New features of the snout and orbit of a therocephalian therapsid from South Africa

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I describe the anterior part of the externally poorly preserved skull of a therocephalian from the Karoo Basin in South Africa, using the method of serial grinding. The skull is incomplete, and its estimated length in life is 130 mm. The skull can be assigned to the Akidnognathidae with some confidence. The stratigraphic age of the specimen and its locality are not known, but the surrounding sediment suggests that it may be from the Upper Permian *Dicynodon* Assemblage Zone. It has five or six postcanine teeth, and a poorly developed crista choanalis. The sinuses and canals of the snout are recognized, and it is believed that the sinus positioned posteriorly in the snout (posterior maxillary sinus) is homologous with the maxillary sinus of anomodonts and cynodonts. It also shows similarities to the infraorbital canal of early mammals, such as *Morganucodon*. An anteriorly positioned sinus (anterior maxillary sinus), situated directly behind the canine root, is homologized with the maxillary sinus of gorgonopsians. In addition, I identify the previously undescribed canal (designated anterior maxillary canal), leading from the anterior maxillary sinus antero-dorsally. No evidence for maxilloturbinals was found in contrast to the condition known in the primitive therocephalian *Glanosuchus*.

Key words: Akidnognathidae, Therocephalia, Therapsida, Synapsida, sinuses, serial grinding, Karoo Basin.

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Introduction

The specimen described in this paper (partial skull of a therocephalian therapsid, associated with parts of lower jaws, PMO 206.702) was found by the late Dr. James Kitching in the Karoo Series in South Africa (presumably Upper Permian *Dicynodon* Assemblage Zone, see below), and handed over to Prof. Wolfgang Maier (University of Tübingen). In October 1999, Prof. Maier offered this specimen to Dr. Jørn H. Hurum (University of Oslo) with permission to study and register it in the collections of the PMO. Dr. Hurum (as my supervisor) suggested to me to study the snout and orbit of this specimen for my Master's thesis. Because of the unsatisfactory state of preservation of the external parts of the specimen (see Fig. 1), the method of serial grinding was applied in this study. The posterior part of the skull, not treated herein, will be described at a later date.

The therocephalians are a group of eutheriodont therapsids occurring from the Late Permian to the Middle Triassic. Their remains are numerous in the Karoo Series in South Africa, but they are also known from Russia (e.g., Tatarinov 1974), China (e.g., Sun 1991; Lucas 2001) and Antarctica (Colbert and Kitching 1981). The therocephalians show a progressive evolution from featuring many primitive or "reptilian" traits to having increasingly advanced "mammalian" morphology. They are regarded as the sister-group of cynodonts (Hopson and Barghusen 1986; Rubidge and Sidor 2001), and the similarity between the advanced therocephalians (the Eutherocephalia) and cynodonts should probably be ascribed to convergent evolution. The eutherocephalians were among the groups of therapsids that survived the mass extinction at the end of the Permian, which might indicate that they had a mammal-like metabolism (Bruce Rubidge, personal communication 2004; Kemp 2005).

The discovery of maxilloturbinal ridges (the supposed attachment sites for respiratory turbinals), in the nasal cavity of the primitive therocephalian *Glanosuchus* (Hillenius 1994), spurred new interest in the group, as this kind of turbinals is currently regarded as the most reliable indication of endothermy in fossil forms (Bennett and Ruben 1986; Hillenius 1992, 1994). Although Mendrez (1975), Van den Heever (1994) and others increased the knowledge of the therocephalians, many questions concerning their phylogenetic relationships, anatomy and physiology still remain unresolved.

The serial sectioning or grinding methods have previously been used in studies of the therocephalians beginning with the work of Broom (1936), who described various sections through skulls of primitive lycosuchid and scylacosaurid therocephalians. However, he did not offer a fully comprehensive picture of the inner structures of the described specimens, and the sinuses of the lateral walls of the snout were not mentioned. Crompton (1955) described the posterior half of the skull of *Ictidosuchops intermedius* by serial sectioning. Brink (1960a) described the anterior part of the snout of *Akidnognathus parvus*, but he did not include the region behind the posterior margin of the choanal openings.
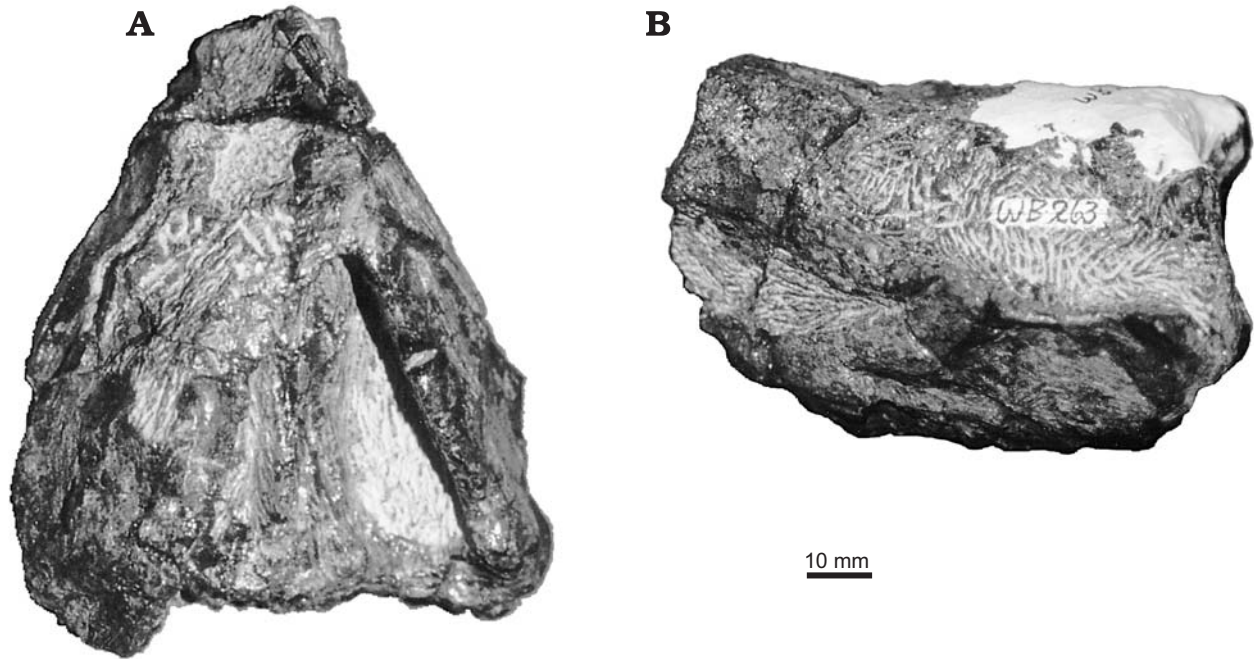
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http://app.pan.pl/acta51/app51-063.pdf

A

B

10 mm

Fig. 1. Akidnognathidae gen. et sp. indet. Upper Permian *Dicynodon* Assemblage Zone, Karoo Basin, South Africa, PMO 206.702 before serial grinding. **A**. Ventral view. **B**. Left lateral view.

Maier et al. (1996) also made use of serial sections in their re-interpretation of the therocephalian palate, but again, only a few sections were described in detail. My study focuses on the area between the canine alveoli and the orbit, a region not fully covered previously.

Institutional abbreviation.—PMO, former Paleontological Museum of Oslo, now incorporated in the Natural History Museum, University of Oslo, Norway.

Material and methods

Material.—The specimen PMO 206.702, described herein, consists of a skull with parts of the lower jaw (Fig. 1). The anteriormost part, including the premaxilla, septomaxilla, and the anterior parts of the vomers, nasals, and maxillary bones, is missing on both sides. The exact locality and age of the specimen are unknown, other than it was found in the Karoo Basin. The matrix is a green-grey mudstone that varies slightly in texture, the lower right side being coarser, darker and more porous. In the finer grained upper left side of the specimen, the pores of the bones have been filled with calcite. As discussed under "systematic position", the studied specimen may be assigned with some degree of confidence to the Akidnognathidae. The akidnognathids of the Karoo Series occur in the *Dicynodon*- and the *Lystrosaurus* assemblage Zones. According to Kitching (1995) and Groenewald and Kitching (1995), the contrast of the sediments of these two zones is quite pronounced, the border between the two marking the Permian–Triassic boundary. Kitching (1995)

described the mudrocks of the *Dicynodon* Assemblage Zone as being grey-green to bluish green in color, with variable texture. This description of the matrix fits the present specimen. In contrast, the color of mudstones of the *Lystrosaurus* Assemblage Zone was described as red or purple (Groenewald and Kitching 1995). Thus, if the attribution of the specimen to the Akidnognathidae is correct, it seems highly probable that the specimen originates from the *Dicynodon*-assemblage zone of the Karoo Series.

Methods.—The anterior part of the specimen was studied with the aid of serial grinding, also called serial lapping, see Sollas (1903), Sandy (1989), and Sutton et al. (2001). Although it was ground rather than sectioned, the surfaces exposed by the grinding will be referred to as "sections" for brevity.

The serial grinding was undertaken using the lapping machine described by Fosse (1968). This machine was originally built for serial grinding of rather small specimens, and therefore the original carrier had to be replaced with a new one able to hold larger objects. The new carrier consists of a guide shaft attached to a series of brass elements fixing the specimen in place next to the object arm rather than under it. The specimen itself was embedded in epoxy resin together with two brass pins which were fixed to the object carrier. Section thickness was set to 100 μm. All in all, 401 sections were made (numbered from the front posteriorly), the last section cutting the middle of the orbit. Each section was scanned digitally using a desktop computer scanner. The images were saved on CD-ROM, and are kept with the specimen in the collections of the PMO. Every tenth section was traced digitally in Corel Photo-Paint 11. The reconstructions

(Figs. 2–5) were made by studying both traced and raw images. The distances between each feature and the plane between the brass pins were plotted manually, slowly building up reconstructed images of the specimen.

Systematic position.—After sectioning the anterior part of the skull PMO 206.702, I assigned the studied specimen to the Therocephalia. Because of the damage to the specimen, the restricted area of the skull studied and the fact that the exact locality from which it was obtained is unknown, the specimen cannot be assigned with confidence to any particular genus or species. However, the details of morphology allow some plausible conclusions.

The anterior fusion of the vomers is a diagnostic feature of the Eutherocephalia (with the possible exception of the Hofmeyriidae see Hopson and Barghusen 1986). PMO 206.702 lacks the extensive palatal exposure of the maxillary bone typical of the advanced therocephalians Baurioidea (Fig. 3) (see Hopson and Barghusen 1986: 96). In addition, the skulls of baurioids are generally more slender, with rows of postcanine teeth extending further back in the jaws.

The studied skull also lacks any trace of the specializations which are typical for the Whaitsiidae, such as the bony bridge between the maxilla and vomers, and the lack of postcanines seen in advanced forms. Nor does it resemble the primitive *Moschowhaitsia*, in which the lacrimo-palatine ridge has become a rod of bone abridging an opening, the "foramen sphenopalatinum" (Tatarinov 1963, 1974), a condition that clearly differs from the studied specimen.

Following this line of reasoning, one is left with the possibility of assigning the present skull to the Akidnognathidae (= the Euchambersiidae of Hopson and Barghusen 1986). The specimen shows a general resemblance to akidnognathid species such as *Akidnognathus parvus* (Haughton 1918; Broom 1932; Brink 1960a) and *Promoschorhynchus platyrhinus* (Brink 1954; Mendrez 1974). In particular, the sections of the snout are more closely comparable to those of *Akidnognathus parvus* (Brink 1960a), than to the available sections made from any other therocephalian. In the shape and size of the skull, as well as in the preserved dentition, the specimen resembles *Promoschorhynchus platyrhinus* as described by Mendrez (1974). It also resembles *P. platyrhinus* in that the maxillo-palatine foramen opens on the palate at the level of the third postcanine tooth. Furthermore, the dorsal ridge on the frontal and the nasal bones are quite prominent in the studied specimen, as in akidnognathids. However, there are also some differences between the studied skull and the skull of *P. platyrhinus*, such as the shape of the posterior part of the vomers. The studied specimen possesses only a rudimentary crista choanalis, which is puzzling, as this feature is well developed in akidnognathids such as *Akidnognathus parvus* (Brink 1960a) and *P. platyrhinus* (Mendrez 1974, 1975), but it is less developed in the akidnognathid genus *Moschorhinus* (Mendrez 1974, 1975). The palatal view of *Moschorhinus*, as figured by Mendrez (1975), shows that the crests do not continue onto the ectopterygoid, as is often the case in other
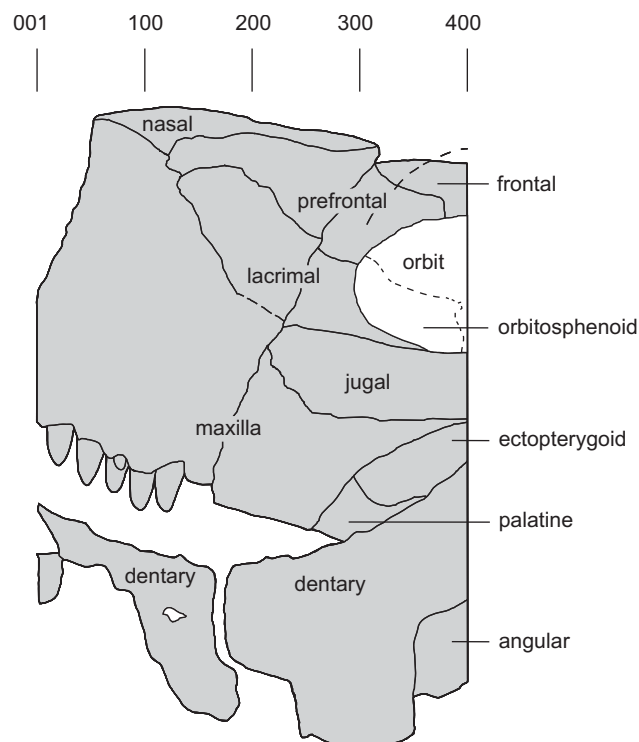

Fig. 2. Akidnognathidae gen. et sp. indet. Upper Permian *Dicynodon* Assemblage Zone, Karoo Basin, South Africa, PMO 206.702. Schematic reconstruction of the anterior part in lateral view. Positions of some sections are indicated above. Some damaged parts are drawn in dashed lines. Distance between 100 sections equals 10 mm.

therocephalians. They continue from the choanae in the direction of the suborbital fenestrae, in front of which they fade away, exactly as in PMO 206.702. Given the general resemblance in most areas of the anterior part of the skull, it seems likely that the PMO 206.702 belongs to the Akidnognathidae.

Description

The studied skull (Figs. 1–5) belongs to a medium sized therocephalian. The preserved part of the skull is 100 mm long and 82 mm in greatest width. The missing anterior extremity of the skull probably had a length of about 30 mm, giving the skull a total length of roughly 130 mm in life. The anterior forty milimetres of the preserved skull (the area between the posterior edge of the canine alveolus, to the middle of the orbits) have been sectioned. The partial lower jaws are poorly preserved, provide no new information, and are not described here, other than in the figures.

Because of the orientation of the ground surfaces relative to the skull, the right side of the skull appears on the left in the figures, and vice versa. Unless otherwise stated, the directions given in the text always refer to the specimen, not to the figures.

Dentition.—The roots of two upper canines are preserved on the left side of the skull. The anterior canine, the root of
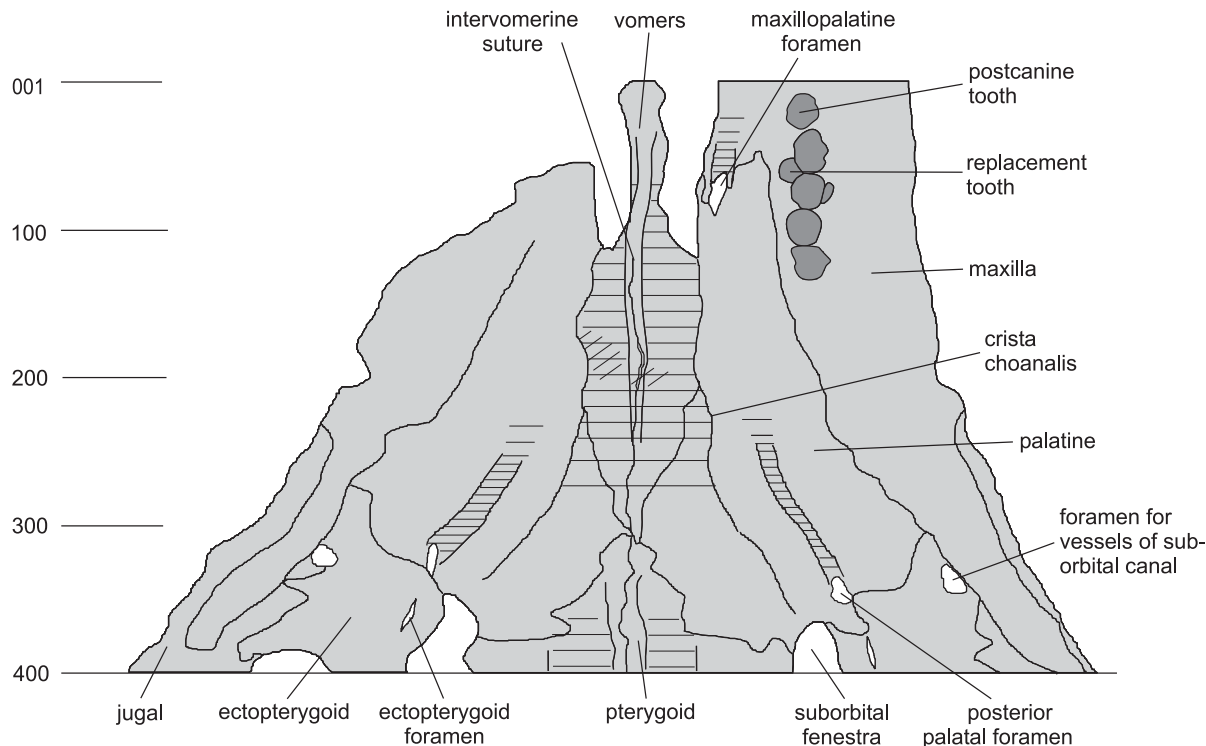
Fig. 3. Akidnognathidae gen. et sp. indet. Upper Permian *Dicynodon* Assemblage Zone, Karoo Basin, South Africa, PMO 206.702. The anterior part in ventral view, as reconstructed from serial grinding. Positions of some sections are indicated on the left. Grooves and troughs are indicated by horizontal hatching. The second and third postcanine teeth are in different stages of replacement. Distance between 100 sections equals 10 mm.
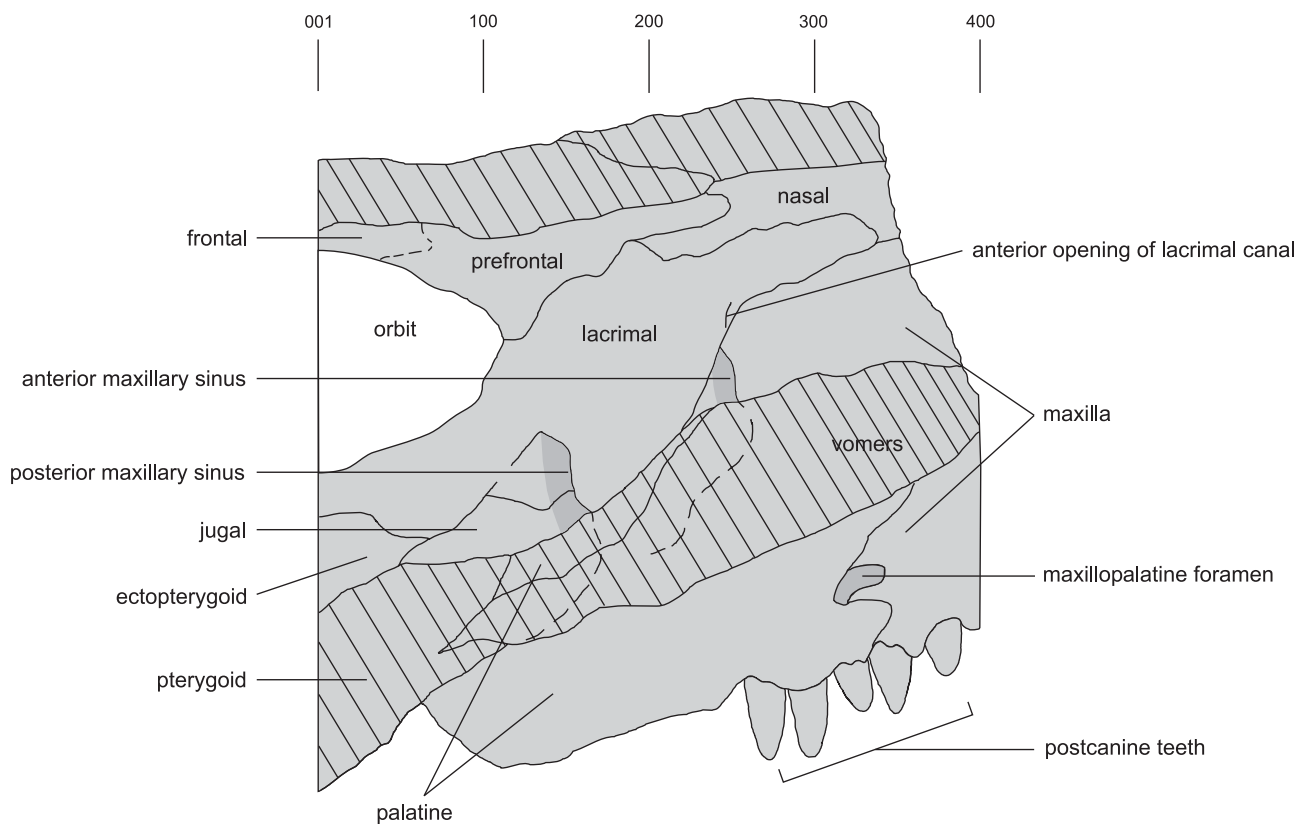

Fig. 4. Akidnognathidae gen. et sp. indet. Upper Permian *Dicynodon* Assemblage Zone, Karoo Basin, South Africa, PMO 206.702. The anterior part in medial view, as reconstructed from serial grinding. Positions of some sections are indicated above. Diagonal hatching indicates areas cut by the plane of view. The orbitosphenoid has been removed, and openings of sinuses are shaded. Distance between 100 sections equals 10 mm.

which is located above that of the posterior canine, was a functional tooth at the time of death. The root of the canine in the posterior position seems to be in development, as the walls are fairly thin and fragile, and it does not appear to be closed at the apex.

The remains of five postcanine teeth of simple cone-shape were found (e.g., Figs. 2, 3). There may be an empty alveolus for a sixth tooth. There is no space between the postcanine teeth. The tooth row reaches only a little past the level of the posterior edge of the choanae (Fig. 3). The postcanine teeth show the alternating pattern of tooth replacement found in many reptiles, including synapsids (Romer 1961; Edmund 1960, 1969).

Maxilla.—Because the anterior part of the snout is missing, the left maxilla is the first bone to be seen in the sections. It is broken off at the ventral opening of the posterior canine alveolus. There are two major cavities associated with the maxillary bone. Although the maxilla constitutes only parts of the walls of these cavities, they will be referred to as the anterior and posterior maxillary sinuses (see below).

Anteriorly the maxilla is higher and thicker than posteriorly due to the swelling around the roots of the canines and the anterior maxillary sinus (Figs. 6, 7A). Posteriorly, the maxilla constitutes the lateral wall of the posterior maxillary sinus and, more posteriorly, the ventral part of the nasal cavity's lateral wall (Fig. 8). The posteriormost part of the maxilla rises steeply dorsally to the base of the zygomatic arch (Fig. 2).

In the region of the choanae, the maxillary bone forms a poorly developed crista choanalis (Figs. 3, 6A). There is no sign of an incipient secondary palate.

Vomers.—Primitively a paired structure, the vomers are referred to in plural in this paper. The anteriormost parts are not preserved. In ventral view (Fig. 3), the posterior part of the vomers has a blade-like shape ending in a sharp point contacting the pterygoid. The anterior interchoanal parts of the vomers are fused medially. The suture between the two elements appears at the posterior end of the internal nares, and continues posteriorly (Figs. 3, 7B). In the internarial part of the skull, the cross sections of the vomers have the shape of a triangle pointing ventrally with a Y-shaped top (Fig. 6A). Posterior to the choanal openings, the vomers are strongly vaulted and the ventral keel is pronounced (Fig. 7B). More posteriorly, the ventral keel becomes shorter, and the vomers gradually narrower, fitting within a recess between the palatine bones (Fig. 8C).

Palatine.—The anteriormost parts of the palatine are sutured with the maxilla above the crista choanalis and around the maxillo-palatine foramen (Figs. 6, 7A). Slightly more posteriorly, the palatine forms part of the medial wall of the anterior maxillary sinus (Fig. 7A). Dorso-medially to the sinus, the contact between the palatine and maxillary bones is very different from the anterior suture. The bones overlap loosely, and there may have been a small opening between the sinus
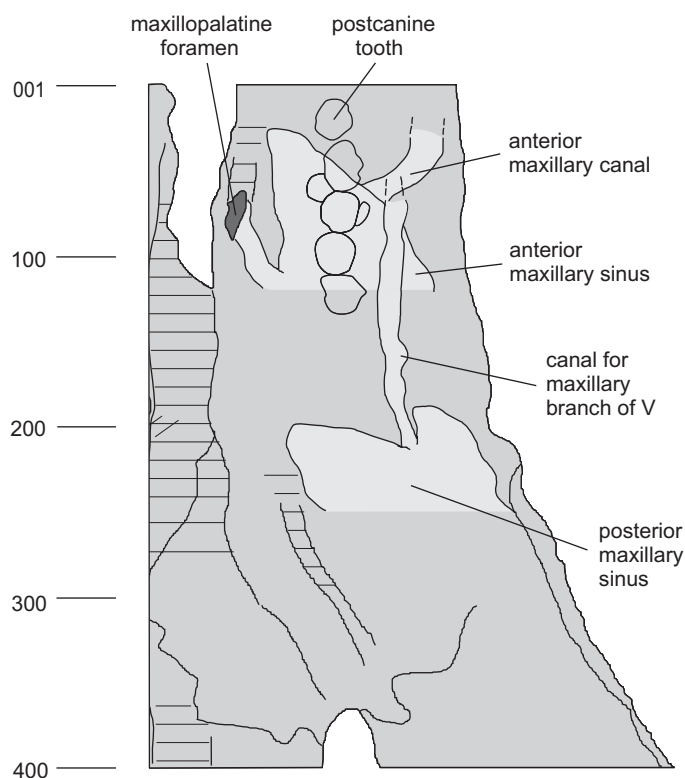

Fig. 5. Akidnognathidae gen. et sp. indet. Upper Permian *Dicynodon* Assemblage Zone, Karoo Basin, South Africa, PMO 206.702. The left anterior part in ventral "transparent" view, showing the major sinuses and canals of the snout. Positions of some sections are indicated to the left. The positions of the preserved teeth are drawn in thin lines and sinuses are shaded. The damaged anterior ends of the canals are drawn in dashed lines. Distance between 100 sections equals 10 mm.

and the inner cavity of the snout at this suture. Posterior to the internal nares, the palatine bone is strongly vaulted as it extends dorsally and medially to meet its fellow in the mid-line of the palate, above the vomers (Fig. 7B). The ventro-lateral parts of the bone clasp the medial part of the maxilla. In this part of the palatine a small anterior pocket of the posterior maxillary sinus appears in section 200 (Fig. 7D).

More posteriorly, the dorso-lateral part of the palatine rises dorsally and laterally to form part of the lateral wall of the nasal cavity, at the same time constituting the medial wall of the posterior maxillary sinus (Figs. 7D, 8A). Also, there is a transverse ridge in this area. In the sections, this ridge can be seen as a thickening of the bone (Fig. 7D). The ridge bridges the lateral trough leading anteriorly to the anterior maxillary sinus. Posteriorly, it continues dorso-laterally on the palatine (Fig. 8A) until it reaches the lacrimal. This ridge has been described as the lacrimo-palatine ridge (Van den Heever 1994). It is immediately anterior to the medial opening of the posterior maxillary sinus. Posterior to the opening of the posterior maxillary sinus, the palatine flattens before being supplanted by the pterygoid medially (Fig. 8B–D).

The crista choanalis continues from the maxilla onto the palatine bone. It runs posteriorly from the lateral sides of the
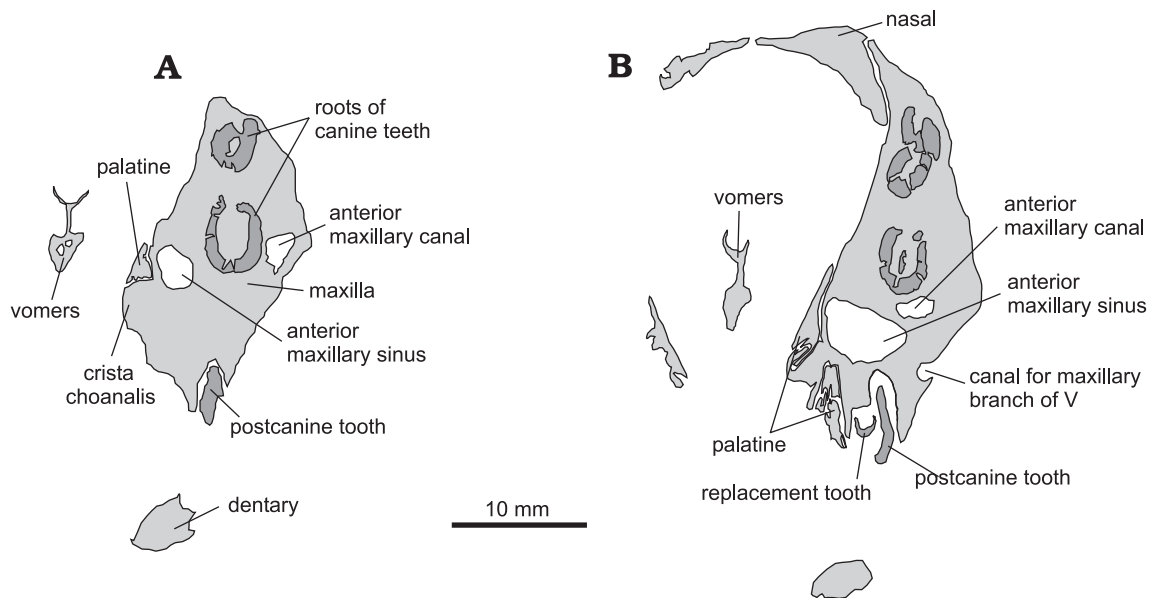
Fig. 6. Akidnognathidae gen. et sp. indet. PMO 206.702. Upper Permian *Dicynodon* Assemblage Zone, Karoo Basin, South Africa. **A**. Section 40, showing the second postcanine tooth. Note the blunt crista choanalis. **B**. Section 60, cutting the second postcanine tooth and its replacement tooth.

choanae, bending laterally (Fig. 3). It is rather indistinct. On the posterior part of the palatine, a groove runs parallel to the crista choanalis, leading to the posterior palatal foramen piercing through the lateral side of the palatine bone (Figs. 3, 9A). On the dorsal side of the palate, immediately anterior and medial to this foramen, the palatine juts sharply upward forming a short ridge (Fig. 8D).

Nasal.—The nasal constitutes most of the dorsal side of the snout, being overlapped laterally by the maxilla. The ventro-lateral edge of the nasal is robust, but there is no clear ridge for the attachment of maxilloturbinals (Fig. 6B). The anterior suture between the nasal and the prefrontal is obscured by weathering. The most plausible, but not the only possible, interpretation is shown in Figs. 2 and 4. Posteriorly, the nasal overlaps the frontal bone, forming a interdigitating suture. A low dorso-median ridge starting at the posterior part of the nasal bone continues onto the frontal. Ridges are also found on the ventral side of the bone. Immediately behind the level of the posterior edge of the internal nares, a pair of ridges, about 3–4 mm lateral to the medial suture, is found on each nasal bone (Fig. 7B). These were presumably the anchoring points for the nasoturbinals.

Prefrontal.—The suture between the prefrontal and nasal bones is often hard to identify. In lateral exterior view, the prefrontal is quite long and slender (Fig. 2). It is positioned dorsal to the lacrimal, and it stretches anteriorly to meet the maxillary bone, preventing the lacrimal from touching the nasal.

In the sections, the prefrontal appears as a thin bone anteriorly (Fig. 8A), but it grows thicker immediately in front of the orbit (Fig. 8C). The prefrontal forms interdigitating sutures with the lacrimal and frontal bones. It does not exclude the frontal from participating in the dorsal orbital rim (Fig. 2).

Lacrimal.—The lacrimal is more extensive on the interior wall of the snout than on the exterior (compare Figs. 2 and 4). It has an anterior process extending out from the main body of the bone, on to the part of the nasal which is overlapped by the maxilla (Figs. 4, 7A). Ventrally, the lacrimal contacts the palatine and, together with this bone and the maxillary and jugal bones, it encloses the posterior maxillary sinus. At this point the lacrimal has a median and a lateral extension ventrally, constituting the dorso-median and dorso-lateral walls of the sinus respectively (Fig. 8A, B). Moving posteriorly, the orbital extension of the lacrimal rests on the dorsal and anterior part of the ectopterygoid (Fig. 9A–C). It forms a thin plate on the internal ventral rim of the orbit (Fig. 4).

Although the area where the lacrimal canal opens into the orbit is very obscure, there were clearly two openings rather than one, as a septum dividing the canal can be seen posteriorly (Fig. 8B). Anteriorly, the lacrimal is thin, and it bulges to an interior ridge around the canal. The lacrimal canal opens anteriorly below the base of the anterior process of the lacrimal (Fig. 4). Close to this point the lacrimal clasps around another bone dorsally, probably a lateral extension of the nasal (Fig. 7C).

Jugal.—Anteriorly, the jugal appears as a sheet of bone bordering the posterior maxillary sinus laterally (Fig. 8B). In this area, its dorsal part fits into a shallow recess in the ventro-lateral part of the lacrimal. It is quite extensive in front of the orbits (Fig. 2). Posteriorly it grows thicker, particularly where it contacts the ectopterygoid. Here, the ventral part of the jugal has a medial shelf on which the dorso-lateral part of the ectopterygoid rests (Fig. 9B–D). The posterior process of the maxillary bone is situated immediately ventral to the shelf and main body of the jugal. In the area where the zygomatic arch diverges from the main body of the skull, the jugal
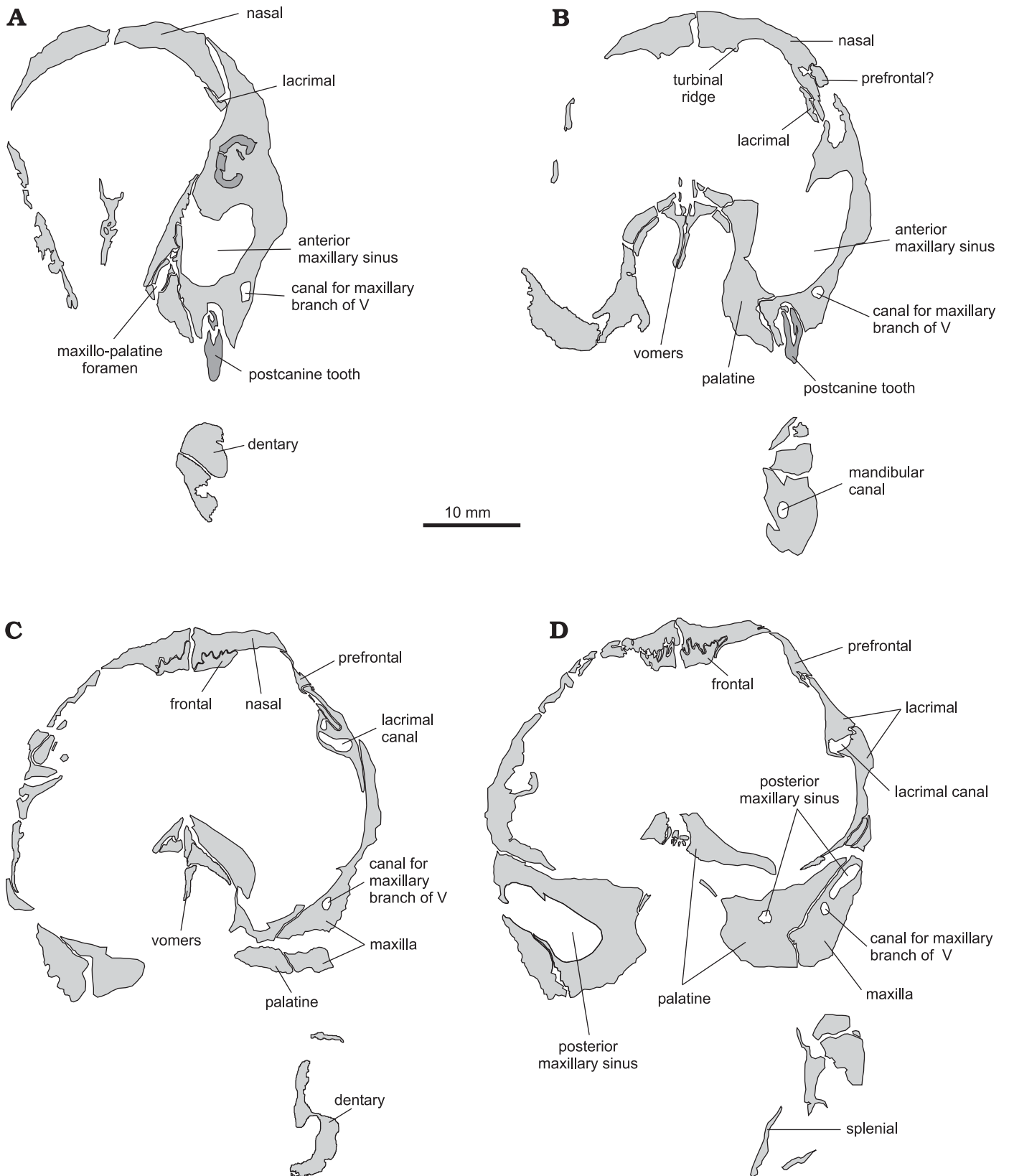
Fig. 7. Akidnognathidae gen. et sp. indet. PMO 206.702. Upper Permian *Dicynodon* Assemblage Zone, Karoo Basin, South Africa. **A**. Section 90, cutting the fourth postcanine tooth. Above it, the root of the third postcanine can be discerned. **B**. Section 130, cutting the fifth postcanine tooth. This is the area immediately posterior to the choanae. Note the appearance of an intervomerine suture. **C**. Section 170. Note the appearance of the frontal bone and the lacrimal canal. **D**. Section 200. Note the appearance of the posterior maxillary sinus. The anterior pockets of the sinus appear in both the maxilla and the palatine. The canal for the maxillary branch of cranial nerve V can be seen on the right side of the figure. It enters the sinus immediately posterior to this section.
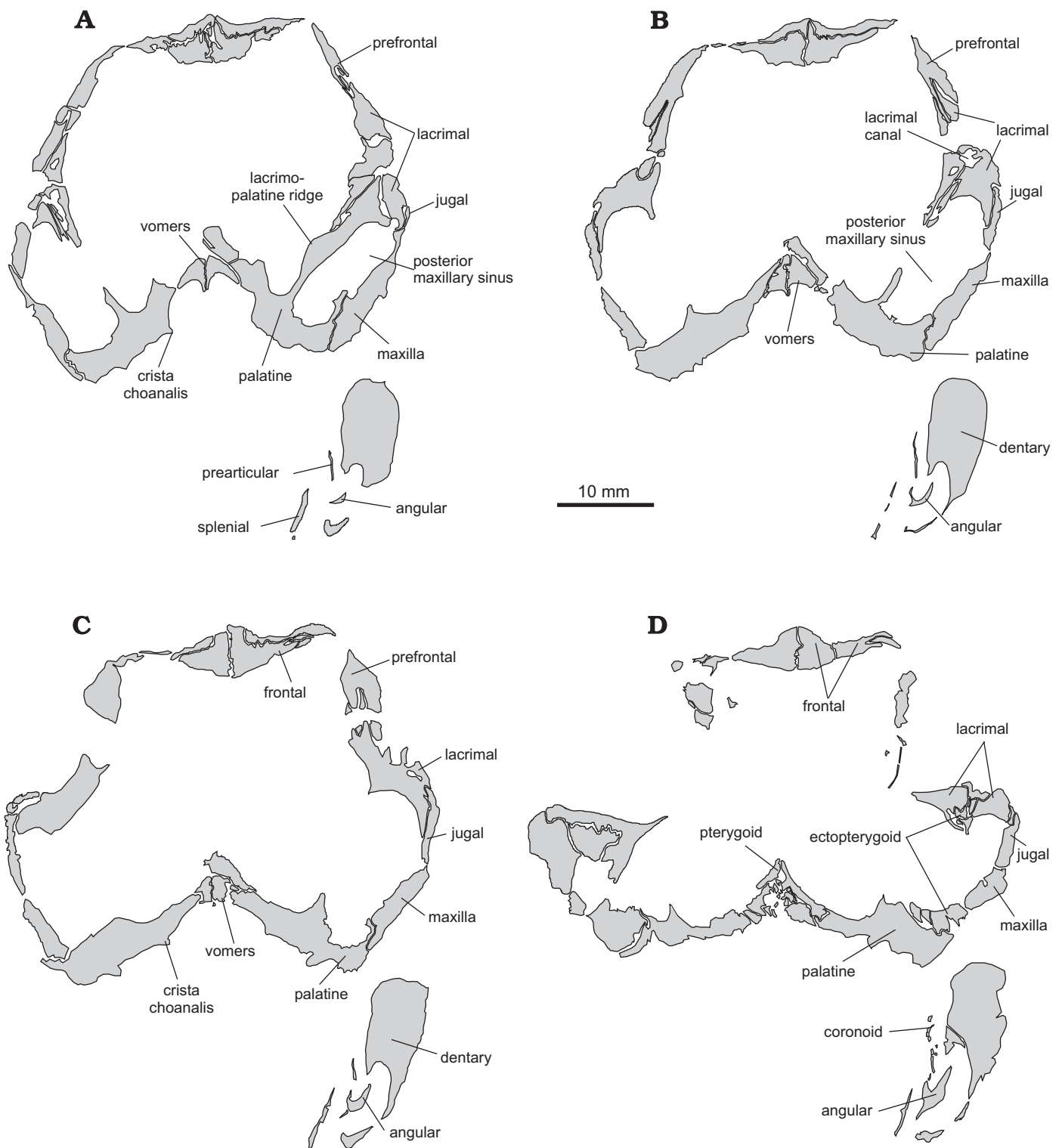
Fig. 8. Akidnognathidae gen. et sp. indet. PMO 206.702. Upper Permian *Dicynodon* Assemblage Zone, Karoo Basin, South Africa. **A**. Section 230, situated at the anterior tip of the jugal. Note also that the lacrimal has two ventral extensions, one on either side of the dorsal extension of the palatine. **B**. Section 250. Note that the posterior maxillary sinus has opened medially. **C**. Section 271. At this level, the frontal finally breaks through to the dorsal surface of the skull. **D**. Section 310, which cuts the anterior extremities of the ectopterygoid.

clasps the postero-lateral (zygomatic) part of the ectoptery-goid dorsally, laterally and ventrally (Fig. 9C, left side of the figure). A little further posteriorly it is the sole element constituting the zygomatic arch (Fig. 9D, left side of the figure).
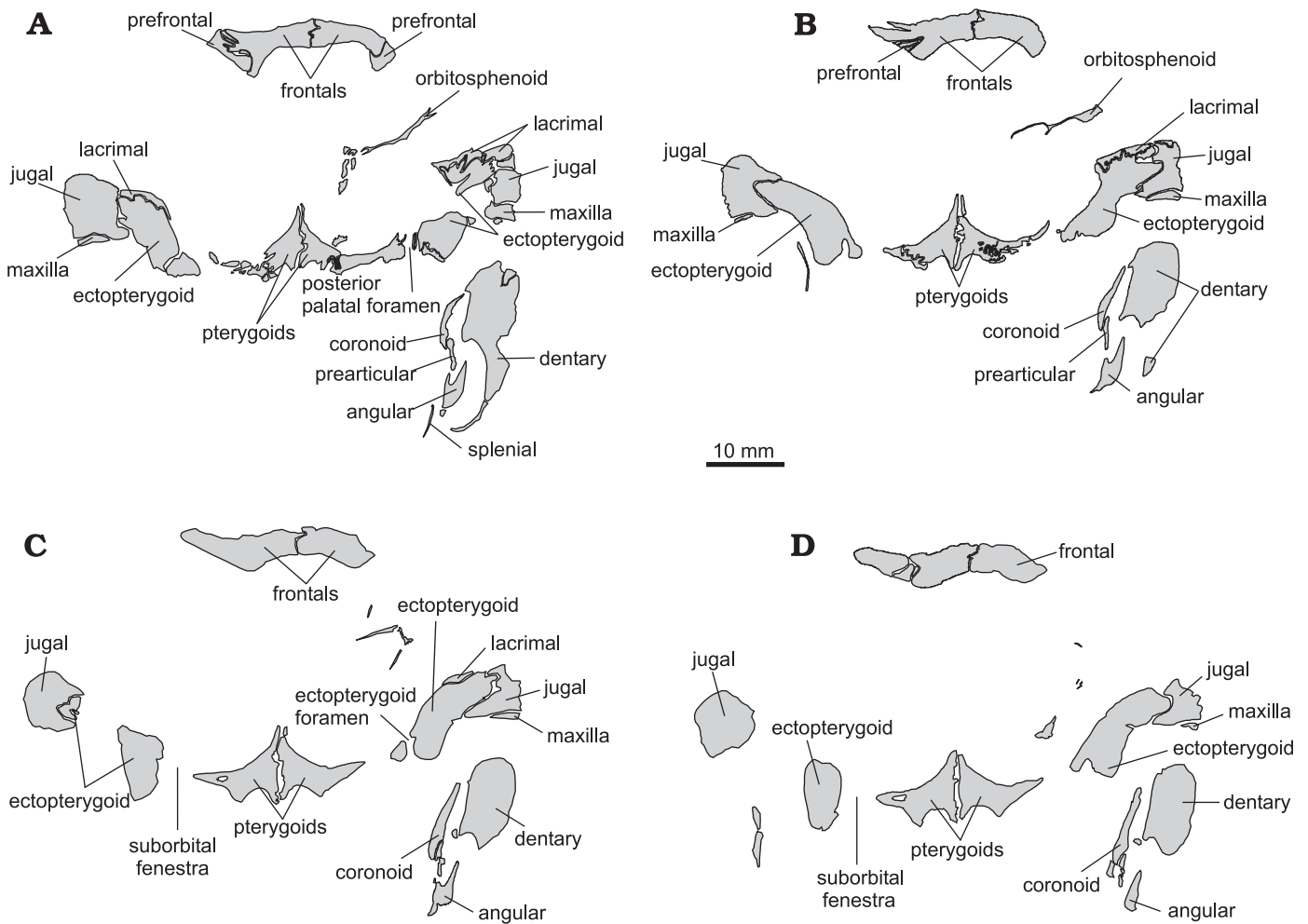
Fig. 9. Akidnognathidae gen. et sp. indet. PMO 206.702. Upper Permian *Dicynodon* Assemblage Zone, Karoo Basin, South Africa. **A**. Section 350. The two anterior extensions of the ectopterygoid can be seen on the right side of this section. Between them, and next to the maxilla and jugal, there is an opening. This is the foramen for the vessels of the suborbital canal as described by Mendrez (1972). **B**. Section 371. **C**. Section 390, located immediately posterior to the level where the zygomatic arch separates from the rest of the skull on the right side (appearing on the left in the figure). **D**. Section 400.

Frontal.—Anteriorly, the frontal is broadly overlapped by the nasal, forming a complex suture with this bone. The median dorsal ridge, which extends from the nasal, becomes more prominent as it continues on to the frontal bone (Fig. 8D). The ridge fades more posteriorly. Above the orbits, the lateral halves of the frontals slope dorsolaterally, the medial parts being slightly domed upwards to meet its fellow in the mid-suture (Fig. 9C). At the angle between the lateral and medial parts of the frontal, there is a slight thickening on the ventral side. This ridge was probably attached to the orbitosphenoid in life.

Ectopterygoid.—This bone has two processes anteriorly. The ventral anterior process is situated immediately dorsal to the lateral rim of the palatine and ventral to the maxilla (Fig. 8D). A little more posteriorly, it expands ventrally and medially and soon constitutes the lateral side of the palate (Fig. 9A). The dorsal process is embraced by the zygomatic extension of the lacrimal, as well as the jugal and maxillary bones

(Fig. 9A). Between the dorsal and ventral processes of the ectopterygoid and bordering on the maxilla, there is an opening on the lateral side of the palate (Figs. 3, 9A). This is equivalent to the "foramen for the vessels of the suborbital canal" of Mendrez (1972) in *Regisaurus jacobi*, and the "foramen nervi palato-nasalis" of Tatarinov (1974) in *Moschowhaitsia*. Posteriorly, the dorsal and ventral parts unite to form the main body of the ectopterygoid (Fig. 9B). In cross section, the dorsal part can be seen to bend laterally, in part constituting the base of the zygomatic arch. Ventrally, there is a short groove leading to a small foramen that penetrates through the palatal part of the bone (the "ectopterygoid foramen" in Figs. 3 and 9C).

Pterygoid.—Only the anterior process of the pterygoid is seen in the sections of the present study. It constitutes the medial edges of the suborbital fenestrae (Fig. 3). The pterygoid has an anterior process that reaches the vomers. Its suture with the palatine is interdigitating, the anterior extensions of

the pterygoid appearing mainly on the dorsal side of the palatine bone, and a smaller process appearing immediately beneath the vomers. These anterior extensions fuse in section 344, and, further posteriorly, the pterygoids expand laterally to supplant the palatine bones as the main element of the palate (Figs. 3, 8D, 9A–D).

The pterygoid is covered with prominent longitudinal ridges. On the dorsal side, the two pterygoids curve upwards to form a ridge on the medial suture. A similar ridge, pointing downwards, is present on this suture ventrally. Moreover, each pterygoid bone has another ventral ridge located laterally to the medial suture (Fig. 9C). No sign of pterygoidal teeth can be seen in the sections.

Orbitosphenoid.—At the level of the anterior edge of the orbits, a number of thin, broken osseous plates is seen in the sections. They seem to have been pushed to the left prior to fossilization, displacing them from a more medial position (Fig. 9A–C). These are presumably the remains of the orbitosphenoid. This bone probably was only partly ossified. Some of the small broken bones found close to the orbit might also be the remains of sclerotic plates of the eye, as has been found in other therocephalians (e.g., Cluver 1969).

Cavities and canals of the snout.—The anterior maxillary sinus is the anterior one of two major cavities found in the lateral wall of the snout (Figs. 4, 5). It appears anteriorly as a small cavity in the maxilla ventro-medially to the lower canine root (Fig. 6A). In section 90 (Fig. 7A) it has expanded dramatically, and is bordered on the medial side by the palatine. Posteriorly, the sinus opens medially into the main nasal cavity (Fig. 7B). It continues as a large lateral aperture of the nasal cavity, giving the ventro-lateral parts of the latter the appearance of deep troughs. There is a canal, which I designate the anterior maxillary canal, originating from the dorsal part the anterior maxillary sinus (Figs. 5, 6A, B). This canal separates from the sinus in sections 71–75, and extends anteriorly and dorsally from this place, bending to the lateral side of the canine roots. It continues into the missing anterior parts of the snout.

The maxillo-palatine foramen (Figs. 3–5, 7A) originates from a groove on the ventral side of the maxilla, and it enters the bone at the level of the third postcanine tooth. It is situated at the anterior suture between the maxillary and palatine bones, although it seems to be embraced by the maxillary bone only (Fig. 7A). It enters the posterior part of the anterior maxillary sinus (Fig. 5).

More posteriorly, the maxilla forms the lateral wall of the posterior maxillary sinus. This cavity is bordered medially by the palatine and dorsally by the lacrimal, and laterally, above the maxilla, the jugal also forms part of its external wall (Fig. 8A, B). Its anteriormost extensions appear in the sections as a pocket in the maxillary bone and, a little more posteriorly, a larger pocket in the palatine (Figs. 5, 7D). More posteriorly these pockets fuse to become a large sinus in the lateral wall of the nasal cavity (Fig. 8A), into which it opens medially immediately posterior to the lacrimo-palatine ridge (Fig. 8B). In much the same way as the anterior maxillary sinus, the posterior sinus continues as a lateral aperture of the posterior nasal cavity.

The main canal for the maxillary branch of the cranial nerve V has its origin in the posterior maxillary sinus (Figs. 5, 7D). From the anterior maxillary extension of the sinus it continues towards the roots of the postcanine teeth. In the sections it can be seen dorso-laterally to the postcanine alveoli (Fig. 7A, B). Small side-branches can sometimes be seen to run from the main canal to the postcanine alveoli. The canal seems to open to the lateral surface in section 120, but this may be the result of damage. Anteriorly, it disappears around section 50. Although it probably ran further anteriorly from this point, its course cannot be determined because of damage to the lateral side of the maxillary.

Discussion

Turbinal ridges.—The ridges on the ventral side of the nasal bones present in PMO 206.702 correspond to those found previously in other therocephalians (e.g., Brink 1960a; Tatarinov 1963; Hillenius 1994). These have been interpreted as evidence for the presence of nasoturbinals, which are primarily of olfactory function. Typical for such turbinals is that they are situated outside the main flow of air in the nasal cavity. This is clearly the case for the specimen of this study, since the ridges found on the nasal bones are located posteriorly to the internal nares.

Hillenius (1994) found in *Glanosuchus* the ridges for the presumed maxilloturbinals on the internal lateral and ventral edges of the nasals continuing onto the lacrimal. However, contrary to the situation reported for *Glanosuchus*, such ridges could not be found in PMO 205.702. As this part of the specimen is well preserved, it is doubtful if maxilloturbinals were present in life.

Lacrimal.—The lacrimal is much more extensive internally than externally, as is typical for therapsids, but differing from the more primitive pelycosaurs (Figs. 2, 4). The internal aspect of the lacrimal still shows a striking resemblance to the condition seen in such sphenacodonts as *Dimetrodon* (Romer and Price 1940). The lacrimo-palatine ridge is also present in the latter genus, but no associated sinus has so far been described.

Maxillary sinuses and canals.—Van den Heever (1994) described three main apertures in the medial side of the lateral walls of the nasal cavity. The first, which he termed the anterior maxillary fossa, is situated immediately anterior to the maxillary bulla, and is not preserved in the studied specimen. The second was termed the posterior maxillary fossa by Van den Heever, but is named the anterior maxillary sinus here. It is identical to the cavity called the maxillary antrum by Brink (1960a), and "the postcanine part of the maxillary sinus" by Tatarinov (1999). The third, called the posterior maxillary sinus in the present paper, was given no name by Van den Heever. It was dubbed "the palatine part of the maxillary sinus" by Tatarinov (1999).

The anterior maxillary sinus is well known in therocephalians (e.g., Brink 1960a; Tatarinov 1974; Van den Heever 1994). In gorgonopsians, it was described in the genus *Arctognathus* by Kemp (1969), and it can also be seen in the section made through the snout of *Lycaenops* as figured by Colbert (1948). In the latter case, it is especially easy to see how similar this structure is to the anterior sinus found in therocephalians. Kemp (1969) suggested that this sinus was an integrated part of the nasal cavity in gorgonopsians, and that it was probably equipped with olfactory turbinals. However, no ridges for such turbinals could be found in the sinuses of the present specimen.

The anterior maxillary sinus apparently disappeared in cynodonts (if it was ever present in the ancestors of this group), as it is not shown in sections of *Thrinaxodon* (Fourie 1974; Rowe et al.1995) and *Scalopocynodon* (Brink 1960b). In the latter two genera the maxillo-palatine foramen pierces through from the ventral to the dorsal side of the newly evolved secondary palate. In contrast, the maxillo-palatine foramen of therocephalians opens into the sinus. From our knowledge about the relationships between cynodonts, therocephalians and gorgonopsians, it seems likely that the anterior sinus was present in the common ancestor of theriodonts, the feature being secondarily lost in cynodonts.

In sphenacodontids, as exemplified by *Dimetrodon*, there is a canine boss with anterior and posterior pockets. A groove runs over this swelling on the medial side (Romer and Price 1940). A comparable condition is seen in the titanosuchid dinocephalian *Microsyodon orlovi* (Ivachnenko 1995). In therocephalians, there is a similar groove leading to the maxillary-palatine foramen (Fig. 3). It is possible that the grooves seen in *Dimetrodon* and *Microsyodon* are homologous with that of the therocephalians. In the latter, the palatine has grown ventrally on the medial side of the canine boss, enclosing the groove, such that it now forms the maxillo-palatine foramen leading into the anterior maxillary sinus.

The presence of a canal running inside the maxilla anteriorly and dorsally from the anterior maxillary sinus (given the name "anterior maxillary canal" in this study) has not been reported previously. It should be noted that this canal extends lateral to the canine roots (Fig. 5). This condition has been reported for the canal for the maxillary branch of cranial nerve V (e.g., Van den Heever 1994). It is possible that the anterior maxillary canal contained a branch of this nerve (James Hopson, personal communication 2005). This would mean that it separated from the main branch posterior to the internal opening of the posterior maxillary sinus.

Van den Heever (1994) proposed that the anterior maxillary sinus of therocephalians and gorgonopsians is similar to, but probably not homologous with, the maxillary antrum described in anomodonts by Watson (1960), and Cluver (1971). In addition, he pointed out that the maxillary antrum in *Thrinaxodon* (Fourie 1974) is homologous with the posterior maxillary sinus. Although these conclusions are accepted here, it should be pointed out that there is a close resemblance between the posterior maxillary sinus of the specimen PMO

206.702 and the "maxillary antrum" in the anomodont *Lystrosaurus*, described by Cluver (1971), and the cynodont *Thrinaxodon* (Fourie 1974). In all three cases the cavity is bordered dorsally by the lacrimal, and this bone has a medial and a lateral process constituting the dorso-medial and dorso-lateral walls respectively. Also in all cases the palatine bone constitutes the medial wall of the sinus, and the maxilla is situated laterally. The contribution of the jugal to the lateral wall varies, but in all cases discussed above it is present laterally.

Another similarity between the posterior maxillary sinus of the studied specimen and that of *Thrinaxodon* is the fact that the canal for the maxillary part of cranial nerve V originates from it. From the drawings of the sections made from the skull of *Lystrosaurus* (Cluver 1971: fig. 35A, B), it seems likely that this is also the case in anomodonts. Kemp (1979) described a maxillary antrum in the primitive cynodont *Procynosuchus*, and the more advanced *Luangwa*. The condition in these forms seems to be similar to that of the species mentioned above. Furthermore, a maxillary sinus bounded by the lacrimal dorsally, the maxilla ventro-laterally and the palatine bone medially was described in the cynodonts *Diademodon* (Brink 1955), and *Kayentatherium* (Sues 1986). Therefore, it seems that the posterior maxillary sinus is generally present in therapsids, or at least in the Neotherapsida, which includes anomodonts, therocephalians and cynodonts (Rubidge and Sidor 2001).

The maxillary sinus has been described in a few early mammals. It is present in docodonts (Lillegraven and Krusat 1991) and multituberculates (Hurum 1993, see also Kielan-Jaworowska et al. 2004). The maxillary sinus of extant mammals is a variable structure, being absent in monotremes and many marsupials (Novacek 1993), but present in the marsupial *Monodelphis domestica* (Macrini 2000). It is almost universally present in eutherian mammals (Moore 1981). Interestingly, contrary to the Fourie's (1974) statement that the maxillary sinus in mammals is bordered by the maxillary bone only, this does not seem to be the case. According to Moore (1981) it extends into the maxillary and lacrimal bones in insectivores. In *Canis* it is bounded by the ethmoid, palatine, and lacrimal bones (Evans 1993). This may indicate that the maxillary sinus, if it is a plesiomorphic feature of mammals, is homologous with the maxillary sinus of therapsids, where it is generally associated with the lacrimal, palatine, and maxilla. Tatarinov (1999) proposed that the posterior maxillary sinus (as defined in the present paper) was homologous with the posterior part of the maxillary sinus of mammals. While this is possible, it is not clear to me why this homologization is restricted to the posterior part. The maxillary sinus of cynodonts is closely associated with the infraorbital canal (Sues 1986; Kemp 1979, 1980). It is possible that the posterior maxillary sinus of therocephalians and cynodonts was differentiated into the infraorbital canal and the maxillary sinus of mammals.

The position of lacrimal above the infraorbital canal in early mammals resembles the condition seen in the posterior maxillary sinus of therocephalians, cynodonts, and *Lystro-*

saurus as described above. The lacrimal of *Morganucodon* possesses two ventral processes bordering the dorsal parts of the infraorbital canal (Kermack et al. 1981: fig. 38), in the same way as is the case for the posterior maxillary sinus of the present specimen (Figs. 8A, B). The way the lacrimal processes borders the jugal and palatine in *Morganucodon* is also similar to the condition in the studied specimen.

Conclusions

The studied skull PMO 206.702 belongs to a medium-sized therocephalian (eutherocephalian). I assign it tentatively to the Akidnognathidae, its closest genus being probably *Promoschorhynchus*. On the other hand, the studied skull lacks the well developed choanal crests and distinctive shape of the vomers found in *Promoschorhynchus*, which might suggest that the studied specimen represents a new species. A study of the posterior part of the skull is needed before any systematic conclusions can be drawn.

The anterior maxillary sinus of therocephalians seems to be homologous to the similar sinus found in gorgonopsians. I conclude that the therocephalian posterior maxillary sinus is equivalent to the maxillary sinus found in dicynodonts and cynodonts. Whether this feature is present in more primitive therapsids and sphenacodontids remains unresolved. I also suggest that the posterior maxillary sinus of studied specimen and the infraorbital canal of early mammals such as *Morganucodon* (Kermack et al. 1981) might be homologous, as both are bordered by the same bones, and both are intimately connected to the maxillary branch of cranial nerve V.

No ridges for maxilloturbinals were found, a fact that might draw into question the condition found previously in *Glanosuchus*. I also recognize in the studied skull a previously undescribed canal (designated anterior maxillary canal), leading from the anterior maxillary sinus antero-dorsally.

Acknowledgements

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