior surface. These features are identical to those illustrated by Kemp (1978:fig. 3) for *Regisaurus*. The fibula is an extremely slender and slightly bowed element, also with expanded proximal and distal ends. The distal end is slightly com-

pressed anteroposteriorly and laterally expanded, presumably for its articulation with the calcaneum (Kemp, 1978; Fourie and Rubidge, 2007).

Disarticulated podial elements scattered throughout the specimen include a slender metapodial and at least eight isolated phalanges. The more proximal phalanges are extremely shortened and wider than they are long, suggesting a compact foot. At least three terminal phalanges are present, which appear as flat but sharp unguals bearing light pitting toward their distal tips. The dorsoventrally flattened unguals resemble those of *Olivierosuchus* in their overall shape and breadth (J. Botha-Brink, pers. comm., 2010).

PHYLOGENETIC ANALYSIS

The phylogenetic relationships of eutheriodonts (including SAM-PK-K10014) were reconstructed based on a cladistic analysis of 32 therapsid taxa and a character matrix of 121 craniodental and postcranial characters. Characters 1–110 were taken from Huttenlocker (2009; herein abbreviated H2009). New characters 111–121 were included for the present study, and the matrix of H2009 was augmented (see Supplementary Data: Appendix S2; available online at www.vertpaleo.org/jvp/JVPcontents.html) to accommodate these characters, as well as the *Promoschorhynchus* specimens (RC 116 and SAM-PK-K10014) and the akidognathid *Cerdops* (RC 58).

The analysis was performed under the criterion of maximum parsimony using the tree-bisection-reconnection (TBR) branch-swapping algorithm on PAUP 4.0 beta 10 (Swofford, 1999). All characters were unordered and had equal weight. A heuristic search was performed using a random addition sequence with 100 replicates. Bootstrap resampling was also performed to observe additional support for recovered clades. A Kishino-Hasegawa (K-H) test (Kishino and Hasegawa, 1989) was also performed to test whether the distributions of character changes across the most parsimonious tree (MPT) were significantly more parsimonious than previously published alternative topologies (i.e., Abdala, 2007; Botha et al., 2007). For this purpose, a backbone constraint tree was constructed following the topology of Botha et al. (2007) and a consensus of trees retaining the backbone constraint topology (Fig. 7A) was saved and tested against the consensus of MPTs (Fig. 7B).

RESULTS AND DISCUSSION

The analysis recovered 12 equally parsimonious minimum length trees (tree length = 310; consistency index [CI] = 0.4935; retention index [RI] = 0.7516; rescaled CI = 0.3709), which differ only in the intra- and interrelationships of scylacosaurids and of the basal baurioids *Ictidosuchus* and *Ictidosuchops*. A strict consensus tree is shown in Figure 7B. The major theropcephalian clades, including the basal Lycosuchidae and Scylacosauridae and the eutheropcephalian groups Akidognathidae, Hofmeyriidae, Whaitsiidae, and Baurioidea, are generally supported (although Hofmeyriidae is shown to be paraphyletic). The resulting trees are illustrated in Figure 7 and in their temporal context in Figure 8.

Monophyly of Therocephalia

The recognition of Therocephalia as a monophyletic taxon has been of great interest recently. Whereas some early authors (Brink, 1960a, 1965) suggested a link between ‘scaloposauroid’ theropcephalians and cynodonts, thus nesting cynodonts within Therocephalia, Romer (1969) argued that the similarities between cynodonts and ‘scaloposaurs’ represent retentions of the plesiomorphic eutheriodont condition. Romer (1969) also argued that theropcephalians possess a number of shared derived features that exclude basal cynodonts from a theropcephalian

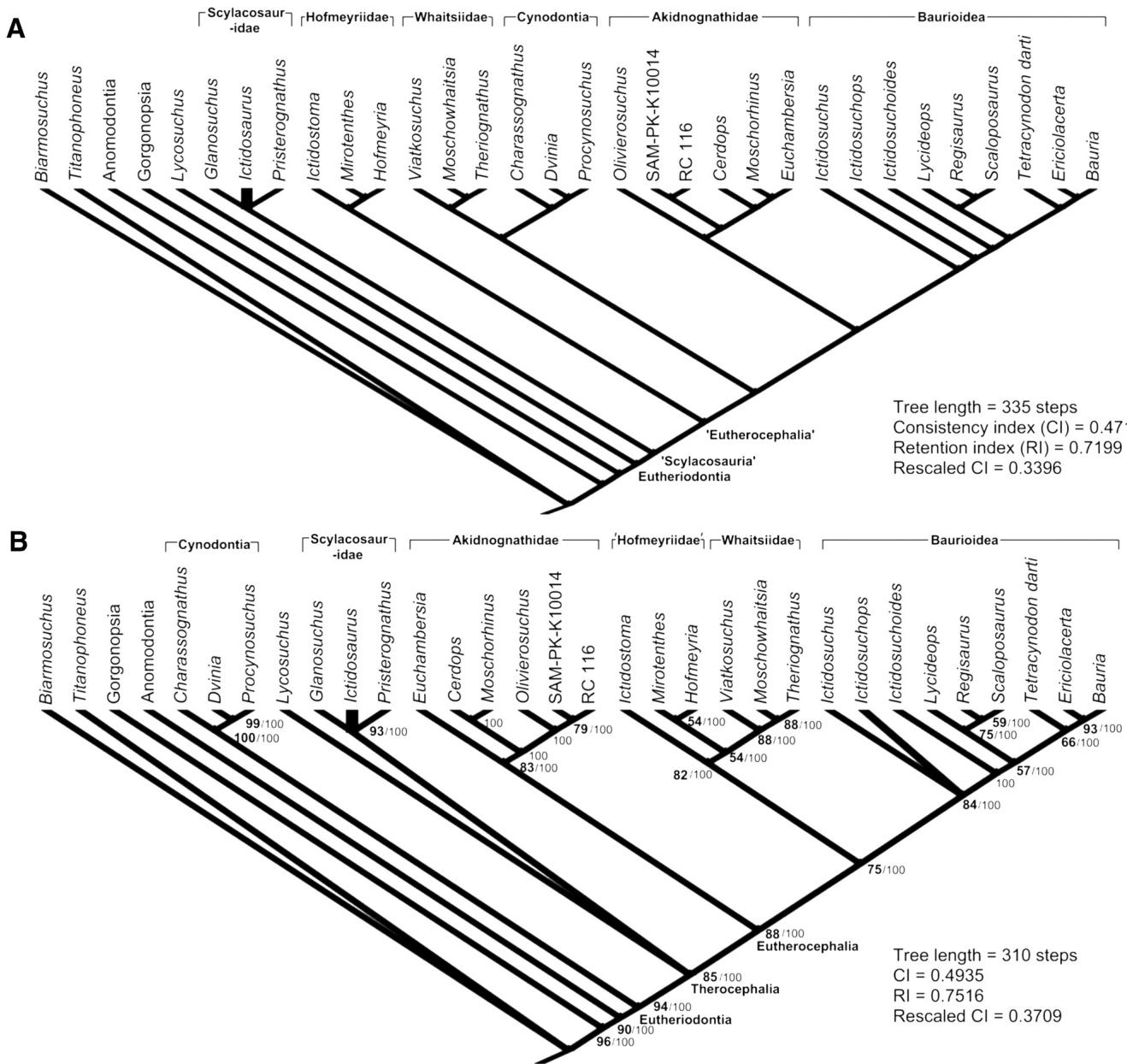


FIGURE 7. Hypotheses of the cladistic relationships of eutheriodont therapsids. **A**, Consensus tree from backbone constraint search using the ‘paraphyletic’ constraint topology of Botha et al. (2007) and Abdala (2007); **B**, strict consensus of 12 MPTs supporting a monophyletic Therocephalia (bold numbers at nodes indicate bootstrap values >50%; consensus indices are provided next to bootstrap values).

ancestry, a view that was adopted by Hopson and Barghusen (1986) in their first cladistic analysis of Eutheriodontia. A few authors have advocated a sister-taxon relationship between cynodonts and the whaitsiid therocephalian *Theriognathus*, largely based on the presence of an expanded epipterygoid ascending process and a quadrate notch in the squamosal (Kemp, 1972; Abdala, 2007; Botha et al., 2007). Nevertheless, bootstrap resampling supported a monophyletic Therocephalia in 85% of trees (compared to 67% in Huttenlocker, 2009), which may be due to the inclusion of more postcranial characters in the present study (Appendix S2, characters 113–121). In addition, the backbone constraint topology (Fig. 7A) of Botha et al. (2007) requires an additional 25 steps for a total of 335 steps ($P = 0.0051$). Thus, the ‘monophyletic Therocephalia’ tree is significantly more parsimonious according to the results of the K-H test. The study of H2009

and the present analysis support Romer’s (1969) and Hopson and Barghusen’s (1986) view of a monophyletic Therocephalia and its sister-taxon relationship with Cynodontia.

Previously offered unambiguous synapomorphies of Therocephalia include (1) vomer widest anteriorly at contact with premaxilla (H2009, 38); (2) large suborbital vacuities bound by palatine, pterygoid, and ectopterygoid (absent in *Theriognathus* and *Euchambersia*; H2009, 19); (3) ventromedian pterygoid tubercle or crest (H2009, 44); (4) posterolaterally expanded pterygoid flanges (reduced in *Euchambersia*; H2009, 46); (5) dorsal process of stapes reduced or absent (reportedly present in *Viatkosuchus*; H2009, 60); (6) sharp anterior process of dorsal iliac blade (H2009, 84); (7) pubis and ischium orientation horizontal with a broad puboischiatic plate (H2009, 85); (8) distinct trochanter minor present on femur (H2009, 87); (9) zygomatic arch lateral

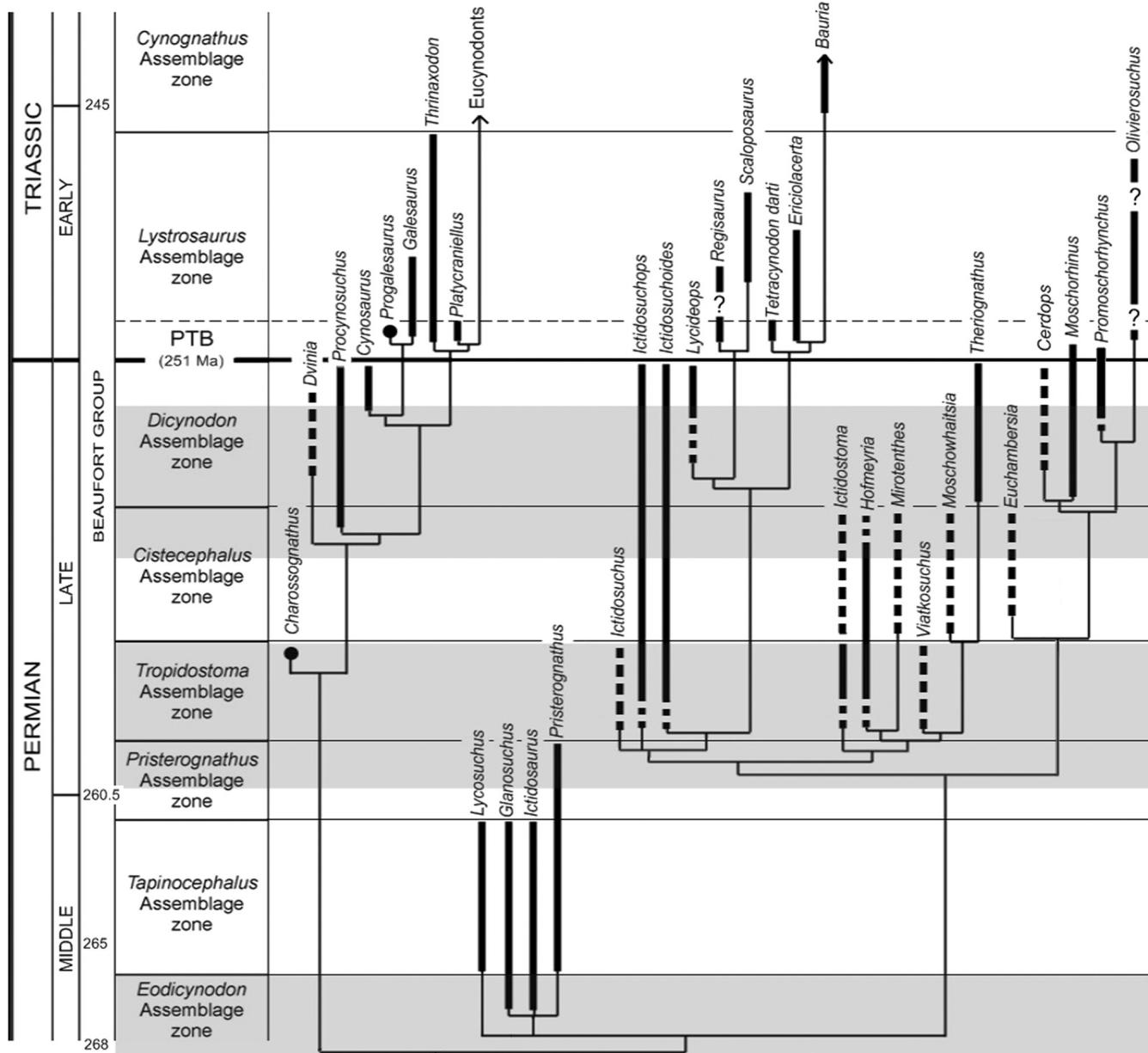


FIGURE 8. Consensus cladistic topology of Figure 7B superimposed onto stratigraphy of the Beaufort Group (Karoo Supergroup). Solid blocks represent observed stratigraphic ranges of OTUs. Dashed blocks represent approximate range of an OTU in which the precise duration is unclear within an interval. Question marks represent disjunct, disputed provenance. Solid dot represents a singleton occurrence. Gray shading indicates major intervals of hypothesized theriodont cladogenetic events prior to the PTB (Middle Permian, end-Middle Permian, and latest Permian diversifications). Dashed line indicates top of Palingkloof Member. Stratigraphic data updated from Botha and Smith (2006), Abdala et al. (2008), and Hutttenlocker (2009). PTB cynodont divergences follow Sidor and Smith (2004). Additional dates (indicated in millions of years [My]) are from Jin et al. (1997, 2000) and Retallack (2005).

expansion greatest at its posterior margin (H2009, 103); (10) lateral dentary sulcus or groove present (absent in hofmeyriids and *Therognathus*; H2009, 110).

Additional characters were offered, but are considered ambiguous due to their presence in other higher-level therapsid clades, including concave ventral margin of suborbital and zygomatic arch (also present in anomodonts; H2009, 19); palatal fenestra for lower caniniform confluent with internal naris (also present in gorgonopsians; H2009, 36); moderately expanded ascending process of epitygoid (variable and also present in cyn-

odonts; H2009, 51); splenial laterally obscured by dentary (either convergent in non-*Procynosuchus* cynodonts or plesiomorphic for Eutheriodontia with a primitive reversal in *Procynosuchus*; H2009, 71); stapedial foramen absent (convergent in anomodonts; H2009, 88). Further postcranial characteristics were discussed by Fourie and Rubidge (2007), including absence of an ectepicondylar foramen (present study, character 114), although this appears to be present in basal lycosuchids (A.K.H., pers. observ.); and caudal vertebral count reduced to less than fifteen (present study, character 119). Thus, as few as 10 and as many as

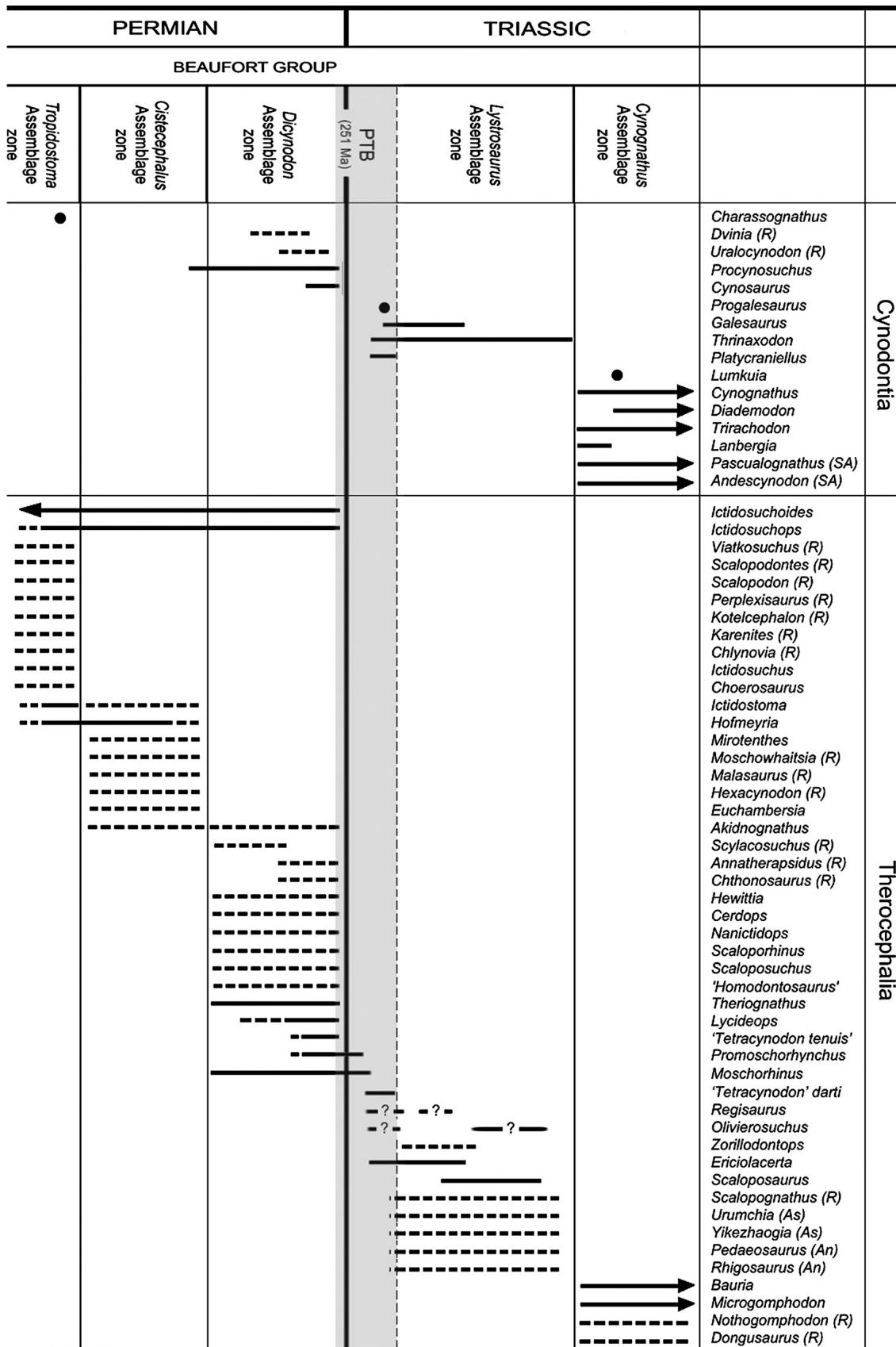


FIGURE 9. Stratigraphic distributions of Upper Permian–Lower Triassic cynodonts and theropcephalians in the upper Beaufort Group (Karoo Supergroup) and equivalent strata. Symbols follow Figure 8. All taxa occur within the Beaufort Group of southern Africa unless otherwise indicated: An = Antarctica-only; As = Asia-only; R = Russia-only; SA = South America-only. The gray-shaded interval bounding the PTB represents the duration of the Palingkloof Member of the Balfour Formation, or equivalent. Stratigraphic data are adapted from Rubidge (1995), Damiani et al. (2003), Sidor and Smith (2004), Tverdokhlebov et al. (2005), Botha and Smith (2006), Abdala et al. (2006, 2008).

17 osteological synapomorphies are currently recognized to diagnose Therocephalia.

Affinities of SAM-PK-K10014 among Akidnognathidae

Cladistic analysis recovered a sister-taxon relationship between RC 116 (see Mendrez, 1974b) and SAM-PK-K10014, supporting assignment of the latter to *Promoschorhynchus*. Within Akidnognathidae, RC 116 and SAM-PK-K10014 form a clade that is united with *Olivierosuchus* to the exclusion of *Moschorhinus* and *Cerdops* (Fig. 7B, C). Some of the characters shared between *Olivierosuchus* and *Promoschorhynchus* are highlighted in the above diagnosis and include presence of a well-developed mastoid process formed by distinct processes of the squamosal and opisthotic; anterior border of orbit positioned on the midline of skull; and a single functional precanine retained in adults (i.e., in contrast to the condition in *Moschorhinus*; Huttenlocker, 2009). Importantly, incomplete specimens of *Olivierosuchus* and *Promoschorhynchus* may be impossible to distinguish unless key generic features are preserved. Although we are confident in our assignment of SAM-PK-K10014 to *Promoschorhynchus*, some features suggest ontogenetic variability within the genus. For example, the specimen exhibits an additional precanine, as in *Cerdosuchus* (bearing two instead of a single precanine, in contrast to BP/1/484 and RC 116) and lacks an ossified posterior apophysis of the epityrgoid (in contrast to the condition in RC 116).

Diversity of Permo-Triassic Eutheriodonts

Permian Diversification—Huttenlocker and Marcot (2007) recognized three peaks in eutheriodont origination and extinction, which correspond to the three regions shaded in light gray in Figure 8. The first two of these events are coincident with the dogmatic ‘stages of diversification’ discussed by Broom (1948), Hotton (1991), and more recently by Abdala et al. (2008). Abdala et al. (2008) emphasized a Middle Permian (Roadian–Wordian) theriodont diversification that included the divergence of the basal therocephalian families Lycosuchidae and Scylacosauridae, and the origins of the higher taxon “Scylacosauria” (scylacosaurids + eutheriocephalians).

The second, early Late Permian, diversification is represented by the abundance of eutheriocephalian genera in strata overlying the *Tapinocephalus* Assemblage Zone (AZ) of southern Africa (i.e., *Pristerognathus*, *Tropidostoma*, and *Cistecephalus* AZs). The diversity of early eutheriocephalians in these strata suggests a divergence by the end-Middle Permian. Moreover, akidnognathids, hofmeyriids, and basal baurioids are inferred to have diverged during this second wave, whereas whaitsiids likely diverged in Laurasia (Russia) shortly thereafter (based on *Viatkosuchus* and *Moschowhaitsia*). However, it is possible that the temporal discordance between the first and second stages is due to poor stratigraphic resolution and the poorly resolved systematics of *Tapinocephalus* AZ theriodont faunas.

A third, Late Permian, diversification is marked by the wealth of derived eutheriocephalians and early cynodonts in the *Dicynodon* AZ. It is within this interval that some of the more derived genera, including *Theriognathus* and *Moschorhinus*, appear within preexisting families that were established in the second stage. Although not included in the current phylogenetic analysis, eutheriodont genera from outside the Karoo Basin conform to the pattern of diversification highlighted here (Fig. 9).

Boundary Crossing Lineages—Sidor and Smith (2004) suggested that at least two major cynodont lineages crossed the PTB, although no individual genus had been recorded from both Permian and Triassic strata in the Karoo. The results of the current study suggest that at least five eutheriocephalian lineages crossed the PTB (reduced from six lineages reported by Huttenlocker, 2009). As a result, many Triassic therocephalian genera found at

PTB localities, such as Bethel 763, represent members of pre-existing Late Permian lineages rather than earliest Triassic diversification (Fig. 8). More importantly, with regards to genus-level diversity, the recognition of SAM-PK-K10014 as pertaining to *Promoschorhynchus* suggests that fossils of at least two therocephalian genera span the PTB (viz. *Moschorhinus* and now *Promoschorhynchus*). Among therapsids, only the dicynodont *Lystrosaurus* shows a comparable pattern (Botha and Smith, 2007).

Shifts in the relative diversities of cynodonts and therocephalians across the PTB have long been documented (Abdala et al., 2008; Abdala and Ribeiro, 2010), although an explanation for this protracted wedge pattern has not been proposed. Therocephalians evidently exhibited lower rates of cladogenesis in the Early Triassic, as well as a significant drop in both taxonomic richness and disparity (Huttenlocker and Marcot, 2007) into the Middle Triassic. Ultimately therocephalians were surpassed in all measures of diversity by their cynodont relatives in the Middle and Late Triassic because this group speciated into a wide array of carnivorous and herbivorous forms (Abdala and Ribeiro, 2010).

CONCLUSIONS

A new record of *Promoschorhynchus* cf. *P. platyrhinus* (SAM-PK-K10014) has been documented on the basis of a nearly complete skull and partial postcranial skeleton from the lowermost Triassic Palingkloof Member of the Balfour Formation, South Africa. Cladistic analysis of 32 therapsid taxa and 121 craniotental and postcranial characters supports the position of the specimen within *Promoschorhynchus* and Akidnognathidae, within a monophyletic Therocephalia. Additional postcranial characters have helped to improve phylogenetic resolution within Therocephalia and further support the monophyly of the clade. The phylogenetic analysis presented here has also allowed for the reconstruction of ghost lineages and suggests at least seven lineages of eutheriodonts (cynodonts and therocephalians) crossed the PTB, the majority of which were therocephalian lineages derived from Late Permian lineages. In spite of their survival across the PTB, rates of cladogenesis in therocephalians appear to have decreased into the Early Triassic, whereas cynodonts continued to diversify during the Triassic. However, the reasons for such a protracted wedge pattern remain to be elucidated and its dynamics (competitive versus opportunistic replacement) should be further investigated in the context of the PTB.

ACKNOWLEDGMENTS

Jude Swales illustrated the specimen (Fig. 3). Hedi Stummer performed initial preparation, and Bruce Crowley helped with final preparation of the specimen. Christian Kammerer and Fernando Abdala provided important discussions of therocephalian taxonomy, and Jennifer Botha-Brink offered additional discussion and comparative material. Greg Wilson and Lauren Berg gave comments on early versions of the manuscript. We thank Randall Irmis, Christian Kammerer, and an anonymous reviewer for improving the content of the final manuscript. This study was supported by the University of Washington Department of Biology Snyder Award and the Society of Vertebrate Paleontology Richard Estes Award to A.K.H., the National Science Foundation (ANT-0838762) to C.A.S., and the National Research Foundation to R.M.H.S.

LITERATURE CITED

- 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., and A. M. Ribeiro. 2010. Distribution and diversity patterns of Triassic cynodonts (Therapsida, Cynodontia) in Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology* 286:202–217.
- Abdala, F., J. Neveling, and J. Welman. 2006. A new trirachodontid cynodont from the lower levels of the Burgersdorp Formation (Lower Triassic) of the Beaufort Group, South Africa and the cladistic relationships of Gondwanan gomphodonts. *Zoological Journal of the Linnean Society* 147:383–413.
- Abdala, F., B. Rubidge, and J. Van Den Heever. 2008. The oldest therocephalians (Therapsida, Eutheriodonta) and the early diversification of Therapsida. *Palaeontology* 51:1011–1024.
- Boonstra, L. D. 1964. The girdles and limbs of the pristerognathid Therocephalia. *Annals of the South African Museum* 48:121–165.
- Botha, J., and R. M. H. Smith. 2006. Rapid vertebrate recuperation in the Karoo Basin of South Africa following the End-Permian extinction. *Journal of African Earth Sciences* 45:502–514.
- Botha, J., and R. M. H. Smith. 2007. *Lystrosaurus* species composition across the Permo-Triassic boundary in the Karoo Basin of South Africa. *Lethaia* 40:125–137.
- Botha, J., F. Abdala, and R. M. H. Smith. 2007. The oldest cynodont: new clues on the origin and early diversification of the Cynodontia. *Zoological Journal of the Linnean Society* 149:477–492.
- Bowring, S. A., D. H. Erwin, Y. G. Jin, M. W. Martin, K. Davidek, and W. Wang. 1998. U/Pb zircon geochronology and tempo of the end-Permian mass extinction. *Science* 280:1039–1045.
- Brink, A. S. 1954. On the Whaitsiidae, a family of therocephalian mammal-like reptiles. *Transactions of the Royal Society of South Africa* 34:43–59.
- Brink, A. S. 1960a. A new type of primitive cynodont. *Palaeontologia Africana* 7:119–154.
- Brink, A. S. 1960b. On some small therocephalians. *Palaeontologia Africana* 7:155–182.
- Brink, A. S. 1963. On *Bauria cynops* Broom. *Palaeontologia Africana* 8:39–56.
- Brink, A. S. 1965. A new ictidosuchid (Scaloposauria) from the *Lystrosaurus*-Zone. *Palaeontologia Africana* 9:129–138.
- Broom, R. 1903. 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. 1905. On the use of the term Anomodontia. *Records of the Albany Museum* 1:266–269.
- 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. 1948. A contribution to our knowledge of the vertebrates of the Karroo beds of South Africa. *Transactions of the Royal Society of Edinburgh* 61:577–629.
- Crompton, A. W. 1955. A revision of the Scaloposauridae with special reference to kinetism in this family. *Navorsinge Van Die Nasionale Museum, Bloemfontein* 1:149–183.
- Damiani, R., J. Neveling, S. Modesto, and A. Yates. 2003. Barendskraal, a diverse amniote locality from the *Lystrosaurus* Assemblage Zone, Early Triassic of South Africa. *Palaeontologia Africana* 39:53–62.
- Durand, J. F. 1991. A revised description of the skull of *Moschorhinus* (Therapsida, Therocephalia). *Annals of the South African Museum* 99:381–413.
- Findlay, G. H. 1968. On the scaloposaurid skull of *Olivieria parringtoni*, Brink, with a note on the origin of hair. *Palaeontologia Africana* 11:47–52.
- Fourie, H., and B. S. Rubidge. 2007. The postcranial skeletal anatomy of the therocephalian *Regisaurus* (Therapsida: Regisauridae) and its utilization for biostratigraphic correlation. *Palaeontologia Africana* 42:1–16.
- Heever, J. A. Van Den. 1994. The cranial anatomy of the early Therocephalia (Amniota: Therapsida). *Annals of the University of Stellenbosch* 1994:1–59.
- Hillenius, W. J. 1994. Turbines in therapsids: evidence for Late Permian origins of mammalian endothermy. *Evolution* 48:207–229.
- Hillenius, W. J. 2000. Septomaxilla of nonmammalian synapsids: soft-tissue correlates and a new functional interpretation. *Journal of Morphology* 245:29–50.
- Hopson, J. A. 1991. Systematics of nonmammalian Synapsida and implications for patterns of evolution in synapsids; pp. 635–693 in H.-P. Schultz and L. Trueb (eds.), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Cornell University Press, Ithaca, New York.
- Hopson, J. A. 1994. Synapsid evolution and the radiation of non-eutherian mammals; pp. 190–219 in D. B. Prothero and R. M. Schoch (eds.), *Major Features of Vertebrate Evolution*. Paleontological Society, Knoxville, Tennessee.
- Hopson, J. A., and H. Barghusen. 1986. An analysis of therapsid relationships; pp. 83–106 in N. Hotton, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), *The Ecology and Biology of Mammal-like Reptiles*. Smithsonian Institution Press, Washington, D.C.
- Hotton, N., III. 1991. The nature and diversity of synapsids: prologue to the origin of mammals; pp. 598–634 in H.-P. Schultz and L. Trueb (eds.), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Cornell University Press, Ithaca, USA.
- Huttenlocker, A. K. 2009. Investigation into the cladistic relationships and monophony of therocephalian therapsids (Amniota: Synapsida). *Zoological Journal of the Linnean Society* 157:865–891.
- Huttenlocker, A. K., and J. Marcot. 2007. The effects of phylogenetic augmentation on analyses of paleodiversity: a case study on Permo-Triassic eutheriodonts (Amniota: Therapsida). *Geological Society of America Abstracts with Programs* 39:589.
- Jin, Y.-G., Q. Shang, and C. Cao. 2000. Late Permian magnetostratigraphy and its global correlation. *Chinese Science Bulletin* 45:698–705.
- Jin, Y.-G., B. R. Wardlaw, B. F. Glenister, and G. V. Kotylar. 1997. Permian chronostratigraphy subdivisions. *Episodes* 20:10–15.
- Kammerer, C. 2008. A new therocephalian from the *Cistecephalus* Assemblage Zone of South Africa and new information on therocephalian systematics. *Journal of Vertebrate Paleontology* 28(3, Supplement):98A–99A.
- 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. 1978. Stance and gait in the hindlimb of a therocephalian mammal-like reptile. *Journal of Zoology* 186:143–161.
- Kemp, T. S. 1982. *Mammal-like Reptiles and the Origin of Mammals*. Academic Press, London, 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.
- Kemp, T. S. 2009. Phylogenetic interrelationships and pattern of evolution of the therapsids: testing for polytomy. *Palaeontologia Africana* 44:1–12.
- Kishino, H., and M. Hasegawa. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order of Hominoidea. *Journal of Molecular Evolution* 29:170–179.
- Mendrez, C. H. 1972. On the skull of *Regisaurus jacobi*, a new genus of Bauriamorpha Watson and Romer 1956 (=Scaloposauria Boomstra 1953), from the *Lystrosaurus*-Zone of South Africa; pp. 191–212 in K. A. Joysey and T. S. Kemp (eds.), *Studies in Vertebrate Evolution*. Winchester Press, New York.
- Mendrez, C. H. 1974a. Etude du crane d'un jeune spécimen de *Moschorhinus kitchingi* Broom, 1920 (?*Tigrisuchus simus* Owen, 1876), Therocephalia, Pristerosauria, Moschorhinidae d'Afrique Austral (Remarques sur les Moschorhinidae et les Whaitsiidae). *Annals of the South African Museum* 64:71–115.
- Mendrez, C. H. 1974b. A new specimen of *Promoschorhynchus platyrhinus* Brink 1954 (Moschorhinidae) from the *Daptocephalus*-zone (Upper Permian) of South Africa. *Palaeontologia Africana* 17:69–85.
- 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; pp. 379–408 in Colloque International C.N.R.S. 218. Problèmes actuels de paléontologie-évolution des vertébrés.
- Nopsca, F. von. 1928. The genera of reptiles. *Palaeobiologica* 1:163–188.
- Retallack, G. J. 2005. Permian greenhouse crises; pp. 256–269 in S. G. Lucas and K. E. Zeigler (eds.), *The Nonmarine Permian*. New Mexico Museum of Natural History and Science Bulletin 30.
- Romer, A. S. 1969. The Chanares (Argentina) Triassic reptile fauna. V. A new chiniquodontid cynodont, *Probelesodon lewisi*—cynodont ancestry. *Breviora* 333:1–24.

- Romer, A. S., and L. I. Price. 1940. Review of the Pelycosauria. Geological Society of America Special Papers 28:1–538.
- Rubidge, B. S. 1995. Biostratigraphy of the Beaufort Group (Karoo Super-group). Geological Survey of South Africa, Pretoria, 46 pp.
- Rubidge, B. S., and C. A. Sidor. 2001. Evolutionary patterns among Permo-Triassic therapsids. Annual Review of Ecology and Systematics 32:449–480.
- Sidor, C. A., and R. M. H. Smith. 2004. A new galesaurid (Therapsida: Cyndontia) from the Lower Triassic of South Africa. Palaeontology 47:535–556.
- Sigurdsen, T. 2006. New features of the snout and orbit of a theerocephalian therapsid from South Africa. *Acta Palaeontologica Polonica* 51:63–75.
- Smith, R. M. H. 1995. Changing fluvial environments across the Permian-Triassic boundary in the Karoo Basin, South Africa and possible causes of tetrapod extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 117:81–104.
- Smith, R. M. H., and J. Botha. 2005. The recovery of terrestrial vertebrate diversity in the South African Karoo basin after the End-Permian extinction. *Comptes Rendus Palevol* 4:555–568.
- Smith, R. M. H., and J. Botha-Brink. 2009. Burrowing as a survival strategy in the earliest Triassic Karoo Basin, South Africa. *Journal of Vertebrate Paleontology* 29(3, Supplement):183A.
- Smith, R. M. H., and P. D. Ward. 2001. Pattern of vertebrate extinctions across an event bed at the Permian/Triassic boundary in the main Karoo Basin of South Africa. *Geology* 29:1147–1150.
- Swofford, D. 1999. PAUP: Phylogenetic Analysis Using Parsimony, Version 4.0 beta 10. Distributed by Sinauer Associates, Sunderland, Massachusetts.
- Tatarinov, L. P. 1963. Novyy pozdneperm'skiy terotsefal (New Late Permian theerocephalian). *Paleontological Journal* 1963:76–84.
- Tatarinov, L. P. 1964. [Contribution to the anatomy of the theerocephalian skull]. *Paleontological Journal* 1964:72–84. [Russian]
- Tverdokhlebov, V. P., G. I. Tverdokhlebova, A. V. Minikh, M. V. Surkov, and M. J. Benton. 2005. Upper Permian vertebrates and their sedimentological context in the South Urals, Russia. *Earth-Science Reviews* 69:27–77.
- Ward, P. D., D. R. Montgomery, and R. M. H. Smith. 2000. Altered river morphology in South Africa related to the Permian-Triassic extinction. *Science* 289:1740–1743.
- Ward, P. D., J. Botha, R. Buick, M. O. de Kock, D. H. Erwin, G. H. Garrison, J. L. Kirschvink, and R. Smith. 2005. Abrupt and gradual extinction among Late Permian land vertebrates in the Karoo Basin, South Africa. *Science* 307:709–714.
- Watson, D. M. S. 1931. On the skeleton of a bauriamorph reptile. *Proceedings of the Zoological Society of London* 1931: 1163–1205.

Submitted December 23, 2009; accepted October 20, 2010.

Handling Editor: Randall Irmis.