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On the stratigraphic range of the dicynodont taxon *Emydops* (Therapsida: Anomodontia) in the Karoo Basin, South Africa

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The dicynodont specimen SAM-PK-708 has been referred to the genera *Pristerodon* and *Emydops* by various authors, and was used to argue that the first appearance of *Emydops* was in the *Tapinocephalus* Assemblage Zone in the Karoo Basin of South Africa. However, the specimen never has been described in detail, and most discussions of its taxonomic affinities were based on limited data. Here we redescribe the specimen and compare it to several small dicynodont taxa from the *Tapinocephalus* and *Pristerognathus* assemblage zones. Although the specimen is poorly preserved, it possesses a unique combination of features that allows it to be assigned confidently to *Emydops*. The locality data associated with SAM-PK-708 are vague, but they allow the provenance of the specimen to be narrowed down to a relatively limited area southwest of the town of Beaufort West. Strata from the upper *Tapinocephalus* Assemblage Zone and the *Pristerognathus* Assemblage Zone crop out in this area, but we cannot state with certainty from which of these biostratigraphic divisions the specimen was collected. Nevertheless, SAM-PK-708 is an important datum because it demonstrates that the stratigraphic range of *Emydops* must be extended below its widely-accepted first appearance in the *Tropidostoma* Assemblage Zone. This range extension is significant because it implies that the divergence between the emydopid and dicynodontid lineages must have occurred no later than *Pristerognathus* Assemblage Zone times, and that most of the major lineages of Permian dicynodonts had emerged by a relatively early point in the history of the group.

Keywords: *Emydops,* Karoo Basin, biostratigraphy, *Pristerognathus* Assemblage Zone, *Tapinocephalus* Assemblage Zone.

INTRODUCTION

The Emydopidae (*sensu* Angielczyk & Kurkin 2003) is a clade of dicynodont therapsids known from the Late Permian to Middle Triassic of South Africa (e.g. King 1988), India (Kutty 1972; Ray 2001), Tanzania (von Huene 1939, 1940, 1942; Cox 1972), Zambia (Drysdall & Kitching 1962; 1963; Kitching 1963), and Antarctica (Cosgriff & Hammer 1979; Hammer & Cosgriff 1981; DeFauw 1989). Although they never achieved the taxonomic diversity of their sister taxon, the dicynodontids, emydopid dicynodonts are noteworthy because some members of the group show diverse and very distinctive modifications of the skull and postcranial skeleton. For example, *Cistecephalus, Cistecephaloides,* and *Kawingasaurus* are highly specialized for a fossorial mode of life (Cox 1972; Cluver 1974, 1978), whereas *Kingoria* shows some of the strongest adaptations for an upright hind limb posture of all dicynodonts (Cox 1959; King 1985; DeFauw 1986). The emydopids also are survivors of the end-Permian mass extinction, with two separate lineages, *Myosaurus* and *Kombuisia,* occurring in the Early and Middle Triassic (Fröbisch and Reisz 2004). Finally, they have played a role in Late Permian terrestrial biostratigraphy for nearly a century (e.g. Broom 1906; Watson, 1914; Kitching 1977; Rubidge 1995).

The most extensively studied emydopid fossil record is found in the Karoo Basin of South Africa. Most recent biostratigraphic studies of the Karoo have suggested that the stratigraphic range of the clade begins with the first appearance of *Emydops minor* in the Late Permian-aged *Tropidostoma* Assemblage Zone or its equivalents (e.g. Kitching 1977; Keyser & Smith 1977–1978; Rubidge 1995), and emydopid-bearing strata outside the Karoo generally have been regarded as coeval with or younger than the *Tropidostoma* Assemblage Zone (e.g. Drysdall & Kitching 1963; Anderson & Cruickshank 1978; Smith & Keyser 1995a,b; Gay & Cruickshank 1999; Ray 2001; Angielczyk 2002a). This pattern of stratigraphic occurrence is somewhat surprising because recent phylogenetic studies (e.g. Angielczyk 2001; Angielczyk & Kurkin 2003) suggest that the lineage including the emydopids and dicynodontids must have diverged by *Tapinocephalus* Assemblage Zone times (Fig. 1). If the phylogenetic hypothesis is accurate, then the apparent absence of stem members of the lineage, or emydopids and dicynodontids themselves, in strata older than the *Tropidostoma* Assemblage Zone in the Karoo implies that the earliest history of these lineages either has been overlooked in the South African fossil record or occurred in a different geographical region.

Here we discuss a single dicynodont specimen, SAM-PK-708, that fills in at least part of the ghost range of the lineage including the dicynodontids and emydopids. SAM-PK-708 is a poorly preserved skull and jaw that Robert Broom described as the holotype of *Opisthoctenodon brachyops* in 1905. Since that time the specimen has been referred to the dicynodont taxa *Pristerodon* and *Emydops* on various occasions (Broom 1915, 1932; Kitching 1977; Cluver & King 1983; King 1988; Keyser 1993; King & Rubidge 1993; Angielczyk & Kurkin 2003), but none of these authors provided a detailed justification for their

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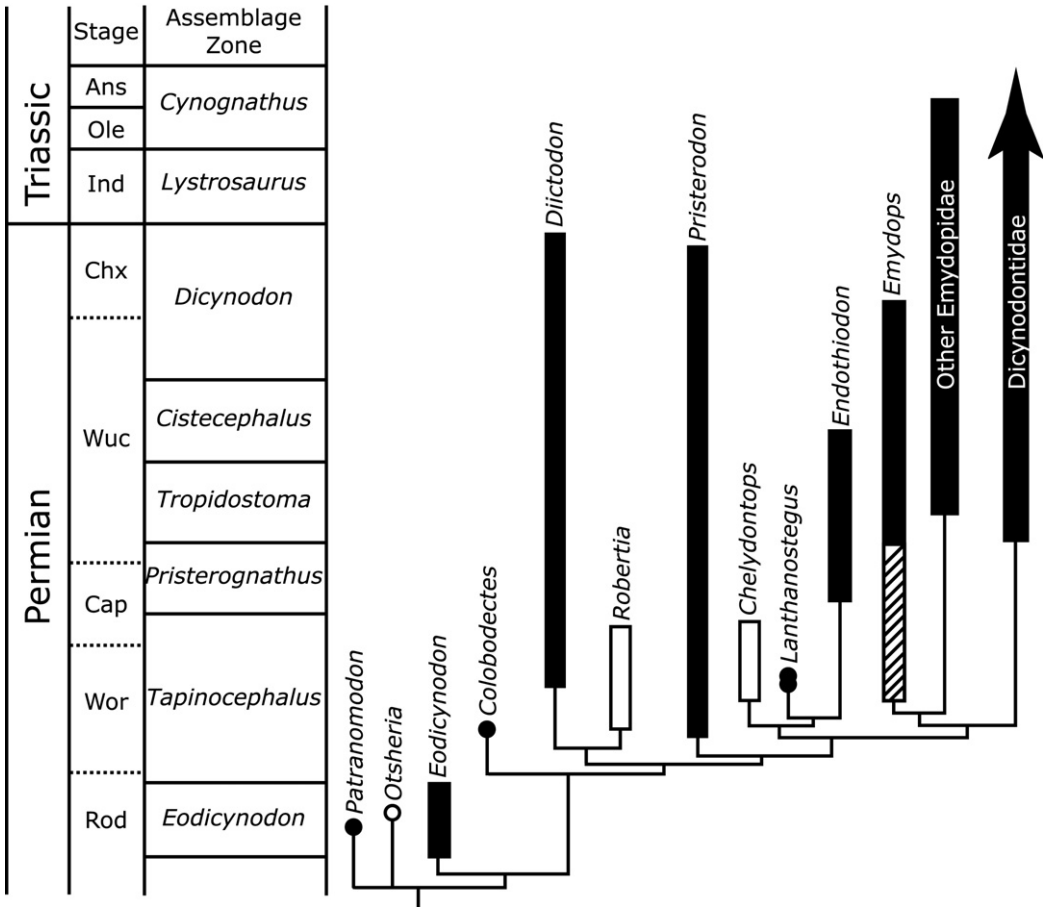

Figure 1. Cladogram drawn to show stratigraphic ranges of *Emydops* and other dicynodonts from the *Tapinocephalus* and *Pristerognathus* assemblage zones. The solid bar for *Emydops* represents its currently-accepted stratigraphic range, whereas the hatched box represents an estimate of the maximum ghost range of the taxon. SAM-PK-708 partially fills this gap, although it is uncertain whether the specimen originated in the *Tapinocephalus* or *Pristerognathus* zones. Topology modified from Modesto *et al.* (2002, 2003) and Angielczyk & Kurkin (2003). Biostratigraphic divisions are based on Rubidge (1995), and ranges of taxa are taken primarily from Rubidge (1995). Correlations of Permian assemblage zones with marine stages are approximate. The stratigraphic occurrences of taxa known from single specimens are represented by dots, whereas ranges of taxa known from multiple specimens are shown by boxes. *Lanthanostegus* is known from two specimens. Ranges for taxa represented by open symbols are poorly constrained.

attributions. We demonstrate that SAM-PK-708 possesses a combination of several features that is found in *Emydops* and no other coeval small dicynodont. Moreover, although the locality data associated with the specimen are vague, it is clear that SAM-PK-708 must have been collected in strata of either the *Tapinocephalus* Assemblage Zone or *Pristerognathus* Assemblage Zone. This finding pushes back the range of the emydopids, and the age of their divergence from the dicynodontids, to at least the *Pristerognathus* zone (Fig. 1). However, we cannot state with certainty that *Emydops* was present in the *Tapinocephalus* Assemblage Zone (contra King 1990; King & Rubidge 1993).

TAXONOMIC HISTORY OF SAM-PK-708

SAM-PK-708 was obtained by Robert Broom from J.R. Joubert on an unknown date. A handwritten note in the accession catalogue of the South African Museum states that Joubert may have collected the specimen in 1881. The locality data, available from subsequent publications and the collections catalogue, are relatively vague and contradictory, and will be discussed in more detail below. In his original description, Broom (1905) made the specimen the holotype of the new species *brachyops,* which he placed in *Opisthoctenodon,* a genus he had only recently erected (Broom 1904). Besides the genotype, *Opisthoctenodon agilis* (AM 4319), SAM-PK-708 is the only specimen that has ever been assigned to this genus. Later, in 1915 Robert Broom re-identified AM 4319 as well as SAM-PK-708 as *Pristerodon.* He based his interpretation on the presence of a number of characters but especially noted the posteriorly serrated 'molars,' which he considered a unique and diagnostic feature of this genus. However, with respect to SAM-PK-708 he stated: 'As the crowns of the molars are unknown it is impossible to be certain that it belongs to *Pristerodon,* but it agrees sufficiently to admit of its being placed here, at least provisionally' (Broom 1915, 358). Several authors (Broom 1932; Haughton & Brink 1954; Kitching 1977; Brink & Keyser 1985) followed Broom's identification of the specimen, but all failed to deliver a detailed diagnosis.

In contrast to the previous authors, Cluver & King (1983) identified SAM-PK-708 as *Emydops,* although they also did not justify their attribution. Moreover, they figured the right lower jaw of the specimen in dorsal and lateral views to show the presence of a short, shallow groove known as the posterior dentary sulcus, a feature that is present in both *Pristerodon* as well as in *Emydops.*

In 1988 King also mentioned SAM-PK-708 in the *Encyclopedia of Paleoherpetology* volume covering the Anomodontia. She referred to the specimen as *Emydops* sp. without ascribing it to any of the eleven recognized *Emydops* species. It is unclear why King (1988) did not use the combination *Emydops brachyops,* but it may be related to the lack of a recent species-level taxonomic revision for the genus at that time.

This situation changed in 1993 when Keyser presented his comprehensive but controversial re-evaluation of what he called the 'smaller Endothiodontidae'. This first and so far only species-level taxonomic revision of emydopids also discussed the two species of the genus *Opisthoctenodon,* called *Pristerodon agilis* and *Pristerodon brachyops* in the paper. Keyser declared the genotype, *P. agilis,* a *nomen dubium,* instead of a synonym of *Pristerodon mackayi,* whereas he regarded the type specimen of *P. brachyops* to be 'an ordinary *Pristerodon*' (Keyser 1993, 24). This statement implies that in his opinion *P. brachyops* (Broom, 1905) is synonymous with *P. mackayi* Huxley, 1868, the only valid species of *Pristerodon.*

In the same year, King & Rubidge (1993) revised the paraphyletic assemblage of small dicynodonts with postcanine teeth at the genus-level and presented generic diagnoses for the taxa they considered valid, i.e. *Pristerodon, Emydops, Eodicynodon,* and *Robertia.* Following Cluver & King (1983) they identified SAM-PK-708 as *Emydops,* but they did not discuss its specific validity. Most recently, Angielczyk & Kurkin (2003) adopted Keyser's (1993) taxonomic identification of SAM-PK-708 as a junior synonym of *Pristerodon mackayi,* but without having personally examined the specimen.

Because of the complex taxonomic history and potential biostratigraphic significance of SAM-PK-708, as well as the fact that most discussions of the specimen have been based on assertions instead of data, we deem it necessary to re-evaluate it in more detail.

COMPARATIVE DESCRIPTION OF SAM-PK-708

SAM-PK-708 consists of a skull and jaw preserved in a single nodule that is broken into four large pieces and a number of smaller fragments. Many of the exposed bone surfaces on the dorsal, anterior and lateral sides of the specimen appear to be weathered, suggesting that they were exposed for some time before the specimen was collected. Because SAM-PK-708 is poorly preserved, we have not endeavored to provide a full description of its morphology. Instead, we focus on documenting features that allow its diagnosis as an *Emydops* specimen, as well as describing similarities and differences between it and other small dicynodonts from the *Tapinocephalus* and *Pristerognathus* assemblage zones.

SAM-PK-708 has a snout–occipital condyle length of approximately 61.2 mm, which is slightly larger than most *Emydops* specimens, but within the known size range of this taxon (e.g. AMNH 5525 = 36.2 mm, BP/1/2366 = 60.0 mm, BP/1/262 = 61.4 mm, SAM-PK-3721 = 47.4 mm, SAM-PK-10148 = 53.0 mm, SAM-PK-10170 = 52.0 mm, SAM-PK-K1671 = 36.1 mm; SAM-PK-K6623 = 52.4 mm). It also is similar to *Pristerodon* (e.g. BP/1/2642 = 67.9 mm, BP/1/2134 = 75.2 mm, BSP 1934-VIII-24 = 77.5 mm, SAM-PK-10153 = 62.6 mm, SAM-PK-K1658 = 55.9 mm), but smaller than is typical for *Brachyprosopus* (FMNH 1561 >107 mm), *Chelydontops* (e.g. SAM-PK-12259 = 128.3 mm), *Colobodectes* (NM QR3329 = 103.3 mm), *Diictodon* (e.g. BMNH R11184 = 95.4 mm, SAM-PK-2354 = 73.1 mm, SAM-PK-10086 = 89.1 mm, SAM-PK-K1242 = 103.2 mm, SAM-PK-K5105 = 91.2 mm), *Robertia broomiana* (e.g. SAM-PK-11461 = 75.0 mm, SAM-PK-11761 = 99.0 mm, SAM-PK-K7807 = 94.1 mm, NMNH 23342 = 103.3 mm), and *Robertia* sp. (e.g. BP/1/1779 = 102.3 mm, NM QR 3145 = 116.5 mm, NMNH 23345 = 113.2 mm). *Lanthanostegus* and *Endothiodon* attain much larger sizes.

The dorsal surface of SAM-PK-708 has been heavily weathered (Fig. 2a), and large portions of the dorsal surface of the snout, interorbital region, and intertemporal region are missing as a consequence. However, it is clear that the intertemporal region of the skull was relatively wide, and the parietals were widely exposed between the postorbitals. A large opening approximately midway along the length of the preserved skull roof likely represents the pineal foramen, whose size has been exaggerated by weathering. A preparietal appears to be present anterior to the pineal foramen, but cracking of the bone in this region of the skull roof makes its exact sutures difficult to trace. The mid-parietal suture can be traced posterior to the pineal foramen, and it meets the suture between the parietals and the postparietal (or interparietal) at the posterior edge of the skull roof. None of the preserved features of the skull roof are exclusive to *Emydops.* However, the fact that the postparietal does not contribute to the dorsal surface of the skull roof argues against the referral of this specimen to *Pristerodon,* a taxon in which the postparietal does contribute to the dorsal surface of the skull roof. The wide exposure of the parietals on the dorsal surface of the skull also is unlike the condition found in *Diictodon,* where the postorbitals nearly completely overlap the parietals.

Little of the occipital surface of the skull is visible when the four main pieces of the nodule are reassembled (Fig. 2d). If the posteriormost piece of the nodule is removed, a transverse section through the occipital plate is exposed (Fig. 2e). Although this does not represent the original external surface of the occiput, some of its characteristics can be inferred. The right side of the occipital plate is damaged so that the lateral profile of the occiput is only preserved on the left side of the skull. The foramen magnum is a large, oval opening that is located to the right of centre on the preserved occipital surface. It is flanked on either side by the posttemporal fenestrae. The left jugular foramen is visible ventrolateral to the foramen magnum. The surface of the bone has undergone extensive cracking, making the sutures between most of the occipital bones difficult to trace. However, the sutures between the opisthotic and the squamosal, and the supraoccipital and the squamosal are visible on the left side. The most diagnostic feature of the occiput is its distinctively squared-off lateral profile (visible only on the left side of the specimen), a morphology that is characteristic of *Emydops* (Fig. 3). Although this morphology can be found

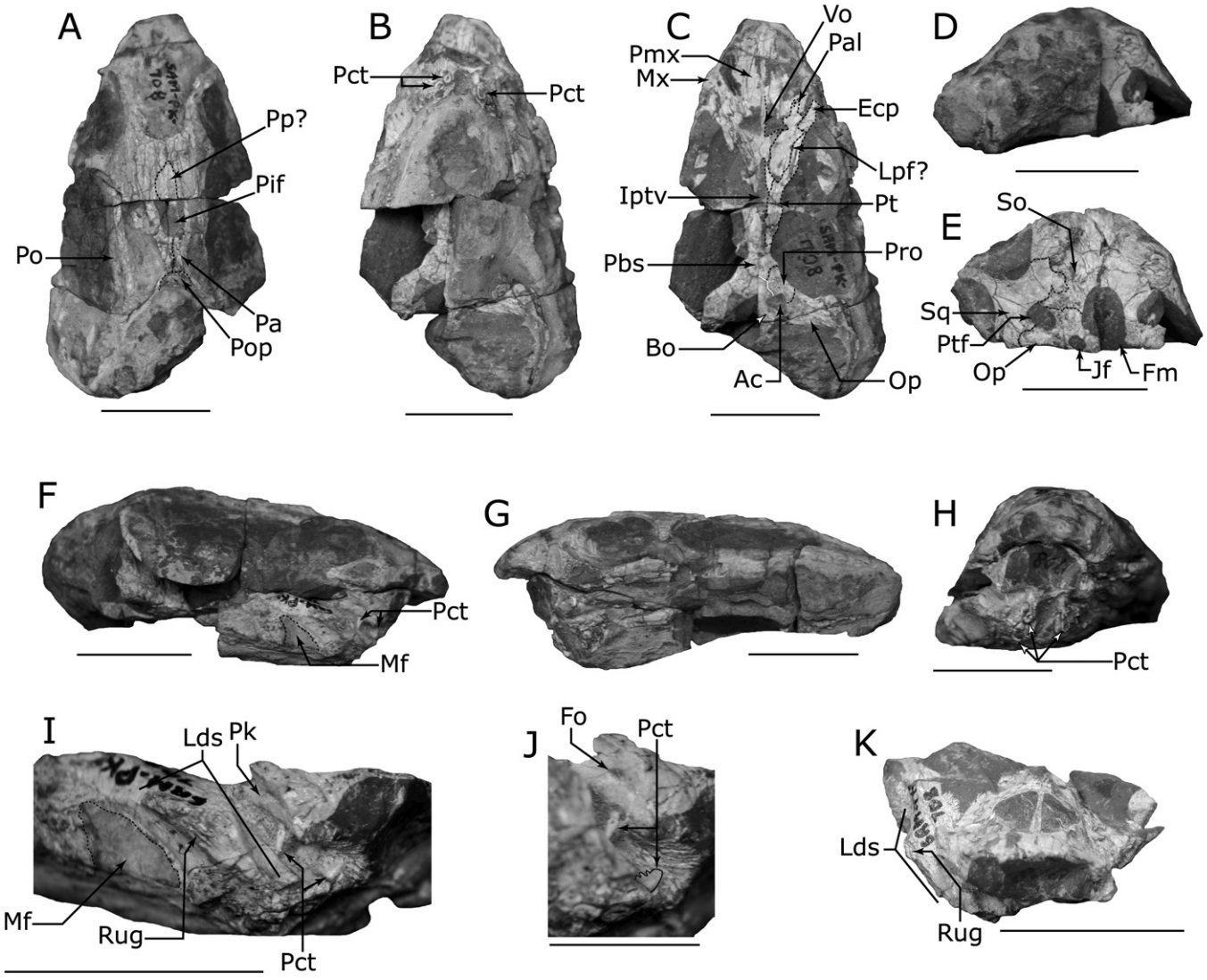

Figure 2. SAM-PK-708. **A**, Dorsal view. **B**, Ventral view, with outer pieces of nodule in place. **C**, Ventral view with outer pieces of nodule removed, exposing coronal section through palate. **D**, Posterior view with outer piece of nodule in place. **E**, Posterior view with outer piece of nodule removed, exposing transverse section through occipital plate. **F**, Right lateral view. **G**, Left lateral view. **H**, Anterior view. **I**, Oblique right lateral view of lower piece of nodule. **J**, Closeup of postcaniniform keel area in I, showing presence of foramen on postcaniniform keel. **K**, Anterodorsal view of the lower piece of nodule, showing dorsal profile of lateral dentary shelf. Scale bar in each panel is 20 mm, except in J, where it is 10 mm. Sutures shown in C and E are as preserved on the specimen, and are not necessarily representative of original sutures that were present on the exterior surfaces of the palate or occipital plate. Note posterior serrations on lower postcanine tooth in I and J.

in some post-*Pristerognathus* zone taxa (e.g. *Myosaurus*), it is not present in any other *Tapinocephalus* or *Pristerognathus* zone dicynodonts (Fig. 3).

Most of the ventral surface of the skull is obscured when the main pieces of the nodule are reassembled, although weathered portions of the postcanine teeth and secondary palate are exposed anteriorly (Fig. 2b). When the two large bottom pieces of the nodule are removed, a section through the ventral surface of the skull is exposed (Fig. 2c). The morphology presented here is typical of dicynodonts. Anteriorly, the secondary palate is formed dominantly by the premaxilla. Its lateral margins are made up by the maxillae, and the palatines and vomer contact it posteriorly. The midventral vomerine plate extends through the middle of the internal nares, and contributions of the palatines and vomer to the dorsal roof of the choanal region also are visible. Ectopterygoids are present lateral to the palatines, and the remains of the lateral palatal foramen may be visible on the left side of the specimen. A relatively large interpterygoid vacuity is present. As is typical in dicynodonts, it is bounded anteriorly by the vomer and laterally and posteriorly by the pterygoids. The remains of the crista oesophagea are present on the median pterygoid plate, and it appears that the crista originally was relatively tall. The anterior pterygoid rami are not well preserved, but appear to have been relatively straight. Posteriorly, the parabasisphenoid is visible between the posterior edge of the median pterygoid plate and the anterior edge of the basioccipital. Contacts between the basioccipital, prootic, and opisthotics, and between the parabasiphenoid and the prootics also are visible. A section through the auditory canal can be seen on both sides of the skull, but is better preserved on the left side of the specimen. Although *Emydops* is characterized by several features of the ventral surface of the skull (e.g. absence of anterior ridges on the

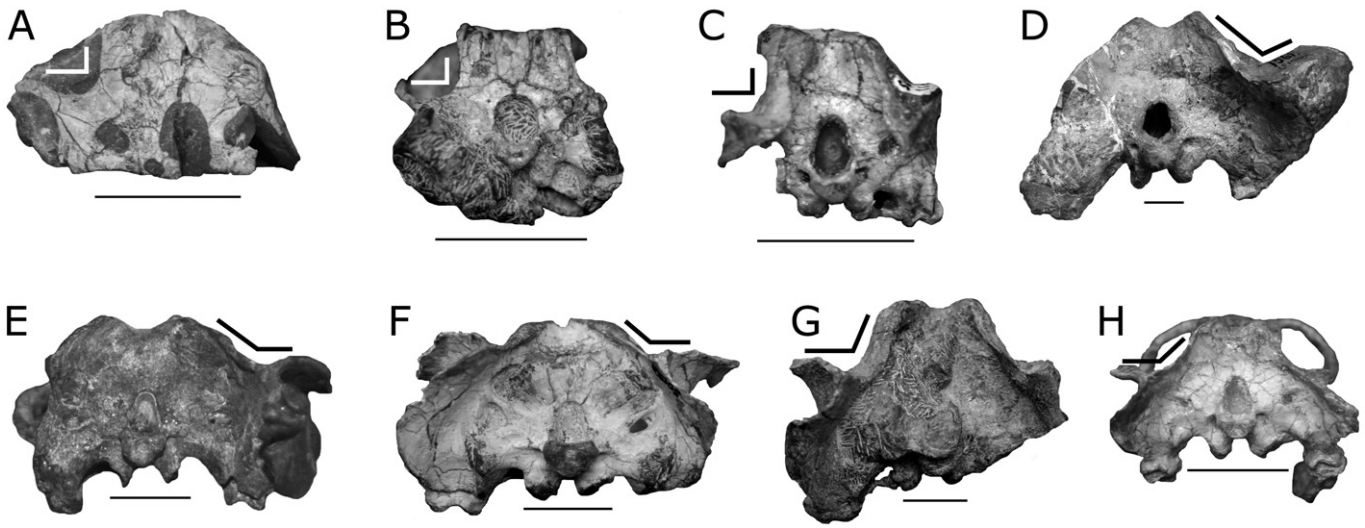

Figure 3. Occipital views of various *Tapinocephalus* and *Pristerognathus* Assemblage Zone dicynodonts for comparison with SAM-PK-708. **A**, SAM-PK-708. **B**, SAM-PK-3721; *Emydops.* **C**, SAM-PK-11060; *Emydops.* **D**, FMNH 1561; *Brachyprosopus.* **E**, SAM-PK-11761; *Robertia.* **F**, SAM-PK-K5105; *Diictodon.* **G**, SAM-PK-11558; *Chelydontops.* **H**, SAM-PK-10153; *Pristerodon.* Compare the distinctively squared-off profile of the occiput in SAM-PK-708 and the two *Emydops* specimens to the more obtuse profile in the other taxa. The occiput of *Colobodectes* is not shown because its lateral margins are highly damaged. Scale bar in each panel is 20 mm.

secondary palate, presence of posterior median ridge on secondary palate, embayment of palatal rim anterior to the caniniform process, square palatal portions of the palatine that are relatively smooth and bear fine vascular foramina), none are preserved or readily visible in the exposed section through the palate of SAM-PK-708.

Anteriorly, much of the snout and all of the dentary symphysis are missing. Thus, the most prominent feature of SAM-PK-708 in anterior view is a large, matrix-filled space representing a transverse section through the buccal cavity (Fig. 2a,h). Sections of the dentary rami also are visible, and weathered sections of several postcanine teeth are present on medial swellings of the dentaries. This postcanine location is typical for most small, toothed dicynodonts of the *Tapinocephalus* and *Pristerognathus* Assemblage Zones. The snout is too damaged to determine whether a nasal boss was present.

Laterally, the left side of SAM-PK-708 is more completely preserved than the right one, but the right side of the specimen retains more diagnostic features. Portions of the snout, suborbital bar, caniniform process, jaw, postorbital bar, and zygomatic arch are present on the left side of the specimen, although they are generally not well preserved or prepared (Fig. 2g). The only potentially diagnostic features preserved on this side of the skull are the presence of a postcaniniform keel and the fact that the caniniform process is at approximately the same level as the anterior margin of the orbit. Both features are characteristic of *Emydops,* but the latter also is found in other *Tapinocephalus* and *Pristerognathus* zone taxa such as *Diictodon* and *Robertia.* The former feature is not present in any of the well-characterized *Tapinocephalus* or *Pristerognathus* zone dicynodonts, although it does occur in several post-*Pristerognathus* zone taxa (e.g. *Cistecephalus, Kingoria, Myosaurus*).

Portions of the snout, suborbital bar, caniniform process, and jaw are visible on the right side of SAM-PK-708 (Fig. 2f). Although the anterior portion of the right caniniform process is damaged, its posterior surface is better preserved than on the left side of the specimen. The postcaniniform keel is particularly pristine, and a single postcanine tooth is present slightly less than halfway along its length. The tooth is well preserved, conical, and appears to lack serrations. Teeth of similar size and morphology can be found along the postcaniniform keel of other *Emydops* specimens (e.g. SAM-PK-11060; Fig. 4c), whereas the upper postcanine teeth of taxa such as *Robertia* or *Pristerodon* tend to be located more medially on the secondary palate.

Just lateral to the postcaniniform keel, a well-developed, round, matrix-filled foramen is present close to the junction of the keel with the ectopterygoid and anterior pterygoid ramus (Figs 2j & 4a). This feature has not been widely reported in descriptions of *Emydops,* although Broom (1905) does refer to it in his original description of SAM-PK-708, calling it a 'depression.' Our personal observations suggest that it is diagnostic for *Emydops* because it is consistently present in specimens in which this region of the skull is preserved and exposed [although the region in question is highly damaged on both sides of the holotype skull of *Emydops* (AMNH 5525)]. A comparable foramen is not found in *Diictodon, Robertia, Pristerodon, Chelydontops, Colobodectes* or *Brachyprosopus* (Fig. 4). A similarly-positioned foramen often is present in *Oudenodon* and *Rhachiocephalus* (e.g. Keyser 1975, p. 24, fig. 18; Maisch 1999), but SAM-PK-708 clearly is not referable to either of these exclusively post-*Pristerognathus* zone taxa. Moreover, we do not consider this foramen to be a potential homologue of the labial fossa or the labial fossa-like features discussed by Cluver (1971), Angielczyk (2001), and Angielczyk & Kurkin (2003) for two reasons. First, the foramen is completely surrounded by the maxilla, instead of a combination of the jugal, palatine, maxilla, pterygoid, and ectopterygoid. Second, the foramen is located farther anteroventrally than is the case for the labial fossa.

Part of the dentary also is well preserved and exposed on

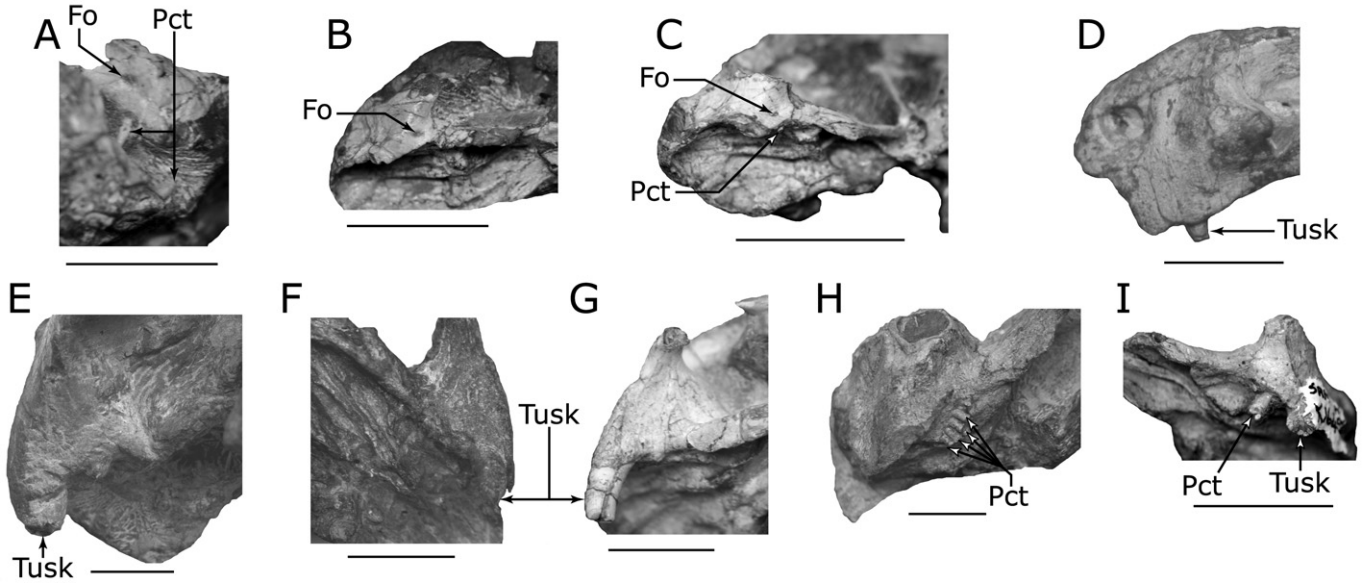

Figure 4. Views of the caniniform process area of various *Tapinocephalus* and *Pristerognathus* Assemblage Zone dicynodonts for comparison with SAM-PK-708. **A**, Right ventrolateral view of SAM-PK-708. **B**, Left ventrolateral view of SAM-PK-6623; *Emydops.* **C**, Left ventrolateral view of SAM-PK-11060; *Emydops.* **D**, Left lateral view of NM QR3329; *Colobodectes.* **E**, Left ventrolateral view of FMNH 1561; *Brachyprosopus.* **F**, Right ventrolateral view of SAM-PK-11761; *Robertia.* **G**, Left ventrolateral view of SAM-PK-K5105; *Diictodon.* **H**, Left ventrolateral view of SAM-PK-11558; *Chelydontops.* **I**, Right ventrolateral view of SAM-PK-K1645; *Pristerodon.* Note that a foramen is present on the posterior surface of the caniniform process in SAM-PK-708 and the two *Emydops* specimens, but in no other taxa. Scale bar in A is 10 mm; in all other panels it is 20 mm.

the right side of the skull (Fig. 2f,i,k). Anteriorly, one postcanine tooth is preserved on a medial swelling of the dentary. It is blade-shaped, larger than the upper postcanine exposed on the right side of the skull, and bears prominent posterior serrations (Fig. 2j). This lower tooth morphology is very similar to that found in several toothed dicynodonts, including *Robertia broomiana, Pristerodon,* and *Endothiodon.* However, it is difficult to determine whether it is also typical for *Emydops* because very few *Emydops* specimens have their lower teeth preserved or exposed. We have personally studied only two *Emydops* specimens with informative lower teeth, SAM-PK-10172 and TM 242 (the holotype of *Emydops minimus*). The lower teeth of SAM-PK-10172 are peg-shaped, whereas those of TM 242 are slightly more blade-shaped. Serrations are not visible in either specimen, but this could be an artifact of incomplete preparation in TM 242. Given these observations, it appears that the lower tooth morphology of *Emydops* was variable. However, the available sample of informative specimens currently is too small to determine whether this variation is of taxonomic or phylogenetic significance.

A shallow posterior dentary sulcus is present lateral to the lower postcanine, and it appears that in life the upper postcanine would have occluded with this sulcus. The lateral wall of the posterior dentary sulcus is slightly taller than the medial wall.

A prominent lateral dentary shelf is present on the lateral surface of the jaw. It begins at the level of the posterodorsal corner of the mandibular fenestra and rapidly expands laterally as it courses anteriorly (Figs 2i,k & 5a). The widest point of the shelf is at the level of the anteroventral corner of the mandibular fenestra, and here its lateral surface bears a prominent rugosity (Fig. 2i,k) that likely represents a muscle scar (presumably for part of the insertion of *M. adductor madibulae externis lateralis*; e.g. Crompton & Hotton 1967; Barghusen 1976; King *et al.*, 1989; Angielczyk 2004). Anterior to its widest point, the shelf narrows and slopes anteroventrally. A weak depression is present on its dorsal surface in this region, and is bounded medially by the lateral wall of the posterior dentary sulcus and laterally by the slightly raised lateral edge of the shelf itself. Little else can be said about the morphology of the jaw because its anterior, posterior, and ventral portions are not preserved on either side of the specimen.

The area of the mandible preserved on the right side of SAM-PK-708 perhaps is the most diagnostic part of the specimen because its morphology is nearly identical to that of the jaws of well-preserved *Emydops* specimens such as SAM-PK-3721 and SAM-PK-6623 (Fig. 5b,c). SAM-PK-6623 has postcanine teeth that are located on a medial swelling, and a shallow posterior dentary sulcus is present lateral to the postcanines (this area is not exposed in SAM-PK-3721). The lateral wall of the sulcus is taller than the medial wall. Both specimens also possess a strong lateral dentary shelf that begins at the level of the posterodorsal corner of the mandibular fenestra and rapidly expands anteriorly. A lateral rugosity is present at the widest point of the shelf in these specimens, and the shelf narrows anteriorly from there. A shallow depression is present on the dorsal surface of the anterior region of the shelf in SAM-PK-6623, but this feature appears to be more weakly developed in SAM-PK-3721.

Moreover, this morphology is different than that of any of the other well-characterized small dicynodonts of the *Tapinocephalus* and *Pristerognathus* Assemblage Zones for which jaws are known (jaw material is not preserved for *Colobodectes* and *Brachyprosopus*). For example, *Diictodon* and *Robertia* lack posterior dentary sulci and have

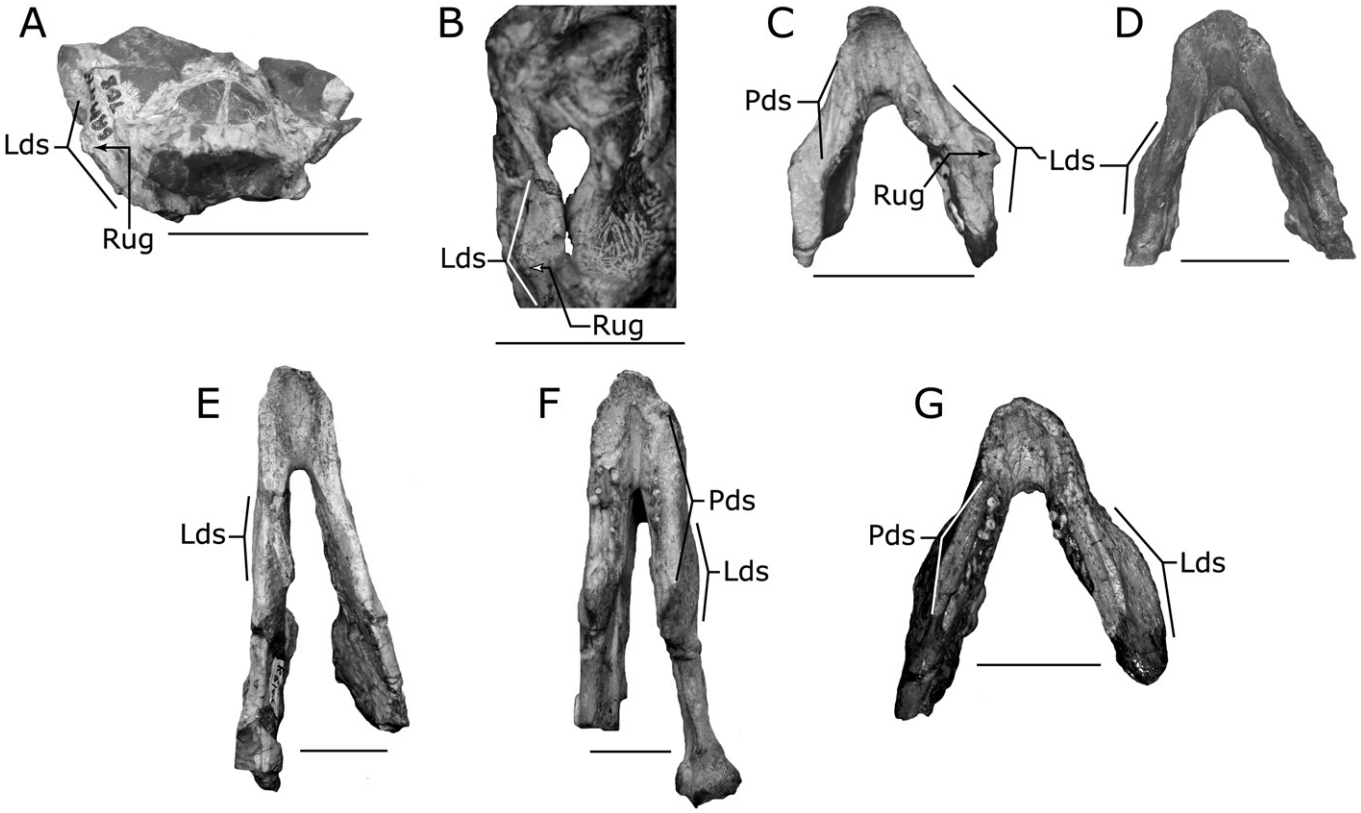

Figure 5. Dorsal views of the jaws of various *Tapinocephalus* and *Pristerognathus* Assemblage Zone dicynodonts for comparison with SAM-PK-708. **A**, Anterodorsal view of the lower piece of nodule of SAM-PK-708, showing dorsal view of right lateral dentary shelf. **B**, Dorsal view of the right jaw ramus of SAM-PK-3721, showing right lateral dentary shelf; *Emydops.* **C**, Dorsal view of SAM-PK-6623; *Emydops.* **D**, SAM-PK-K7807; *Robertia.* **E**, Dorsal view of SAM-PK-K5105; *Diictodon.* **F**, Dorsal View of SAM-PK-12259; *Chelydontops.* **G**, Dorsal view of CGP FL102; *Pristerodon.* Note that SAM-PK-708 and the *Emydops* specimens are the only specimens in which the lateral dentary shelf is strongly developed with a prominent rugosity on its lateral edge. Scale bar in each panel is 20 mm.

much less prominent lateral dentary shelves (Fig. 5d,e). *Chelydontops* does possess a posterior dentary sulcus, but it is more strongly developed in this taxon than in *Emydops* (Fig. 5f). It also lacks a prominent lateral dentary shelf (Fig. 5f). *Pristerodon* has a posterior dentary sulcus and a prominent lateral dentary shelf, but the morphology of these features is different that that of *Emydops* (Fig. 5g). The posterior dentary sulcus in *Pristerodon* is longer and deeper than that of *Emydops,* and bears a closer resemblance to that of *Chelydontops.* Although well developed, the lateral dentary shelf of *Pristerodon* tends to be of a more constant width along its length, instead of narrowing rapidly anteriorly and posteriorly as in *Emydops.* It also lacks the lateral rugosity at its widest point and the shallow depression on its anteriormost dorsal surface. Finally, it is noteworthy that Cluver and King considered the jaw of SAM-PK-708 to be sufficiently typical of *Emydops* to use a drawing of the specimen to illustrate the jaw morphology of this taxon (1983, p. 250, fig. 33a,b).

STRATIGRAPHIC OCCURRENCE OF SAM-PK-708

Broom presents conflicting information about the provenance of SAM-PK-708 in his published accounts of the specimen. In the 1905 paper in which the specimen was first described as the holotype of *Opisthoctenodon brachyops,* Broom states that it likely came from an uncertain locality in the Beaufort West District. However, in 1915 he did not mention a geographic locality for the specimen, but speculated that it likely originated in *Cistecephalus* zone strata. He provided no information about its geographic or stratigraphic occurrence in *The Mammal-like Reptiles of South Africa and the Origin of Mammals* (1932).

A potential clue to the origin of SAM-PK-708 exists in the accession catalogue of the South African Museum. A handwritten note there states that the specimen was collected in the Gough, in the magisterial district of Beaufort West. The Gough (a.k.a., the Koup or the Gouph) is a Khoisan word coined by the early settlers to refer to the expansive, flat, semi-arid scrublands of the Great Karoo. Today the area is fairly accurately delimited by the 'Great Nama Karoo' vegetation type. The southern boundary of the Gough is defined by the East–West trending Groot Swartberge mountains of the Cape Fold Belt; the northern and western margins are clearly defined by the escarpments of the Nuweveldberge and Komsberge mountain ranges. The eastern boundary of the Gough is not defined by any topographic feature; it is based on changes in vegetation at the transition into the 'Eastern Nama Karoo' vegetation zone. Within the collection database and the palaeontological literature of Karoo fossils in South Africa, the term has not been used for any localities east of Beaufort West.

The Gough region contains outcrops of Beaufort Group rocks of the Abrahamskraal and the lower Teekloof forma-

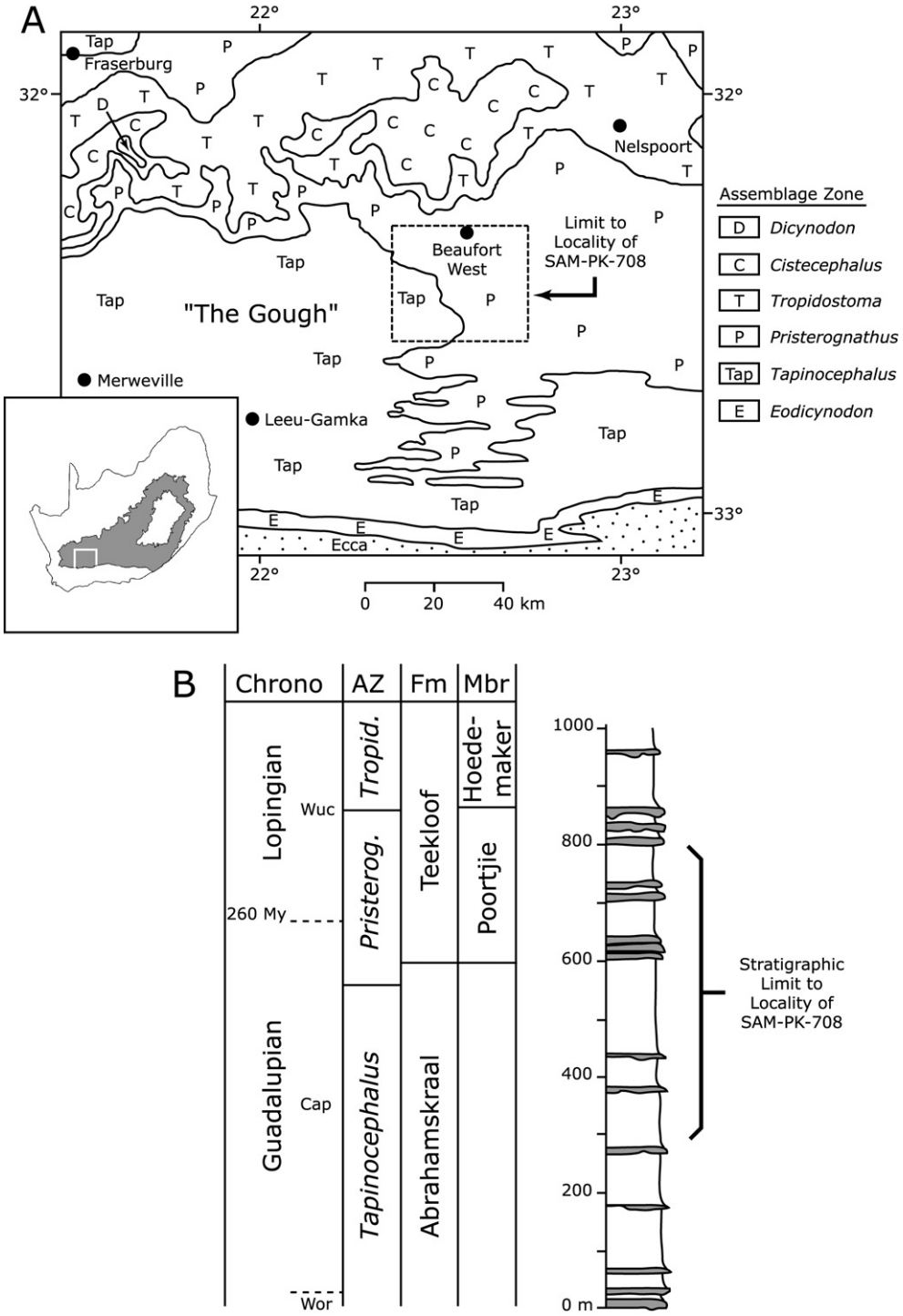

Figure 6. Map and stratigraphic column showing provenance of SAM-PK-708. **A**, Geological map of the Gough region of the Karoo Basin, showing the geographic area from which SAM-PK-708 was collected. Inset map shows the approximate outcrop area of Beaufort Group Strata in South Africa, and the area covered in the geologic map. **B**, Stratigraphic column showing the chronostratigraphy, biostratigraphy, and lithostratigraphy of the Gough region. The portion of the section from which SAM-PK-708 was collected is highlighted.

tions. Kitching (1977) noted that this 'locality' represented a relatively large geographic area, but suggested that most of the material that had been collected there (including the holotype of *O. brachyops*) originated in strata in his *Tapinocephalus* Zone. Since that time the biostratigraphic subdivision of these rocks has been modified, and strata cropping out in the region have been assigned to the *Eodicynodon, Tapinocephalus,* and *Pristerognathus* Assemblage Zones (Rubidge 1995). If the data recorded in the accession catalogue are correct, and the specimen SAM-PK-708 was collected in the Gough in the magisterial district of Beaufort West, we can limit its provenance to an area extending some 40 km south of Beaufort West (Fig. 6). It is therefore possible to confine SAM-PK-708 to a 500 m thick stratigraphic interval that spans the top of the *Tapinocephalus* Assemblage Zone and most of the *Pristerognathus* Assemblage Zone. Based on these data we can state that *Emydops,* and by extension the emydopid lineage, appeared in the Karoo no later than *Pristerognathus* Assemblage Zone times, but we cannot rule out the possibility that the first appearance of *Emydops* occurred late in *Tapinocephalus* Assemblage Zone times.

DISCUSSION

Comparison with published diagnoses of *Emydops*

Because SAM-PK-708 is poorly preserved, we have attempted to use several detailed comparisons between it and better preserved specimens of *Emydops* and other small *Tapinocephalus* Assemblage Zone and *Pristerognathus* Assemblage Zone dicynodonts to confirm its identity as an *Emydops* specimen. However, the specimen also compares favourably with published diagnoses of *Emydops* as well.

Nearly all of the species of *Emydops* were described by Broom or Toerien, although the species *Emydops arctatus* (Owen, 1876) is a notable exception. Neither Broom, who erected the taxon *Emydops,* nor Toerien provided a modern-style definition of the taxon. Broom's 'species descriptions' essentially are brief descriptions of individual specimens, but it appears that he considered a broad intertemporal region with wide exposure of the parietals, small size, and the presence of unserrated postcanine teeth to be characteristic of all *Emydops* species (see e.g. Broom 1912, 1913, 1921, 1932, 1935, 1936; Broom & Haughton 1917). Toerien (1953) considered individual variation more thoroughly than Broom, and questioned whether the lack of serration and number of postcanine teeth could be used to effectively distinguish *Emydops* from other taxa. Instead, he suggested that relatively large palatines that contact the premaxilla and the presence of upper postcanines along the alveolar margin were characteristic of the taxon. It also appears that he considered a broad intertemporal region and relatively large postfrontals typical of *Emydops,* if not completely diagnostic.

Several revised diagnoses of *Emydops* have appeared more recently in the literature (e.g. Cluver & King 1983; King 1988; Keyser 1993; King & Rubidge 1993; Ray 2001). Although these diagnoses do not agree on all points, they do share several common features. For example, all of these authors include small size, the presence of a wide intertemporal region with widely exposed parietals, and prominent lateral dentary shelves. Most also incorporate a jaw symphysis that is drawn into a sharp cutting edge, the presence of a shallow posterior dentary sulcus, the presence of an embayment on the medial surface of the palatal rim, relatively straight anterior pterygoid rami, a crista oesophagea that does not extend onto the anterior pterygoid rami, and the presence of a small number of irregularly-placed postcanine teeth.

Although some of these features are not preserved or exposed in SAM-PK-708, many are present, including a wide intertemporal region with wide exposure of the parietals, a prominent, triangular lateral dentary shelf, a shallow posterior dentary sulcus, relatively straight anterior pterygoid rami, the apparently small number of upper and lower postcanine teeth, and the presence of upper postcanines on the postcaniniform keel. When taken together with the detailed similarities noted in the comparative description, we assert that the generally close correspondence between SAM-PK-708 and the published diagnoses of *Emydops* form a strong argument for the referral of this specimen to the taxon. Even if further investigation should show that SAM-PK-708 is not part of *Emydops,* its referral to the Emydopidae is still relatively certain given that it possesses two of the synapomorphies of that clade recognized by Angielczyk & Kurkin (2003) (presence of a postcaniniform keel, straight contour of the squamosal in posterior view; incompleteness and/or poor exposure prevents the assessment of other synapomorphies for the clade).

We have not considered the specific affinities of SAM-PK-708 in detail. As noted above, this specimen is the holotype of the species *Pristerodon brachyops* (Broom, 1905) [= *Emydops* sp. of King (1988) and King & Rubidge (1993)]. In addition, several other species have been referred to *Emydops,* and King (1988) recognized a total of eleven valid species. Keyser (1993) reviewed these species and considered most of them to be synonyms of *Pristerodon mackayi* Huxley, 1868, including the type species of *Emydops, E. minor* Broom, 1912. He recognized only two valid species, *platyceps* Broom & Haughton, 1917, and the new species *tener* Keyser, 1993, both of which he referred to the new genus *Emydoses.* Although we agree with some of his synonymies (e.g. *E. longiceps* Broom, 1913, likely is a synonym of *P. mackayi*) others seem less certain, and we see no need for the erection of the name *Emydoses* because the holotype of *E. minor* (AMNH 5525) is a poorly preserved *Emydops* specimen (also see Ray 2001; Angielczyk & Kurkin 2003). Also noteworthy is the fact that our observations of the type specimen (BMNH R1690) of the species *arctatus* Owen, 1876, suggest that it belongs to *Emydops,* and is not a synonym of *P. mackayi.* This species is considerably older than any of the other described species of *Emydops,* raising the possibility that it may be a senior synonym of names such as *E. minor.* Given these and other taxonomic issues, we consider it premature to speculate on the specific relationships of SAM-PK-708 until the species of *Emydops* are reconsidered, preferably in a phylogenetic framework. However, the early stratigraphic occurrence of SAM-PK-708 does raise the possibility that it might be part of a species lineage that is distinct from later forms.

Stratigraphic range of *Emydops*

Uncertainty surrounds the stratigraphic range of *Emydops* in the Karoo Basin, with different authors placing the first appearance of the taxon in the *Tapinocephalus* Assemblage Zone (King 1990; King & Rubidge 1993) or the *Tropidostoma* Assemblage Zone (Kitching 1977; Keyser & Smith 1977–1978; Rubidge 1995). Some of this ambiguity stems from the question of whether SAM-PK-708 actually is an *Emydops* specimen or not. Although the specimen is poorly preserved, we feel that the question can be answered strongly in the affirmative, eliminating identification as a source of uncertainty.

However, the vagueness of the available locality information for SAM-PK-708 does not allow a complete resolution of the issue. As we have shown, it is possible to narrow down the occurrence of the specimen to a relatively restricted geographic area and stratigraphic interval, but these include strata assigned to both the *Tapinocephalus* and *Pristerognathus* assemblage zones. Thus, although we

can state that the first appearance of *Emydops* cannot be younger than *Pristerognathus* Assemblage Zone times, we cannot place a confident lower boundary on the age of the first appearance. Further collecting and/or identification of known locality *Emydops* specimens in museum collections will be needed to determine whether the first appearance of this taxon in South Africa is in the *Tapinocephalus* zone or in the *Pristerognathus* zone. Given that more *Pristerognathus* zone strata crop out in the area from which SAM-PK-708 likely was collected (Fig. 6), it may be most conservative to place the first appearance of *Emydops* in the *Pristerognathus* zone for the time being.

Finally, the identification of SAM-PK-708 has implications for studies of dicynodont phylogeny. Several recent analyses have compared the fit of phylogenetic hypotheses to the fossil record (Angielczyk 2001, 2002b; Angielczyk and Kurkin 2003), and all of these works assumed that *Emydops* appeared during the *Tropidostoma* Assemblage Zone. Pushing the first appearance of *Emydops* back into at least the *Pristerognathus* zone may slightly improve the fit of the phylogenetic hypotheses presented in these analyses, and this range extension must be taken into account in future works. At a broader scale, extending the stratigraphic range of *Emydops* implies that the divergence between the emydopid and dicynodontid lineages must have occurred no later than *Pristerognathus* zone times, and possibly as early as late *Tapinocephalus* zone times. This fact is significant because it means that most of the main lineages of Permian dicynodonts had diverged by a relatively early point in the history of the group.

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ABBREVIATIONS

Institutional

AM	Albany Museum, Grahamstown, South Africa
AMNH	American Museum of Natural History, New York City, U.S.A.
BMNH	The Natural History Museum, London, U.K.
BP	Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany
CGP	Council for Geoscience, Pretoria, South Africa
FMNH	Field Museum of Natural History, Chicago, U.S.A.
NM	National Museum, Bloemfontein, South Africa
NMNH	National Museum of Natural History (Smithsonian Institution), Washington, D.C., U.S.A.
SAM	South African Museum, Cape Town, South Africa
TM	Transvaal Museum, Pretoria, South Africa.

Anatomical

Ac	auditory canal
Bo	basioccipital
Ecp	ectopterygoid
Fm	foramen magnum
Fo	foramen
Iptv	interpterygoid vacuity
Jf	jugular foramen
Lds	lateral dentary shelf
Lpf?	lateral palatal foramen?
Mf	mandibular fenestra
Mx	maxilla
Op	opisthotic
Pa	parietal
Pal	palatine
Pbs	parabasisphenoid
Pct	postcanine tooth
Pds	posterior dentary sulcus
Pif	pineal foramen
Pk	postcaniniform keel
Pmx	premaxilla
Po	postorbital
Pop	postparietal
Pp?	preparietal?
Pro	prootic
Pt	pterygoid
Ptf	posttemporal foramen
Rug	rugosity
So	supraoccipital
Sq	squamosal
Vo	vomer

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