

**Adult morphology of the therocephalian *Simorhinella baini* from the middle Permian of South Africa and the taxonomy, paleobiogeography, and temporal distribution of the Lycosuchidae**

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# ADULT MORPHOLOGY OF THE THEROCEPHALIAN *SIMORHINELLA BAINI* FROM THE MIDDLE PERMIAN OF SOUTH AFRICA AND THE TAXONOMY, PALEOBIOGEOGRAPHY, AND TEMPORAL DISTRIBUTION OF THE LYCOSUCHIDAE

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**ABSTRACT**—The Middle Permian tetrapod fauna of the South African Beaufort Group is taxonomically diverse and includes representatives of all major therapsid groups, including the earliest records of Eutheriodontia. In the Middle Permian, eutheriodonts are represented mainly by large therocephalians, which made up a large proportion of the vertebrate predators in these faunas. Here we describe the skull and partial skeleton of a large therocephalian from the uppermost *Tapinocephalus* Assemblage Zone (AZ) of South Africa. A combination of features, including the short snout, presence of three to four upper postcanines and presence of teeth on the pterygoid processes, indicates that the new specimen belongs to the earliest-diverging therocephalian family, Lycosuchidae. The presence of a well-developed midline ridge on the ventral surface of the vomer indicates that the new specimen can be referred to *Simorhinella baini*, a species previously represented only by a tiny juvenile skull. The new specimen forms the basis for a taxonomic re-evaluation of the Lycosuchidae as well as of the geographic and stratigraphic range of the family. We recognize two valid species within the Lycosuchidae: the type species *Lycosuchus vanderrieti* represented by five specimens and *Simorhinella baini* represented by two specimens, with an additional 22 specimens currently identifiable as *Lycosuchidae incertae sedis*. Lycosuchid specimens range throughout the *Tapinocephalus* and *Pristerognathus* AZs; specimens of *Simorhinella* are restricted to the *Tapinocephalus* AZ, whereas *Lycosuchus* specimens are documented in both the *Tapinocephalus* and *Pristerognathus* AZs.

## INTRODUCTION

**I**MPORTANT CHANGES in the taxonomic composition of amniote faunas occurred during the Middle Permian, the most significant being the explosive emergence of therapsids. The earliest therapsids are known from Middle Permian of China, Russia and, perhaps slightly later, Tanzania, Zambia, South Africa, and Brazil (Abdala et al., 2008; Cisneros et al., 2011, 2012; Liu et al., 2009; Simon et al., 2010; Sidor et al., 2014; Angielczyk et al., in press). The Middle Permian tetrapod record of the South African Karoo Supergroup is particularly rich and includes the oldest known representatives of two major therapsid lineages, dicynodonts and theriodonts (Rubidge, 2005). Of the latter group, the oldest records are the scylacosaurid therocephalians *Glanosuchus macrops* Broom 1904 and *Ictidosaurus angusticeps* Broom 1903b, and an unidentified gorgonopsian from the *Eodicynodon* Assemblage Zone (AZ), the lowermost tetrapod assemblage zone of the Permo–Triassic Beaufort Group (Abdala et al., 2008). The overlying *Tapinocephalus* AZ records a dramatic diversification of therapsid genera (Boonstra, 1969; Smith and Keyser, 1995; Rubidge, 2005), mostly of the same broad taxonomic groupings already present in the *Eodicynodon* AZ. The most dramatic increase in generic richness occurred amongst the herbivorous dinocephalians and dicynodonts, although carnivorous therocephalians also show a significant increase in diversity and abundance: from two specimens in the *Eodicynodon* AZ to at least 75 specimens in the *Tapinocephalus* AZ (Smith et al., 2012; Day, 2013).

The Therocephalia is a morphologically heterogeneous group initially represented by large-bodied forms that were important predators during the Middle Permian. A general reduction in average body size and a clear increase in morphological and ecological diversity occurred in this lineage in the Late Permian (Huttenlocker, 2014). Recent phylogenies have resulted in different hypotheses regarding the interrelationships of Therocephalia. Abdala (2007) and Botha et al. (2007) found Therocephalia to be paraphyletic with regards to Cynodontia, with both basal families (Lycosuchidae and Scylacosauridae) and the whaitsiid *Theriognathus* placed outside of the core group of therocephalians (Eutherocephalia). Conversely, recent contributions by Huttenlocker (2009), Huttenlocker et al. (2011), and Sigurdson et al. (2012) recovered a monophyletic Therocephalia using expanded taxon sampling.

Two main basal therocephalian families are present in the *Tapinocephalus* AZ and can be readily distinguished by snout proportions: Scylacosauridae have a long and comparatively narrow snout, whereas in the Lycosuchidae the snout is short and broad (van den Heever, 1994). Ten nominal species have been recognized in Lycosuchidae (Table 1, Fig. 1) that were reduced to two species by van den Heever (1987).

*Simorhinella baini* Broom 1915 from the *Tapinocephalus* AZ is represented by only the holotype, which is the snout and partial lower jaw of a very small therocephalian (Fig. 2). This species was described by Broom (1915) and, after a period of uncertainty regarding its taxonomic placement, it was reinstated as a valid therocephalian by Mendrez (1975). Here, we describe a new specimen of a short-snouted basal therocephalian

TABLE 1—Taxonomy of the Lycosuchidae after revision of basal therocephalian by van den Heever (1987) and referral in this work. Specimens include individuals assigned to some of the above taxa that were also considered as member of the Lycosuchidae. The last two specimens are unpublished and were assigned by van den Heever (1987). Abbreviation: *i.s.=incertae sedis*.

Specimen	Original name	van den Heever (1987)	Current referral
US D173	<i>Lycosuchus vanderrieti</i> Broom 1903	valid	valid
SAM-PK-632	<i>Scymnosaurus ferox</i> Broom 1903	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-633	<i>Lycosuchus mackayi</i> Broom 1903	Therapsida <i>i.s.</i>	Gorgonopsia <i>i.s.</i>
SAM-PK-1079	<i>Hyaenasuchus whaitsi</i> Broom 1908	<i>Lycosuchus vanderrieti</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-1076	<i>Trochosuchus acutus</i> Broom 1908	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
AMNH 5543	<i>Trochosaurus major</i> Broom 1915	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-2756	<i>Trochosaurus intermedius</i> Haughton 1915	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
TM 275	<i>Trochorhinus vanhoepeni</i> Broom 1936	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-9005	<i>Scymnosaurus major</i> Boonstra 1954	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-12185	<i>Zinnosaurus paucidens</i> Boonstra 1964	<i>Lycosuchus vanderrieti</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-3430	( <i>Scymnosaurus ferox</i> )	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-9084	( <i>Scymnosaurus ferox</i> )	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-10556	( <i>Scymnosaurus major</i> )	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-8999	( <i>Scymnosaurus</i> sp.)	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
SAM-PK-11961	( <i>Scymnosaurus</i> sp.)	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
NHMUK R5747	<i>Trochosaurus major</i>	Lycosuchidae <i>i.s.</i>	Lycosuchidae <i>i.s.</i>
NHMUK 49422	<i>Simorhinella baini</i> Broom 1915		valid
CGS M793		<i>Lycosuchus vanderrieti</i>	<i>Lycosuchus vanderrieti</i>
CGS C60		" <i>Lycosuchus keyseri</i> sp. nov."	Lycosuchidae <i>i.s.</i>

(BP/1/5592) from the *Tapinocephalus* AZ. The presence of a short snout, five upper incisors, and palatal teeth on the transverse process of pterygoid suggests a link with lycosuchid therocephalians (van den Heever, 1994). Based on the presence of a longitudinal midline crest on the palatal portion of the vomer we refer the new specimen to *Simorhinella baini*, representing the first known adult of the species.

In contrast to most previously described *Tapinocephalus* AZ therocephalians, the new material has well-established geographic and stratigraphic provenance data. This paper is the first of a series of contributions intended to update the alpha-taxonomy and the geographic and stratigraphic distribution of therocephalians from the *Tapinocephalus* and *Pristerognathus* AZs of the Karoo Basin. We expect that this exercise will have important ramifications for the analysis of diversity and abundance of basal therocephalians and other amniotes from the Middle Permian.

#### SYSTEMATIC PALEONTOLOGY

*Institutional abbreviations.*—AMNH, American Museum of Natural History, New York; BP, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg; CGS, Council for Geosciences, Pretoria; FMNH, Field Museum of Natural History, Chicago; MB, Museum für Naturkunde, Berlin; NHMUK, Natural History Museum, London; NMQR, National Museum, Bloemfontein; SAM, Iziko: South African Museum, Cape Town; TM, Ditsong National Museum of Natural History (formerly Transvaal Museum) Pretoria; US, University of Stellenbosch, Stellenbosch.

Order THERAPSIDA Broom, 1905  
 Suborder THEROCEPHALIA Broom, 1903c  
 Family LYCOSUCHIDAE Nopsca, 1923  
 Genus SIMORHINELLA Broom, 1915  
*Simorhinella baini* Broom 1915

*Diagnosis.*—*Simorhinella baini* is distinguished from *Lycosuchus vanderrieti* by the presence of a wide and uniform sagittal crest behind the pineal foramen; proportionally narrower extension of the vomer in the posterior margin of the choana; choana pinched lateromedially by the bulbous expansion of the canine alveolus; smooth quadrate trochlea without clear distinction of the medial and lateral condyles and a well-developed median ridge of the vomer extending to the central length of the

bone, a character shared with scylacosaurids and euterocephalians.

*Description.*—See detailed description section below.

*Holotype.*—NHMUK 49422 (Fig. 2). Weltevreden, Gough, Prince Albert District, Western Cape Province.

*Material.*—BP/1/5592: skull (lacking lower jaw), series of vertebrae, partial scapula and a complete ulna (Figs. 4, 5, 6.1, 7, 8, 9). The specimen was found in the farm Rhebokfontein 74 (S 31°5.829', E 23°2.407'), Victoria West district, Northern Cape Province, South Africa (Fig. 3A). Uppermost *Tapinocephalus* Assemblage Zone, Abrahamskraal Formation, Beaufort Group, Karoo Supergroup, Middle Permian. Rhebokfontein 74 occupies land exposing rocks of the upper Ecce and lower Beaufort groups in this part of the Karoo Basin. BP/1/5592 was recovered from immediately above the base of the Beaufort Group but due to the diachroneity of this contact, the lowest Beaufort strata here are of upper *Tapinocephalus* AZ age. The *Eodicynodon* AZ and lower *Tapinocephalus* AZ are not present at this part of the basin. This is confirmed by the presence of the dinocephalian *Anteosaurus* at the same locality (BP/1/5591) and of the dicynodont *Diictodon* (NMQR 3455) close to the contact on the farm Bastardsfontein, Carnarvon district, Northern Cape Province (Day, 2013).

*Remarks.*—*Simorhinella baini* can be recognized as a lycosuchid by the presence of five or fewer incisors; no precanines; five or fewer postcanines; transverse process of the pterygoid bearing a single row of teeth; pterygoid bosses lacking teeth; anterior processes of pterygoid separated by a broad interpterygoid vacuity; ventromedial tubercle anterior to the vacuity; short snout; broad interorbital region; broad suborbital bar; discrete and rounded pterygoid boss; rugose maxillary ridge on the palate; well-developed internal boss of the maxilla around the canine constricting the choana.

Additional specimens that were examined for this study are shown in Table 2. They represent nearly all the specimens recognized in the Family Lycosuchidae.

#### DESCRIPTION

*General preservation.*—The skull of BP/1/5592 is relatively complete and the bone texture is well preserved, but it has suffered dorso-ventral compression such that the dorsal portion of the skull has been displaced posteriorly relative to the ventral side (Fig. 4). The palate is well preserved, lacking only the tip of the right transverse process of the pterygoid. Most of the teeth are missing or broken, but their alveoli are well defined. The skull lacks the dorsal portion of the snout (including both nasals) and the zygomatic arches. The occiput is partially preserved, with the

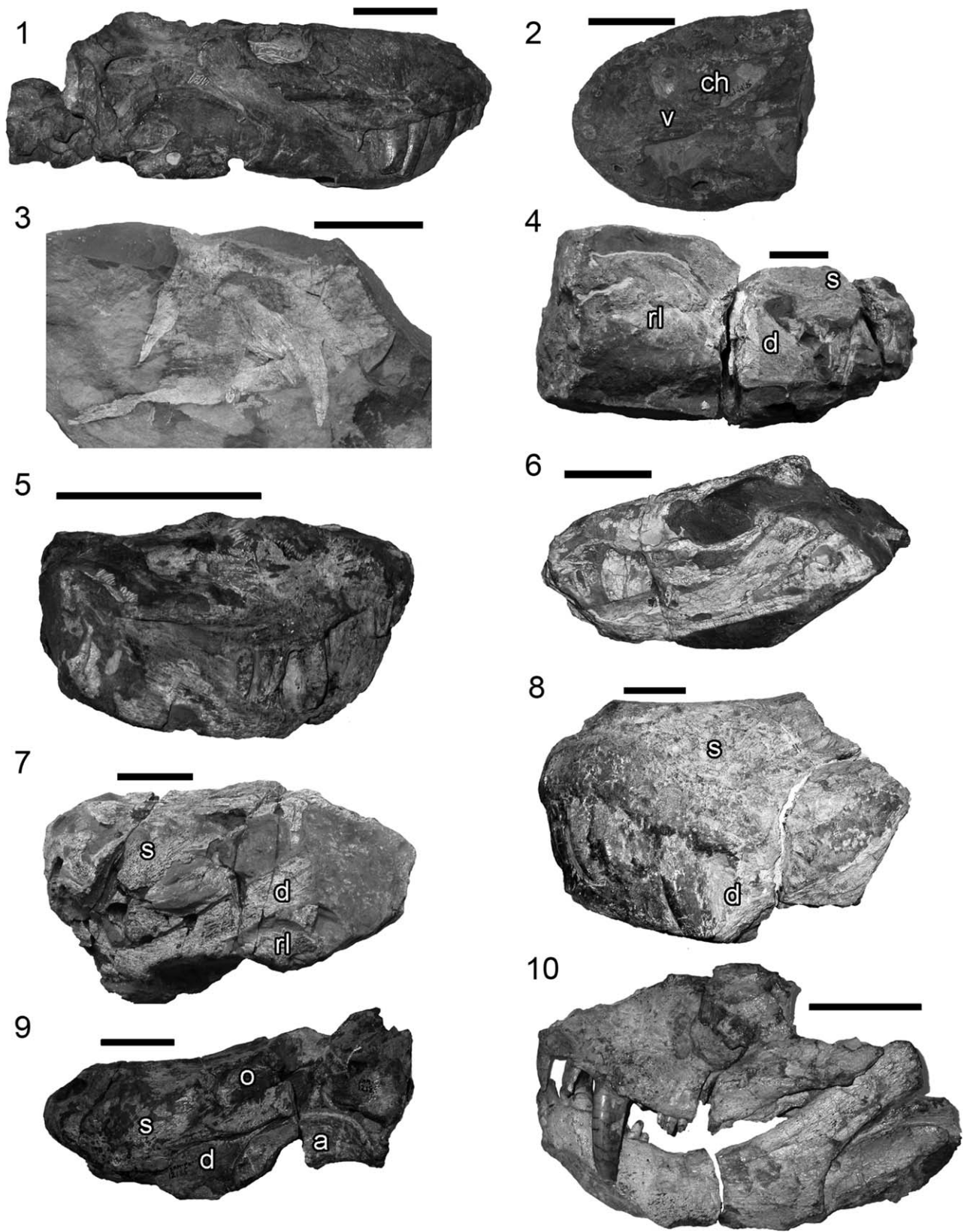


FIGURE 1—Photographs of the holotypes of Lycosuchidae. 1, *Lycosuchus vanderrieti* Broom 1903 (US D173); 2, *Scymnosaurus ferox* Broom 1903 (SAM-PK-632); 3, *Lycosuchus mackayi* Broom 1903 (SAM-PK-633); 4, *Hyaenasuchus whaitsi* Broom 1908 (SAM-PK-1079); 5, *Trochosuchus acutus* Broom 1908 (SAM-PK-1076); 6, *Trocosuchus major* (Broom 1915) (AMNH FARB 5543); 7, *Trochosaurus intermedius* Haughton 1915 (SAM-PK-2756); 8, *Scymnosaurus major* Boonstra 1954 (SAM-PK-9005); 9, *Zinnosaurus paucidens* Boonstra 1964 (SAM-PK-12185); 10, '*Lycosuchus keyseri*' (CGS C60). Abbreviations: a=angular; ch=choana; d=dentary; o=orbit; rl=reflected lamina; s=snout; v=vomer. Scale=5 cm.

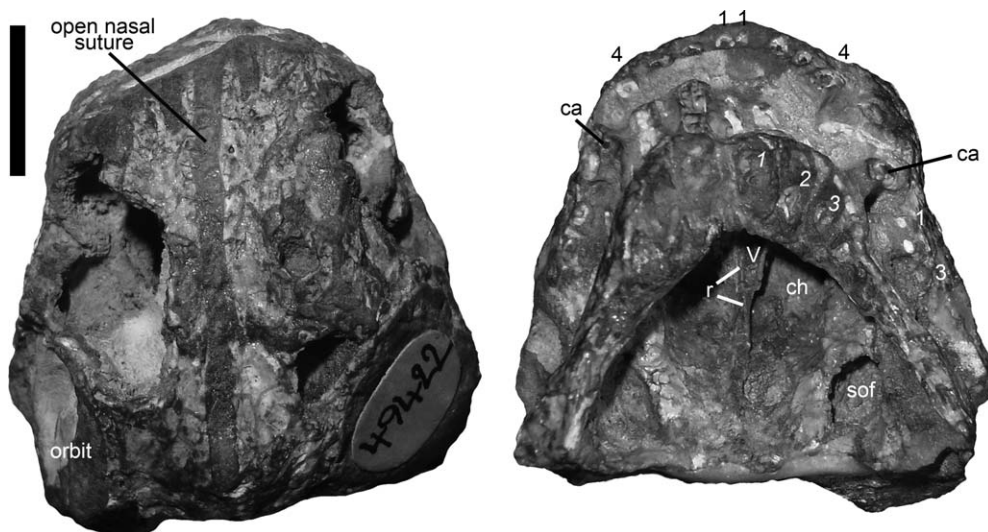


FIGURE 2—Holotype of *Simorhinella baini* Broom 1915 (NHMUK 49422). Photographs of the skull in dorsal and ventral views. Abbreviations: ch=choana; r=central ridge on the vomer; sof=suborbital fossa; v=vomer. White numbers in italics are lower incisors. Scale=1 cm.

left side complete. This is one of the largest lycosuchid skulls recovered, with a total skull length of ~370 mm (see Table 3 for additional measurements of the skull).

**Snout.**—The premaxilla forms the anterior end of the snout and is in contact with the maxilla posteriorly below the external naris and the nasal dorsally (Figs. 4.1, 4.3, 5.1, 5.3). In dorsal view the midline premaxillary suture is not visible but is obvious on the palate. Within the external naris the premaxilla forms a medial platform that is in contact with the anterior edge of the

septomaxilla. A small portion of the right intranarial process of the septomaxilla is preserved close to the base of the broken ascending process. The left process is more complete and has a slightly concave lateral surface (Figs. 4.1, 5.1). The base of the intranarial plate extends anteriorly, broadly superposing the premaxilla (a feature not known in other basal theropcephalians).

In palatal view, the premaxilla forms a broad ventral plate that encompasses the alveoli of the five upper incisors (Figs. 4.2, 5.2). Posteromedially it meets the vomer with a short triangular

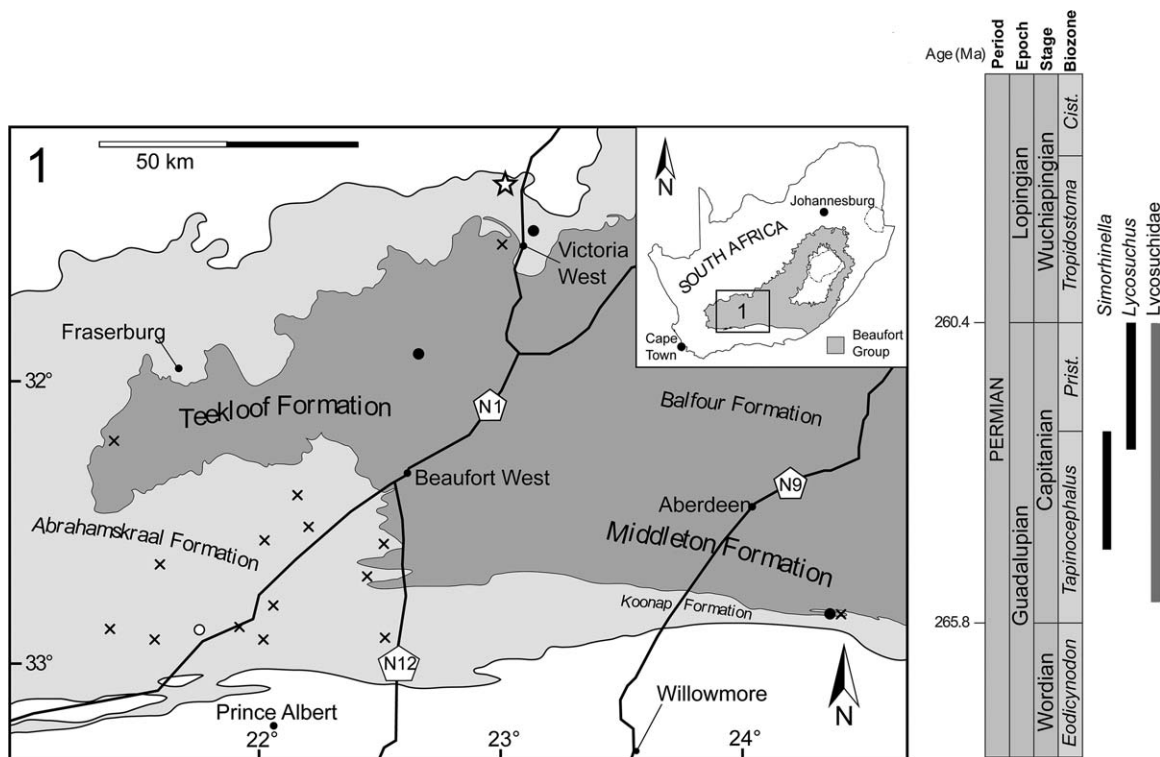


FIGURE 3—Geographic and temporal distribution of Middle Permian Lycosuchidae from the Beaufort Group. Map of the south-western portion of the Karoo Basin. Star represents locality of new specimen BP/1/5592; filled circles represent localities with records of *Lycosuchus vanderrieti*, unfilled circle represents *Simorhinella baini* and crosses represent indeterminate lycosuchids (see also Table 2). Note the long distance separating the two records of *S. baini*. Abbreviations of assemblage zones are: *Prist.*=*Pristeroagnathus*, *Cist.*=*Cistecephalus*.

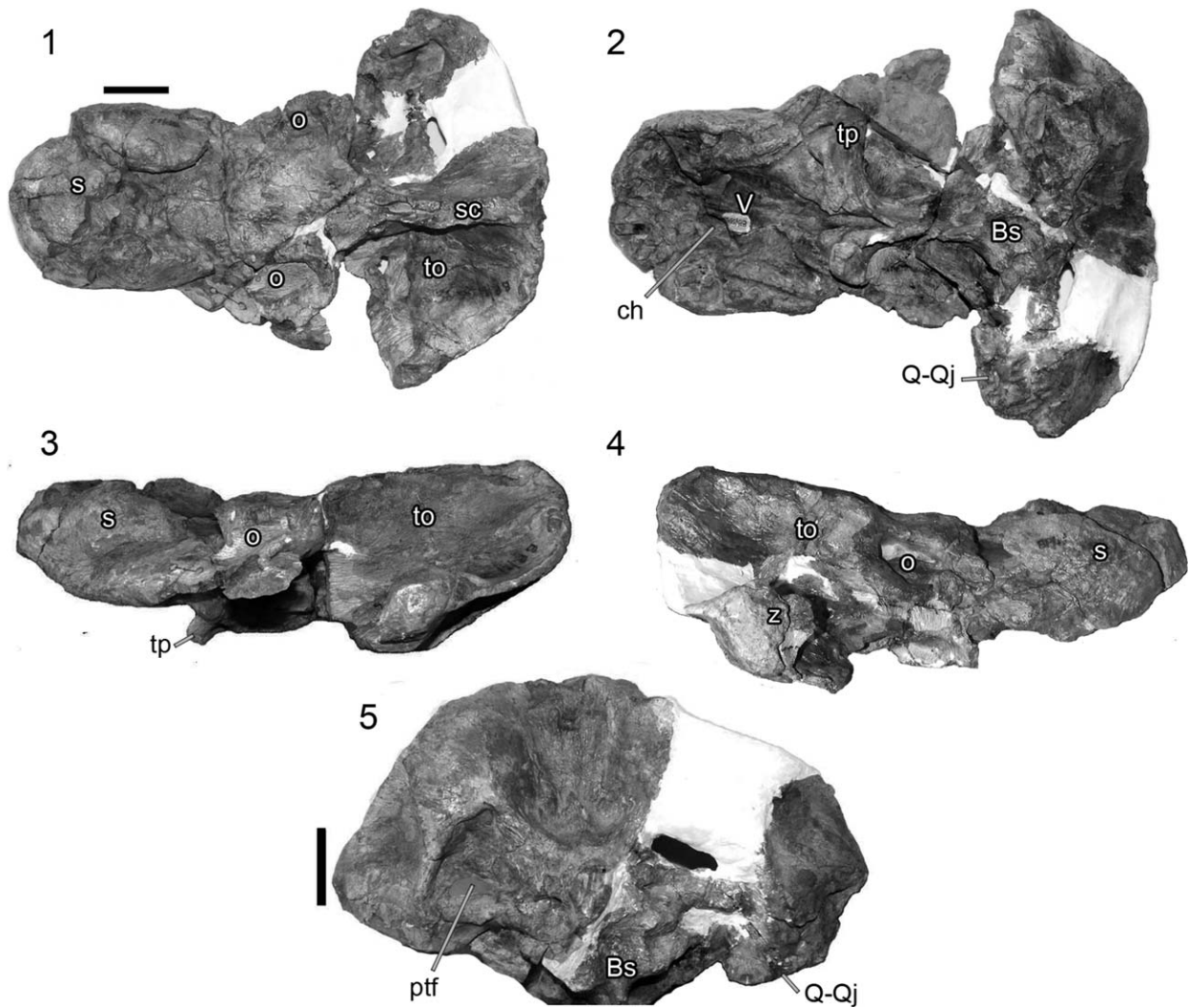


FIGURE 4—Photographs of skull of *Simorhinella baini* (BP/1/5592) in different views. 1, dorsal; 2, ventral; 3, lateral; 4, right lateral; 5, occipital. Abbreviations: Bs=basisphenoid; ch=choana; o=orbit; ptf=posttemporal foramen; Q-Qj=quadrate-quadratojugal complex; s=snout; sc=sagittal crest; to=temporal opening; tp=transverse process; V=vomer; z=zygoma. Scale=5 cm.

posteriorly-directed vomerine process. On the left side, the suture between the premaxilla and maxilla extends anteriorly in front to the canine alveolus and continues up to the external naris on the side of the snout in line with the last incisor.

The external surface of the maxilla is damaged but in lateral view it appears that the height of the bone is taller than the length of the canine root. In lateral view the ventral margin of the maxilla is remarkably convex (Figs. 4.3, 5.3) but is slightly concave in front of the level of the canine alveolus. The posteroventral margin of the maxilla forms a short laterally directed flange that borders the jugal on its dorsal side. The flange in this specimen is relatively small compared to that of the holotype of *Lycosuchus vanderietii* (US D173), where a ridge or crest separating the lateral surface of the maxilla from the postcanine maxillary margin is more prominent.

In ventral view, the suture between the maxilla and palatine extends almost parallel with the lateral margin of the skull on the medial side of the postcanine row (Figs. 5.2, 6.1). In addition, the palatine is positioned slightly more dorsally than the maxilla. The maxilla has broad exposure medial to the canine alveolus, causing the choana to narrow in this region (Figs. 4.2, 5.2, 6.1). The crescent shaped choana extends the length of the canine alveolus

and is bordered laterally by the maxilla, anteriorly by the premaxilla, medially by the vomer, and posteriorly by the vomer and palatine.

Anterior to the canine the maxilla has a thin shelf overlapping the posterior portion of the premaxilla at the level of the last incisor, whereas posterior to the canine the maxilla is constricted and gradually narrows posteriorly.

**Orbital region.**—The jugal extends halfway along the anterior border of the orbit where it is in contact with the lacrimal on the dorsal side, makes up the suborbital portion of the bar, and extends dorsally to form the ventral half of the posterior border of the orbit. Dorsally and posteriorly the jugal is in contact with the postorbital (Figs. 4.1, 5.1).

In lateral view, the postorbital bone has a narrow exposure on the postorbital bar between the jugal on the ventral side and the postfrontal dorsally, such that the latter bone forms only the anterodorsal part of the postorbital bar (Figs. 4.3, 5.3). On the skull roof the postorbital expands posteriorly as a broad plate forming the anterolateral border wall of the intertemporal bar (Figs. 4.3, 5.3).

The postfrontal comprises a ventral and posterior projection. The ventral projection, which tapers posteroventrally, extends halfway down the postorbital bar (Fig. 5.1) and in lateral view

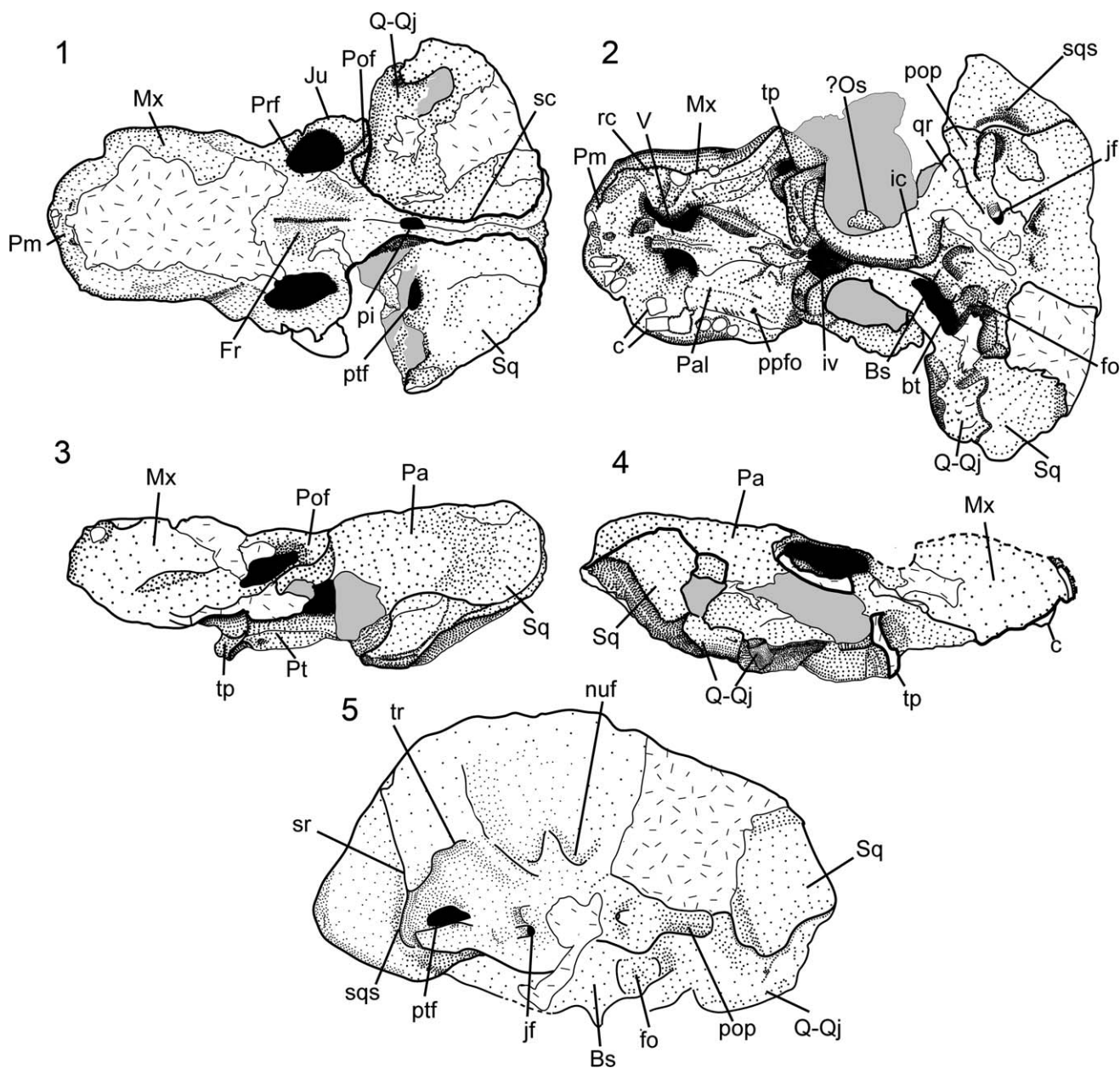


FIGURE 5—Interpretive drawings of skull of *Simorhinella bairi* (BP/1/5592) in different views. 1, dorsal; 2, ventral; 3, left lateral; 4, right lateral; 5, occipital. Abbreviations: Bs=basisphenoid; bt=basal tubera; c=canine; fo=fenestra ovalis; Fr=frontal; Ju=jugal; ic=internal carotid foramen; iv=interpterygoid vacuity; jg=jugular foramen; Mx=maxilla; nuf=nuchal fosa; ?Os=orbitosphenoid; Pa=parietal; Pal=palatine; pi=pineal foramen; Pm=premaxilla; Pof=postfrontal; pop=paroccipital process; ppfo=posterior palatine foramen; Prf=prefrontal; Pt=pterygoid; ptf=posttemporal foramen; Q-Qj=quadrate-quadratojugal complex; qr=quadrate ramus of the pterygoid; rc=replacement canine; sc=sagittal crest; Sq=squamosal; sqs=squamosal sulcus; sr=squamosal ridge; tp=transverse process; tr=tabular ridge; V=vomer; Broken line pattern is broken; gray indicates sediment. Scale=5 cm.

forms a diagonal suture with the postorbital. The posterior projection makes up the anterolateral end of the intertemporal region and forms a shelf that overhangs the postorbital.

The dorsal margin of the orbit is formed by the prefrontal, frontal, and a small contribution of the postfrontal (Figs. 4.1, 5.1). On the dorsal surface of the skull, the frontal is a wide bone with a midline ridge that is more prominent anteriorly. A longitudinal depression is present on either side of this ridge (Fig. 5.1). The posteromedial part of the frontal slopes dorsally and forms the anterior portion of the strongly arched intertemporal bar.

Only the posterior region of the right prefrontal is preserved, and forms the anterodorsal margin of the orbit. Ventral to this, a

poorly preserved lacrimal bone is present on the anterior margin of the orbit.

A slightly convex laminar bone, present in the interorbital region of the skull, visible in ventral view, is interpreted as the orbitosphenoid (Figs. 4.2, 5.2). This bone was recognized previously in only one specimen of basal theriocephalian ('theriocephalian B'; Olson, 1944), but this specimen has been demonstrated to be a gorgonopsian (van den Heever and Hopson, 1982). This element, however, has been described in several eutheriocephalians (Kemp, 1972a; Sigurdson, 2006; Sigurdson et al., 2012; Abdala et al., 2014). The lack of orbitosphenoid in other basal theriocephalian specimens is not surprising as this bone in BP/1/5592 is a remarkably thin lamina.

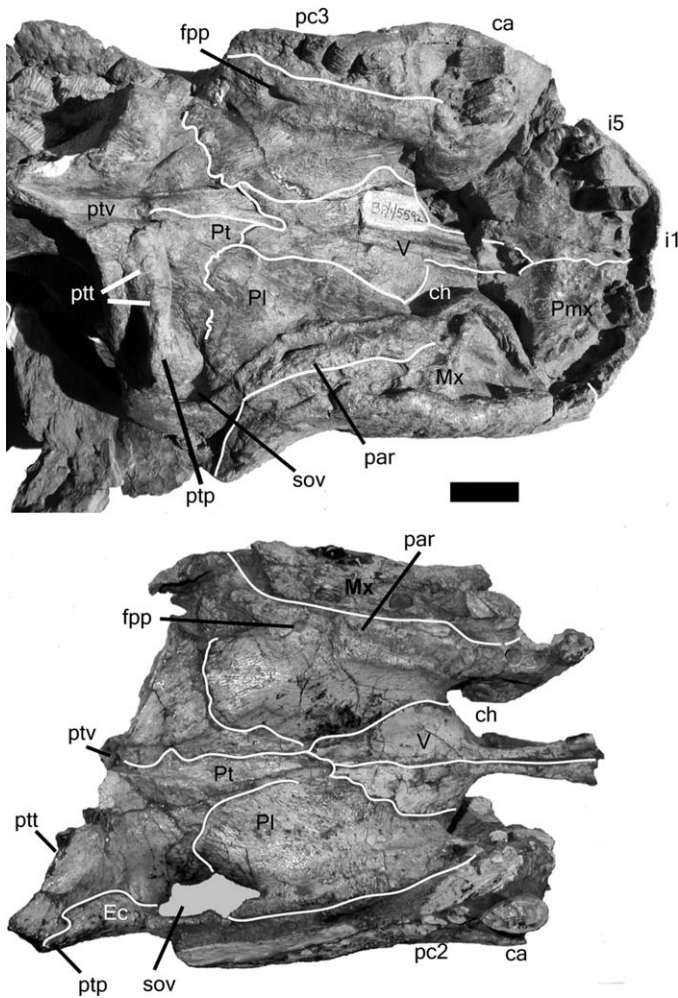


FIGURE 6—Photograph of the palate of *Simorhinella baini* (BP/1/5592) and *Lycosuchus vanderrieti* (CGS M793). Abbreviations: ca=canine; ch=choana; Ec=ectopterygoid; fpp=foramen palatine posterior; i=incisor; Mx=maxilla; par=palatine ridge; pc=postcanine; P=palatine; Pmx=premaxilla; Pt=pterygoid; ptp=pterygoid process; ptt=pterygoid teeth; ptv=interpterygoid vacuity; sov=suborbital vacuity; V=vomer. Scale=2 cm.

The parietal forms a long, tall sagittal crest and contributes to the anterior portion of the occipital crest (Figs. 4.1, 4.3, 4.4, 5.1, 5.3, 5.4). Posterolaterally, the parietal is in sutural contact with the dorsal process of the squamosal, and this suture is visible on both sides of the skull. The internal process of the squamosal is anteroposteriorly concave and contributes to the dorsal margin of the anterior opening of the post-temporal canal. The quadrate ramus of the squamosal, which is more robust than the other sections of the bone, has an anteriorly depressed area to receive the quadrate and quadratojugal. Only a reduced portion of the prootic is visible. It is in contact with the medial portion of the parietal, and contributes to the medial margin of the post-temporal canal.

**Basicranium and palate.**—The large, robust, ventrally projected basal tubera are bisected by the transverse suture between the basioccipital and basisphenoid. The tubera extend obliquely across the basicranium and taper anteriorly to meet at the base of the tall parasphenoid rostrum. Clearly defined carotid openings are present (Fig. 5.2). The anterior portion of the parasphenoid rostrum is not preserved but appears to have ended anteriorly close to the posterior margin of the interpterygoid vacuity. The

large interpterygoid vacuity separates the transverse processes and palatal bosses of the pterygoid (Figs. 5.2, 6.1). A prominent medial tubercle of the pterygoid limits the vacuity anteriorly.

The pterygoid is typically a tripartite bone comprising a quadrate ramus, transverse process, and anterior boss. Only the left transverse process of the pterygoid is completely preserved and bears four teeth in a straight line along its ventral margin (Figs. 5.2, 6.1). Prominent ridges extend anteromedially from the medial margin of the transverse process and form the lateral wall of the interpterygoid vacuity. These ridges extend ventrally as in scylacosaurids and differ from those of *Lycosuchus*, in which they typically extend ventrolaterally (see van den Heever, 1994, fig. 8). The lateroventrally expanded pterygoid bosses are rounded and poorly developed. The pterygoid has a short anteromedial contact with the vomer, thus excluding contact between the palatine and vomer (Figs. 5.2, 6.1). A relatively small ectopterygoid overlies the anterolateral portion of the transverse process and is in contact with the pterygoid on its posterior and medial sides, the palatine anteriorly, and the maxilla laterally.

Anteriorly, the pterygoid contacts the palatine by means of a suture that runs on both sides at the anterior base of the palatal bosses (Fig. 6.1). The palatine bears a posteromedial boss and a tongue-shaped anterior extension. The edentulous palatal bosses are rounded, in contrast to the more elongate morphology present in *Lycosuchus*. As is typical in lycosuchids, the palatine decreases in width anterior to the boss and has a smooth, medial surface and a raised, strongly rugose lateral portion, close to its contact with the maxilla (Fig. 6.1, 6.2). The laterally situated rugose region is wide and is bordered by a long, narrow, medially positioned ridge. A prominent posterior palatine foramen, which is directed anteriorly, is present on the posterior portion of the palatine.

The paired vomer, which has a posteromedial contact with the pterygoid, extends the length of the choana to meet the vomerine process of the premaxilla at its anterior end (Fig. 6.1). The vomer is narrow at its contact with the pterygoid and broadens anteriorly to its greatest width immediately behind the choana. From here it tapers toward the front end of the skull such that the anterior part of the vomer is narrow (Figs. 5.2, 6.1). The anterior part of the vomer has a high midline ridge with a lower lateral one on either side. This ridge extends posteriorly two-thirds the length of the vomer.

**Quadrate-quadratejugal complex.**—The right quadrate-quadratejugal complex is preserved and is articulated to the squamosal (Fig. 7). This complex is displaced ventrally from its life position. A clear suture separating the quadrate from the quadratojugal is visible in anterior view and a well-developed quadrate foramen is bordered laterally by the dorsal process of the quadratojugal and medially by the medial process of the base of the quadratojugal and the dorsal process of the quadrate (Fig. 7.1). The dorsal process of the quadrate is long with a slight concavity directed anteriorly. The quadratojugal is a robust element with an anterior crest on the dorsal process and a lateral process that is dorsoventrally broad (Fig. 7.1, 7.2). In lateral view, this process is dorsoventrally lenticular. The lateral margin of the dorsal process of the quadratojugal forms a clear concavity, bounded medially by a ridge. The quadrate foramen is exposed posteriorly with the lateral margin formed by quadratojugal and quadrate on the medial side (Fig. 7.2). A depressed area is also present on the posterior side of the dorsal process of the quadratojugal, and a series of crests on the posterior side of the dorsal process of the quadrate served to connect with the anterior surface of the squamosal cavity. The trochlea, formed by the quadrate, is an ellipsoid surface oriented anteroventrally. It has a medial projection for the stapes that arises from the anterior margin of the trochlea, and a lateral projection extending from the posterior margin of the trochlea, which is in contact with a thin lateral



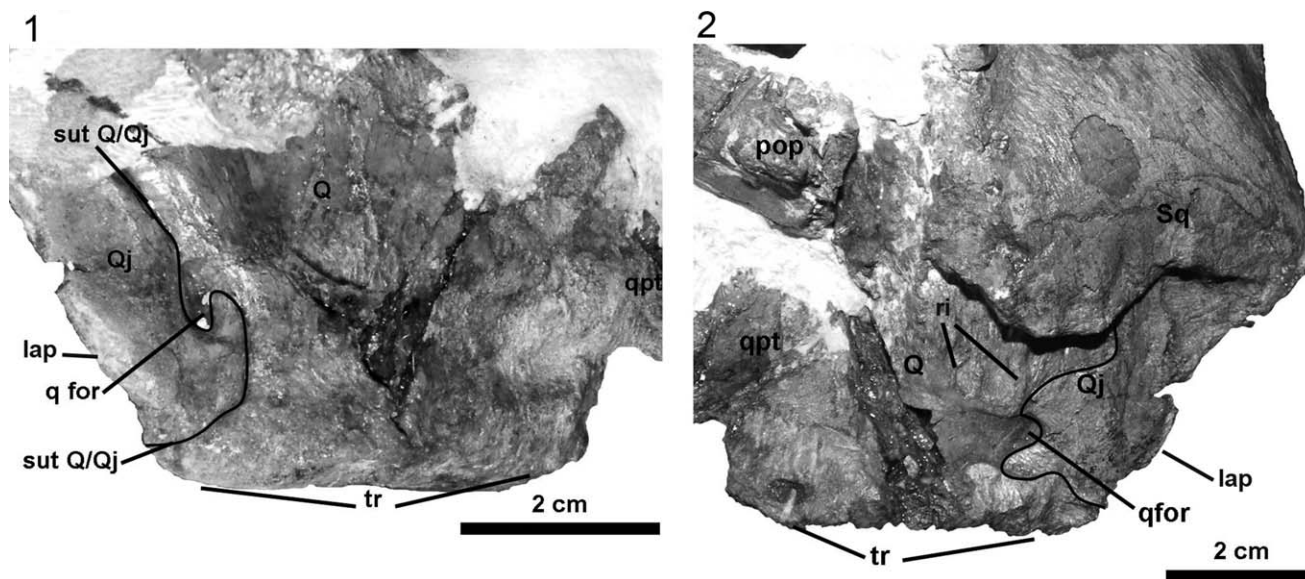


FIGURE 7—Photographs of the quadrate-quadratejugal complex in *Simorhinella baini* (BP/1/5592). 1, latero-anterior view; 2, posterior view. Abbreviations: lap=lateral process of the quadratejugal; pop=paroccipital process; Q=quadrate; qfor=quadratejugal foramen; Qj=quadratejugal; qpt=quadrate ramus of the pterygoid; ri=ridges; Sq=squamosal; sut Q/Qj=suture between quadrate and quadratejugal; tr=trochlea of the quadrate. Scale=2 cm.

portion of the quadratejugal. The quadrate-quadratejugal complex contacts the quadrate ramus of the pterygoid anteromedially and paroccipital process of the opisthotic on the posteromedial side (Fig. 7.2).

**Occipital plate.**—The complete left and part of the right side of the occiput is preserved (Figs. 4.5, 5.5). A central depressed area of the supraoccipital is present above the foramen magnum and is bisected by a nuchal ridge, which is more developed at its base. A second well-developed depression is located above the post-temporal canal; it is formed by the lateral process of the supraoccipital and by the tabular ridge and appears deeper than the same depression in other therocephalians. This second depression is separated from a third depressed area by a medial squamosal ridge, which contributes to form the squamosal sulcus (Figs. 4.5, 5.5). The occipital condyle and foramen magnum are poorly preserved and it is not possible to establish the suture between the basioccipital and exoccipital. The paroccipital process of the opisthotic forms the ventral margin of the post-temporal canal and, in ventral view, separates the quadrate from the mastoid process. The latter process is incompletely preserved and lacks the lateral portion that contacts the squamosal. The medial portion of the paroccipital process forms the lateral margin of the jugular foramen and the posterior margin of the fenestra ovalis.

**Dentition.**—The dental formula is five incisors, one canine, and three postcanines. None of the left incisors are present apart from a partial root in the fourth alveolus, but from the right side it is apparent that the incisors decrease in size posteriorly. The third right incisor is the only tooth preserved with enamel intact and bears serrations on its keeled posterolateral surface. The right 14 and 15 show no evidence of serrations, but this is probably because of their poor preservation. A diastema is present between the last incisor and the extremely wide, mediolaterally expanded canine alveolus (Figs. 4.2, 5.2). Two poorly preserved canines, positioned side by side (Figs. 4.2, 5.2), are present on the right side and we interpret the lateral one to be a replacement tooth. The well-preserved tip of a replacement canine, with a well-developed serrated keel on its posterior side, is positioned on the anterior side of the left alveolus. Three postcanine teeth are preserved on the right side, and only the root of a single postcanine (probably PC2) is preserved on the left side (Fig. 5.2). There is no diastema between the canine and the first postcanine.

The postcanines are robust, positioned close to each other, and decrease in size posteriorly (see Table 3). They are oval in cross-section and slightly longer anteroposteriorly than mediolaterally. The tooth row curves posterolaterally such that the last postcanine is positioned further laterally than the first.

**Axial skeleton.**—Three sets of poorly preserved, articulated amphicoelous vertebrae are represented in BP/1/5592: the first is made up of two complete, articulated centra and two partial centra that are considered to be cervicals (Fig. 8.1); the second, interpreted as representing the transition between thoracic and sacral regions, includes three complete articulated and two partial centra (Fig. 8.2); the third includes three vertebrae and a partial fourth element, considered caudals (Fig. 8.3). The centra of the cervical vertebrae are all approximately the same size (Table 4, Fig. 8.1). The complete centrum has a ventral keel, which is prominent in the second vertebra and somewhat widened in the third one (Fig. 8.1). Vertebral keels have also been described for the therocephalian *Olivierosuchus* (Botha-Brink and Modesto, 2011), but unlike that taxon there is no preserved intercentrum in BP/1/5592. The transverse processes, which have a robust base, are partially preserved and the postzygapophyses are uniform in size and are separated from the base of the transverse process by a wide notch (Fig. 8.1). The prezygapophyses are relatively longer than the postzygapophyses and their articular surfaces (as observed in the fourth vertebra) are oriented obliquely and medially. The neural spines are broken and are triangular in cross-section, with a narrow base at the anterior end, a condition also described in cervical vertebrae of the scylacosaurid *Glanosuchus* (Fourie and Rubidge, 2009).

The set of posterior dorsal-to-sacral vertebrae have a centrum with a midline depression bordered by a weak ridge on either side. The prezygapophyses are transversely broader than those of the cervicals and are expanded and directed laterally (Fig. 8.2). The third, fourth, and fifth centra have partially synostosed ribs. The rib of the third vertebra is broken and preserved ventrally to the point of articulation. The articulated ribs of the fourth and fifth vertebrae have a broad medial attachment portion, which is better preserved in the fourth rib. The preserved lateral portion is narrower than the medial end. The ribs of the fourth and fifth vertebrae differ greatly in dorsoventral and anteroposterior robustness (Fig. 8.2). This type of differentiation is observed

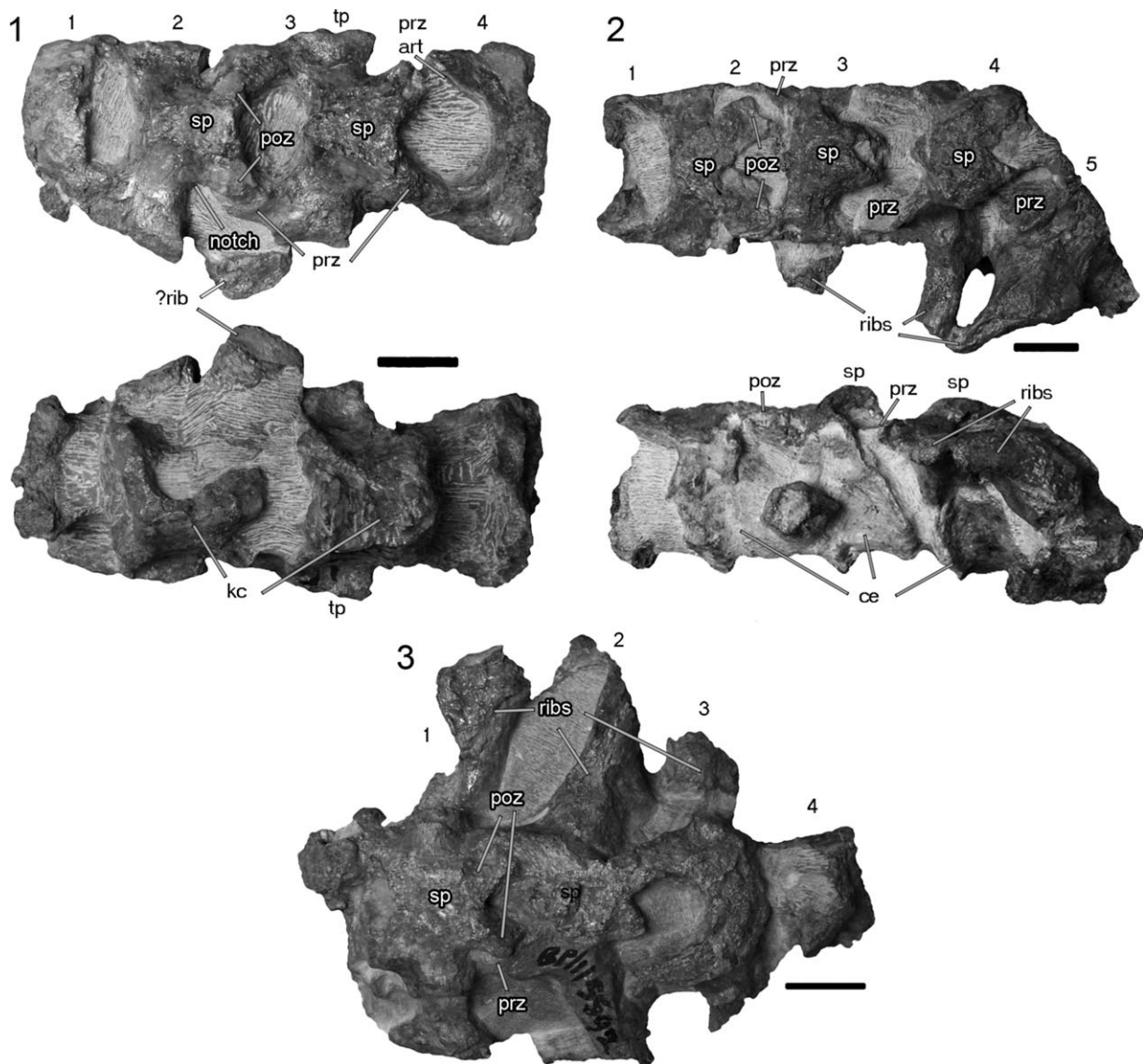


FIGURE 8—BP/1/5592. Photographs of vertebral series of *Simorhinella baini* (BP/1/5592). 1, dorsal and ventral views of cervical series; 2, dorsal and lateral view of posterior dorsal and anterior sacral; C3 dorsal view of posterior ?sacral and caudal. Abbreviations: ce=centrum; kc=keeled ventral portion of the centrum; prz=prezygapophysis; prz. art=articular surface of the prezygapophysis; poz=postzygapophysis; sp=neural spine; tp=transverse process. Number indicates vertebral count for each portion. Scale=2 cm.

between the last lumbar and the first sacral of the basal therocephalian described as *Cynariognathus* by Cys (1967, text-fig. 1) and because of this, we consider that the last (fifth) vertebra of this set is most likely the first sacral element.

The last set, comprising possible sacral and caudal vertebrae that decrease in size posteriorly (Fig. 8.3), is associated with an unidentified bone that might represent a girdle element. The prezygapophyses are relatively short and robust in comparison with those of the posterior dorsal and sacral regions, whereas postzygapophyses are relatively smaller. The bases of the postzygapophyses are closer together than those of the posterior dorsal and sacral regions. The ribs of the first vertebra are expanded laterally and curve anteriorly (Fig. 8.3). Remaining ribs are damaged and all point posteriorly. Although the ends of these ribs are broken there is no evidence of the expansion observed in the first vertebra.

*Scapula*.—Only the base of the scapula is preserved and has a similar general morphology to that of other basal therocephalians (Boonstra, 1964; Cys, 1967, text-fig. 3). It is a robust bone, which

is convex towards the base of the lamina but concave above the rim of the glenoid (Fig. 9.1). The anterior margin of the blade is thin at the base, as described in *Erciolacerta* (Watson, 1931), and as also seems to be the case in bauriids (King, 1996, fig. 5B), whereas it is rounded on the posterior margin. On the posterior margin, close to the glenoid, is a protuberance that probably served as the area of origin of the scapular head of the triceps (Jenkins, 1971). Projections of this kind are not common in therocephalian scapulae, but a well-developed projection at a similar location was also recognized in the holotype of *Zinnosaurus paucidens* (Boonstra, 1964, fig. 19). In addition, a long, moderate protuberance is observed in the same area in the basal therocephalian described by Cys (1967, text-fig. 3), although Cys (1967) does not describe this trait. A notable concavity is present laterally, close to the contact with the procoracoid. On the medial side, the scapula blade is divided in two areas by a ridge, with the posterior area being larger (Fig. 9.1).

*Ulna*.—The right ulna is relatively well preserved and has a length of 149.6 mm. The general morphology of the bone is

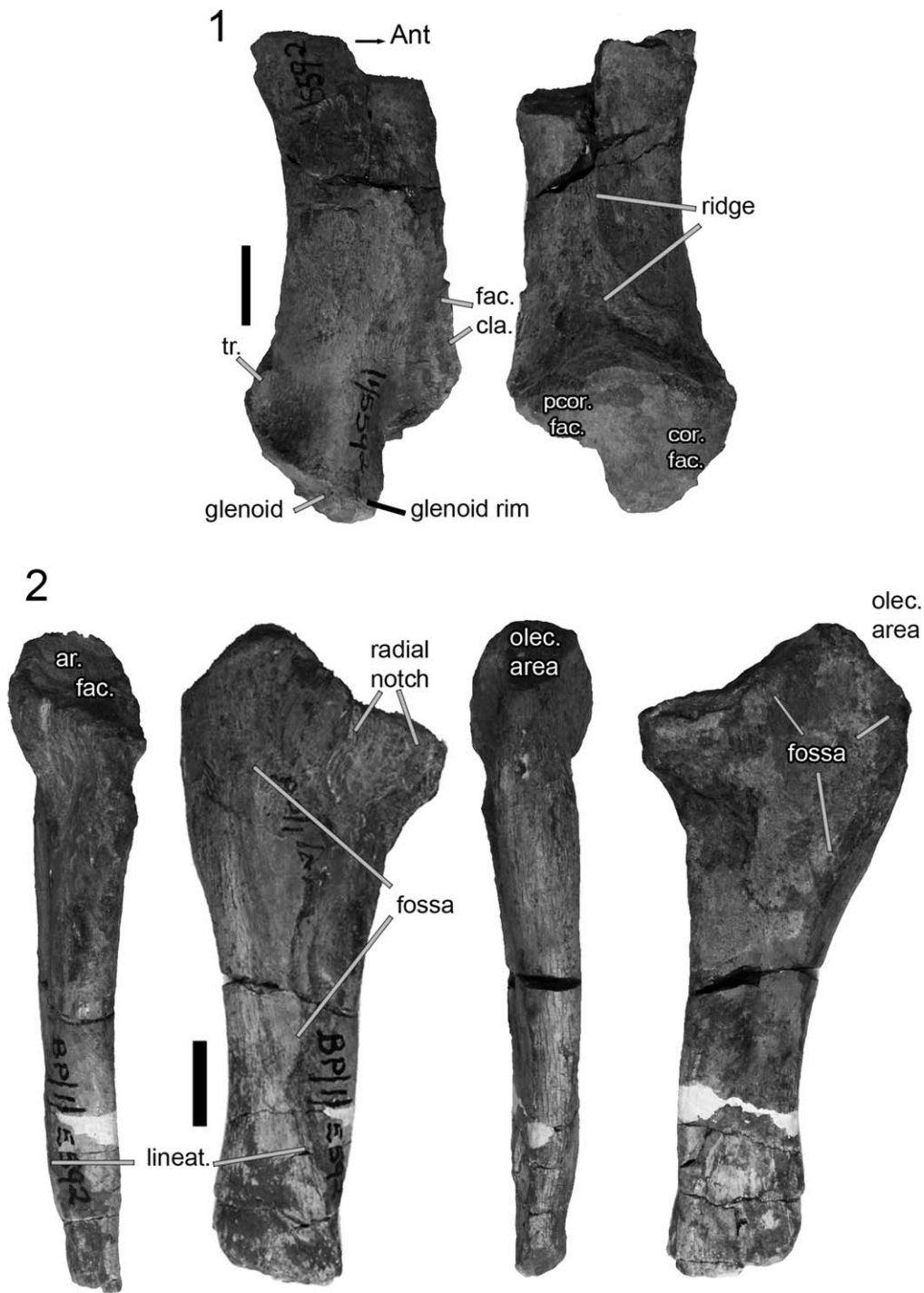


FIGURE 9—BP/1/5592. Photographs of *Simorhinella bairi* (BP/1/5592). 1, partial right scapula in lateral and medial views; 2, right ulna in anterior, lateral, posterior and medial views. Abbreviations: ar.fac.=articulation facet; cor.fac.=facet for the coracoid; fac. cla.=facet for the clavicle; lineat.=lineation; olec.=olecranon; pcor.fac.=facet for the procoracoid; tr.=protuberance for the triceps. Scale=2 cm.

similar to that of SAM-PK-9005 (holotype of *Scymnosaurus major*). The ulna is a relatively straight element with a low degree of proximo-distal (sigmoid) curvature (Fig. 9.2). There is a short, broad olecranon (Fig. 9.2). The presence of an olecranon process is an important distinction from other theriocephalians, which either lack an ossified process (e.g., Regisauridae indeterminate; Kemp, 1986, p. 225) or have it weakly developed (e.g., the bauriid *Microgomphodon oligocynus*, King, 1996, p. 387; for taxonomic identification of the specimen see Abdala et al., 2014). The development of the olecranon in lycosuchids is probably

related to the large body size of this group. The proximal facet is irregular, being wider in proximity to the olecranon and narrower anteriorly (Fig. 9.2). The radial notch is well developed, extending over half of the proximo-lateral surface of the bone. On the lateral surface of the ulna, there is a posterior longitudinal extensor fossa that starts at the level of the end of the radial notch (Fig. 9.2). This fossa extends distally for three-quarters of the length of the bone and is continued by a lineation directed anteriorly and somewhat medially. On the medial face of the ulna there is a wide, shallow flexor fossa delimited posteriorly by a

TABLE 2—Geographical distribution of specimens of Lycosuchidae. \*For Kitching (1977) the locality is Fraserburg Road (now Leeu Gamka Station), Prince Albert, southwest of Beaufort West. Abbreviations: S=specimens of *Simorhinella baini*; L=specimens of *Lycosuchus vanderrieti*.

Specimen	District	Farm
NHMUK 49422 (S)	Prince Albert	Weltevreden, Gouph
BP/1/5592 (S)	Victoria West	Rheboksfontein 76
US D173 (L)	Prince Albert	Groot Vlatke between Prince Albert, Beaufort West, and Willowmore*
CGS MJF68 (L)	Victoria West	Uitzigt 171
BP/1/7162 (L)	Jansenville	Hilary 53
MB.R.995 (L)	Beaufort West	'Beaufort West'
SAM-PK-751	Prince Albert	Seekoiegat
SAM-PK-1076	Prince Albert	Rietfontein 56
SAM-PK-1079	Prince Albert	Rietfontein 56
SAM-PK-2756	Prince Albert	Abrahamskraal 29
SAM-PK-3430	Prince Albert	Jan Willemsfontein 32
AMNH 5543	Prince Albert	Rietfontein 56
TM 275	Prince Albert	Abrahamskraal 29
CGS RMS1013	Prince Albert	Antjiesfontein
CGS RMS990	Prince Albert	Rietfontein 56
FMNH 1707	Prince Albert	About 3 miles NW of a dam, Stinkfontein
SAM-PK-9005	Beaufort West	Klein Koedoes Kop 310
SAM-PK-9084	Beaufort West	Riet Kuil 387
SAM-PK-10556	Beaufort West	Knoffelfontein, Van der Bylskraal 265
SAM-PK-12185	Beaufort West	Meyers Poort 326
CGS RMS 888	Beaufort West	Putfontein
SAM-PK-11936	Laingsburg	Bosluiskraal
SAM-PK-11961	Laingsburg	Dikbome 53
CGS MJF21	Victoria West	Amsterdam 126
CGS C60	Fraserburg	Tygerhoek 468
SAM-PK-8999		unknown
CGS RMS869		unknown
SAM-PK-632		unknown
NHMUK R5747		unknown

strong posterior crest. This fossa extends up to halfway along the ulna (Fig. 9.2). An incipient ulnar crest is present on the proximal region near the articular surface, but could not be discerned further distally.

DISCUSSION

*Basal therocephalians from the Middle Permian.*—The therocephalians from the *Eodicynodon* and *Tapinocephalus* AZs of the Beaufort Group are the oldest and most primitive representatives of this group. They also include the largest known therocephalians and would have been important predators in the Middle Permian. Lycosuchids are typical Middle Permian therocephalians, with large body size and well-developed incisor serrations. The taxonomic revision of van den Heever (1987) drastically reduced the number of recognized lycosuchid species from ten to only two. Van den Heever (1987) identified four specimens referable to the species *Lycosuchus vanderrieti*, including the holotypes of *Hyaenasuchus whaitsi* and *Zinnosaurus paucidens* (Table 1). The second species he recognized, "*Lycosuchus keyseri*," is a *nomen nudum*, as it was never proposed outside of van den Heever's (1987) unpublished Ph.D. thesis. In addition, he considered five species as *Lycosuchidae incertae sedis*, one as probably referable to the Lycosuchidae and *Lycosuchus mackayi* Broom 1903b as Therapsida *incertae sedis*. Three teeth are visible in the holotype of the latter taxon: a recurved functional canine, a replacement canine in the posterior alveolus, and a single, strongly posteriorly-canted postcanine (Fig. 1.3). Both canines bear fore and aft serrations. The Late Permian age, serrated canines, and posteriorly-canted postcanine are all consistent with a gorgonopsian identification for this specimen. We consider the taxon *L. mackayi* to be a *nomen dubium*, and refer it to *Gorgonopsia incertae sedis*.

The newly described specimen BP/1/5592 shows clear similarities in general skull morphology to lycosuchids, and is herein referred to that family. With a dorsal skull length of 370 mm (Table 5), this specimen is one of the largest lycosuchids (and

TABLE 3—Cranial measurements of BP/1/5592 (in mm).

Total skull length (dorsal)	370
Basal skull length	289
Interorbital width	79
Temporal region	133
Snout width at level of the root of the canines	138
Snout length	182
Orbital width	54
Occipital plate height above foramen magnum	108
Occipital plate base (paroccipital processes)	172
Occipital plate base (squamosal margin)	233
Left width canine alveolus	27
Maximum maxillary width at canine position	47
Orbital length	62
First postcanine length	11
Second postcanine length	0.9
Third postcanine length	0.8
Interpterygoid vacuity width (between transverse processes)	11
Width of basal tubera left	27
Width basal tubera (right) midpoint-edge	30
Minimum width of the choana (right side/left side)	10/0.7
Width basal tubera restricted to tubera (right side/left side)	20/20

indeed, therocephalians) known, roughly the same size as the partial skull of SAM-PK-632 (holotype of *Scymnosaurus ferox*), which has a snout length of 180 mm. In the palate, this specimen is remarkably similar to CGS M793, perhaps the best-preserved lycosuchid specimen (Fig. 6.1, 6.2). Among these similarities are: the morphology of the vomer, which is narrow in the choanal portion and expands laterally on the posterior one-third of this bone; a narrow anterior pterygoid ramus; the location and development of the posterior palatine foramen; the strong lateral margin of the choana defined by the maxillary christa choanalis; and a palatine that has a series of well-defined rugosities medial to the postcanine teeth. The most remarkable difference in the palate of BP/1/5592 compared to other lycosuchids is the presence of a sharp median crest between the choanal and the anterior portions of the expanded vomer (compare Fig. 6.1 and 6.2). A similar condition is present in the scylacosaurids, but this crest is fragile and "not often seen in prepared specimens" (van den Heever, 1994, p. 21).

*Simorhinella baini* from the *Tapinocephalus* AZ was previously known only from the holotype, comprising the snout and orbital portion of the skull, and part of the lower jaw (NHMUK 49422; Fig. 2). The small size of the specimen and the very open suture between the nasals, amongst other characters, indicates that this specimen is a juvenile. Another feature clearly indicative of juvenile status is an extremely reduced snout in which postcanine teeth are positioned below the orbits, an unusual condition in therocephalians. Based on the combination of these features and the presence of only four or five incisors (Mendrez, 1975), and possibly four postcanines, we interpret the holotype of this taxon as a juvenile lycosuchid. NHMUK R49422 also has a vomerine median crest, similar to that described in BP/1/5592. Because of this character and the extremely large size of BP/1/5592, we consider the new specimen to represent an adult of *S. baini*. A palatal view is necessary to observe most characters differentiating this species from *Lycosuchus vanderrieti*, therefore some specimens previously identified as *L. vanderrieti* (e.g., SAM-PK-1079: holotype of *Hyaenasuchus whaitsi*; SAM-PK-12185: holotype of *Zinnosaurus paucidens*), are here considered as *Lycosuchidae incertae sedis*. Further preparation of the palate of these specimens will be necessary to establish a specific taxonomic assignment within Lycosuchidae.

Some features of *Simorhinella* (e.g., median vomerine crest, ventral extension of ridges from the transverse processes of the pterygoid) are shared with scylacosaurids to the exclusion of *Lycosuchus*, raising the possibility that Lycosuchidae (as made up

TABLE 4—Measurements (mm) of vertebral elements of BP/1/5592. They are numbered according preserved portion not anatomical location of the elements. Anteroposterior length was measured at the middle of the centrum; height is from the base of the center to above the origin of the transverse process.

	Anteroposterior length	Maximum width center	Height
<b>Cervicals</b>			
First vertebra	30	32	45
Second vertebra	31	32	46
<b>Transition dorsal-sacral</b>			
First vertebra	29	38	47
Second vertebra	30	42	48
Third vertebra	30	41	49
<b>Caudal</b>			
First vertebra		41	
Second vertebra		35	
Third vertebra	27	33	35
Fourth vertebra		30	

of *Lycosuchus* and *Simorhinella*) is paraphyletic with regards to Scylacosauria (Scylacosauridae + Eutherocephalia). A robust test of the phylogenetic relationships of lycosuchids and scylacosaurids will require a taxonomic revision of the latter family, as the number of valid species of scylacosaurids is uncertain. Additionally, further information on the morphology of Middle Permian gorgonopsians is needed, so as to polarize characters at the base of Eutheriodontia. Few Middle Permian gorgonopsian specimens have been described, and most are poorly-prepared or incomplete (Kammerer, 2014).

*Canine replacement in lycosuchids.*—One of the key characters originally used to diagnose the Lycosuchidae was the presence of two functional canines in each maxilla (Haughton and Brink, 1954; Kermack, 1956). A study of all available lycosuchid material led van den Heever (1980) to consider this diagnostic character for the family to be invalid, and proposed that the presence of double canines was related to tooth replacement. We agree with this interpretation, but it is interesting to note that in most of the specimens studied (10 of 18; Table 6) there is evidence of canine replacement. This suggests a rapid rate of canine replacement in lycosuchids, and the fact that in some specimens the functional and replacement canines are similar in size indicates that the final shedding of the old canine occurred

TABLE 5—Skull measurements and number of incisors and postcanines in specimens assigned to the Lycosuchidae. Dorsal skull length and snout length in mm. Specimens are ordered by skull size. When the skull was incomplete the order is by the length of the snout. In specimens represented by fragment of the snout (e.g., SAM-PK-632) we used the length from the tip of the snout to the last incisor to infer placement in the size series.

Specimen	Skull length	Snout length	Incisors	Postcanines
SAM-PK-9005		226	5	2(?)
BP/1/5592	370	182	5	4(?)
SAM-PK-632		180	5	At least 3
TM 275			5	2(?)
SAM-PK-9084		181	5	3 to 4
FMNH 1707		163	5	4
BP/1/7162	298	149	5	?3
SAM-PK-1079	296	130	5	3(?)
CGS M793	~275			2
SAM-PK-2756	~237		5	4
CGS C60		119	4(?)	3
CGS RMS 1013	234	117	5	3
US D173	232	114	5	3
CGS RMS888		114	5	3
SAM-PK-12185	223	102	5	2(?)
CGS MJF68	220	121	5	3
AMNH 5543	219	126	5	3
CGS RMS 990	218	105	5	3
SAM-PK-1076		101	5	3
NHMUK R 49422		21	4	3

TABLE 6—Upper canine replacement status in specimens referred to the Lycosuchidae. Abbreviations: ACE=anterior canine erupting; RA=anterior canine replacing the posterior; RP=posterior canine replacing the anterior; R?=replacement occurring but it is not possible to know which one is the new element. Specimens have the same order as in Table 5.

Specimen	Left	Right
SAM-PK-9005	1	1
BP/1/5592	ACE	1
SAM-PK-632	1	1
TM 275	R?	?
SAM-PK-9084	1	1
FMNH 1707	1	1
BP/1/7162	RP	RA
SAM-PK-1079	1	1
SAM-PK-2756	RP	RP
CGS M793	RA	1
CGS C60	RP	RP
CGS RMS1013	1	RA
US D173	RA	R?
CGS RMS888	1	1
SAM-PK-12185	RA	
CGS MJF68	1	1
AMNH 5543	RA	
CGS RMS990	1	1
SAM-PK-1076	1	RA
NHMUK R 49422	1	1

when the new tooth was almost in its final placement. Canine replacement is represented in the entire series of specimens and not restricted to a particular skull size. The common condition in lycosuchid canine replacement is the new tooth erupting anterior to the upper functional canine. This condition is represented in eight out of 10 specimens showing canine replacement (Table 6). Variation in the canine replacement pattern is illustrated by specimen BP/1/7162, the only case in which the new canine is erupting anterior to the functional one on the right side but posterior to the functional tooth on the left.

*Suspensorium.*—The new specimen BP/1/5592 provides fresh information on the quadrate-quadratojugal, a complex that is usually not preserved or is concealed because of the articulation with the lower jaw. The dorsal portion of the quadrate is not embayed as observed in *Glanosuchus* but appears to be rather flat. The trochlea in *Simorhinella baini* is smooth, without clear distinction of the medial and lateral condyles and is thus different to that of other therocephalians, including other lycosuchids (e.g., *Scymnosaurus ferox*; Boonstra, 1953; van den Heever, 1994). The continuity of the lateral and medial condyles on the trochlea has also been reported for whatsiids (Kemp, 1972b), whereas Laurin (1998) mentioned the lack of differentiation between the quadrate condyles in the gorgonopsian *Lycaenops* but attributed this condition to overpreparation. A lateral process of the quadratojugal is not commonly mentioned in descriptions of the therocephalian suspensorium but was also present in the Russian therocephalian *Purlovia maxima*, although the process is more projected laterally and less high than in *S. baini* (Ivakhnenko, 2011, fig. 11b). The quadratojugal foramen, as observed in the posterior view of the scylacosaurid specimen CGS RS330 (van den Heever, 1994, fig. 11b), is much larger than that of *S. baini*. The dorsal process of the quadrate is robust and possesses a depressed area on its anterior face, possibly homologous with the area interpreted in the quadrate of Gorgonopsia for the insertion of the posterior pterygoid muscle (Kemp, 1969). The partially visible posterior portion of the dorsal process of *S. baini* is flat and shows some ridges and small depressions. The posterior side of the process in Gorgonopsia is concave but, like *S. baini*, has a series of ridges and pits (Kemp, 1969). The displacement of the quadrate complex in relation to the articulation notch of the squamosal suggests a movable connection between these bones. Kemp (1969) suggested the presence of a streptostylic condition in gorgonopsians after analyzing the suspensorium of specimens from Tanzania. Laurin (1998), however, argued against a

streptostylic condition between the quadrate and the squamosal, although he recognized a loose contact between these bones. However, he stated that a similar kind of contact between squamosal and quadrate “prevailed in early synapsids (the quadrate was even less tightly linked to the squamosal in Permo-Carboniferous synapsids)” (Laurin, 1998, p. 774).

*Abundance of basal therocephalians in the Lower Beaufort Group.*—Determining the stratigraphic provenance of specimens in the lower portion of the Beaufort Group is complicated by the folded nature of strata of the Abrahamskraal Formation in the south of the Karoo Basin, resulting from the Cape orogenic event. A further problem is that specimens in museum collections that were collected long ago lack good stratigraphic provenance data. However, a detailed study of stratigraphic distribution of fossil tetrapods in the Abrahamskraal Formation has recently been achieved (Day, 2013). This utilized the GIS database of georeferenced Beaufort Group tetrapod fossils (Nicolas, 2007), combined with long-term targeted stratigraphic fossil collecting, refined stratigraphic mapping, and the systematic measurement of stratigraphic sections in the Abrahamskraal and lower Teekloof formations by the researchers at the Evolutionary Studies Institute. The updated taxonomic review of the lineages represented in the *Eodicynodon*, *Tapinocephalus* and *Pristerognathus* AZs, in combination with the more accurate assessment of stratigraphic and geographic distribution of species in the last decade, has permitted renewed understanding of patterns of distributional change in fossil tetrapods from these biozones.

In the lower three assemblage zones of the Beaufort Group, therocephalians are important components of the tetrapod fauna, with medium to large forms that were subordinate only to the dinoccephalian *Anteosaurus* within the predator guild. Therocephalians are represented by two specimens in the *Eodicynodon* AZ, 66–83 in the *Tapinocephalus* AZ and 18–40 in the *Pristerognathus* AZ (the uncertainty in numbers is due to many specimens being collected close to the boundary of the latter two assemblage zones). Middle Permian therocephalians belong almost exclusively to one of two families: Lycosuchidae and Scylacosauridae. Only scylacosaurids are currently known in the *Eodicynodon* AZ, and thus represent the oldest known therocephalians (Abdala et al., 2008). Scylacosaurids remained the dominant group throughout the Middle Permian of the Karoo sequence: within the three lower assemblage zones, the Scylacosauridae are represented by at least 77 specimens versus 30 recognized for Lycosuchidae, giving a ratio of approximately 2.3:1.

At the top of the *Pristerognathus* AZ and the base of the overlying *Tropidostoma* AZ therocephalians experienced taxonomic turnover that led to an increase in generic diversity and morphological heterogeneity (i.e., evolution of Eutherocephalia, Huttenlocker et al., 2011; Sigurdson et al., 2012) concurrent with a reduction in average body size (Huttenlocker, 2014). This transition also resulted in the disappearance of the Lycosuchidae and Scylacosauridae, which are unknown above the *Pristerognathus* AZ.

*Stratigraphic and temporal distribution of the Lycosuchidae in the Lower Beaufort Group.*—*Lycosuchus vanderrieti* has a stratigraphic distribution that corresponds to the *Pristerognathus* AZ and the uppermost *Tapinocephalus* AZ (Fig. 3). The lower limit of this range is suggested by two geographically disparate specimens, CGS MJF 68 and BP/1/7162. CGS MJF 68 was found on the farm Uitzigt 171 to the north of Victoria West. This specimen is from the uppermost Abrahamskraal Formation and hence from the upper *Tapinocephalus* AZ. BP/1/7162 was recovered from the upper Koonap Formation on the farm Hilary, Jansenville district, from the Eastern Cape Province, and, although the biostratigraphic position of this fossil is less secure, it is likely that this corresponds to the upper *Tapinocephalus* AZ

as well (Day et al., 2013). The stratigraphically highest specimen is CGS M793 from the farm Drie Kop 396, Beaufort West district, which can be constrained to the uppermost Poortjie Member (*Pristerognathus* AZ).

The type specimen of *L. vanderrieti*, US D173, was described by Broom (1903a) as coming from the ‘Groot Vlake between Prince Albert, Beaufort West and Willowmore.’ This area exposes strata of the Abrahamskraal Formation and Poortjie Member of the Teekloof Formation and thus both the *Tapinocephalus* and *Pristerognathus* AZs (Rubidge et al., 1995; Van der Walt et al., 2010). An additional historic specimen, MB.R.995, is reported to come only from the vague area of ‘Beaufort West’ and therefore its stratigraphic provenance is too broad to be of use. Kitching (1977) reports a specimen of *L. vanderrieti* from Fraserburg Road (now Leeu-Gamka), but this cannot be substantiated.

The two specimens attributed to *S. baini* (NHMUK 49422 and BP/1/5592) were both recovered from the southwestern part of the Karoo Basin (Fig. 3). The holotype, NHMUK 49422, comes from the farm Weltevreden in the Prince Albert district, which exposes strata from the upper few hundred meters of the Abrahamskraal Formation; this constrains it only broadly to the *Tapinocephalus* AZ, although likely lower within it than BP/1/5592. The current record of *S. baini* therefore restricts this species to the upper *Tapinocephalus* AZ.

The majority of lycosuchid specimens have been found in the Abrahamskraal Formation, but the stratigraphic range of the family can be constrained with relative certainty only to the upper 450 m of the formation. The stratigraphically lowest specimens (SAM-PK-2756 and TM 275) were collected on the farm Abrahamskraal in the Prince Albert district and could potentially have been recovered from strata up to 800 m below the top of the Abrahamskraal Formation; the associated fossil taxa from the farm Abrahamskraal show that these specimens are from the *Tapinocephalus* AZ. The stratigraphically highest specimen is CGS M793 (*L. vanderrieti*), from the upper Poortjie Member. This indicates that the stratigraphic range of the family Lycosuchidae probably includes most of the *Tapinocephalus* AZ and succeeding *Pristerognathus* AZ (Fig. 3).

Because the base of the *Pristerognathus* AZ has been dated to >261.24 Ma and the top of the *Pristerognathus* AZ to approximately 260 Ma (Rubidge et al., 2013), the temporal range of the Lycosuchidae corresponds to the late Capitanian (Shen et al., 2013). This is corroborated by tetrapod biostratigraphic correlation with Russia (Rubidge, 2005) and is consistent with an early Capitanian age derived from the mid-Abrahamskraal Formation at Ouberg Pass (Lanci et al., 2013).

#### CONCLUSION

The first adult specimen of the lycosuchid therocephalian *Simorhinella baini* is described, representing one of the largest skulls known for a therocephalian from the *Tapinocephalus* AZ (basal skull length of ~370 mm). A diagnostic feature for *Simorhinella baini*, unique amongst Lycosuchidae, is the presence of a sharp crest in the mid-line of the vomer, a feature previously reported in scylacosaurid therocephalians from the same Assemblage Zone. Two species of Lycosuchidae are thus recognized: the type species *Lycosuchus vanderrieti*, represented by four specimens, and *Simorhinella baini*, represented by the holotype NHMUK 49422 and the new specimen described here.

Therocephalia is represented by two families of large carnivores in the Middle Permian of South Africa: Lycosuchidae and Scylacosauridae. The latter family is more abundant in the three Middle Permian assemblage zones of the Karoo Basin, with a proportion of 2.3:1. Lycosuchidae is documented by 30

specimens (see Table 2), which are known from the upper *Tapinocephalus* AZ and the entire *Pristerognathus* AZ. Recent radiometric dating constrains the age of the Family Lycosuchidae to the late Capitanian.

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