The cranial anatomy of *Kombuisia frerensis* Hotton (Synapsida, Dicynodontia) and a new phylogeny of anomodont therapsids

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Redescription of the small Triassic dicynodont *Kombuisia frerensis* Hotton reveals new information about its cranial anatomy. On the basis of the new data, the previously suggested hypothesis of a close relationship of *Kombuisia* and the Permian genus *Kingoria* is tested within a phylogenetic framework. For this a total evidence analysis of Permian anomodont relationships was performed by combining existing data matrices into a comprehensive data set that includes basal anomodonts, dicynodonts and a large number of morphological characters. The resulting phylogenetic hypothesis corroborates the sister-taxon relationship of *Kombuisia* and *Kingoria*. This is based on a number of synapomorphies, including the narrow intertemporal region that forms a sagittal crest, a reduced mandibular fenestra, the presence of a dorsolateral notch in occipital view of the squamosal, a relatively wide mid-ventral plate of the vomer and a dorsal stapedial process. The general topology of this phylogeny supports the main aspects of recent hypotheses of anomodont relationships, and not only resolves critical nodes at the base of the Dicynodontia that were previously obscured by polytomies, but also introduces new hypotheses of relationships. Furthermore, the phylogenetic position of *Kombuisia* has implications for the survivorship of the Dicynodontia across the Permian–Triassic boundary. With consideration of ghost lineages there are at least four dicynodont lineages that extend beyond the end-Permian extinction event. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **150**, 117–144.

ADDITIONAL KEYWORDS: Anomodontia – Beaufort Group – *Cynognathus* Assemblage Zone – Emydopidae – Karoo Basin – Middle Triassic – Permian extinction – P/T boundary – South Africa – survivorship.

INTRODUCTION

The extinct Dicynodontia were the dominant terrestrial herbivores of the Late Permian. In the latest Permian, the diversity of dicynodonts was reduced down to a few genera, as the result of the end-Permian mass extinction, but in the Triassic the clade recovered and had a second, albeit less pronounced, radiation. In the eyes of most authors, the Triassic dicynodonts, except the genera *Myosaurus* (King, 1988; Angielczyk, 2001) and *Lystrosaurus* (Keyser & Cruickshank, 1979; Maisch, 2001, 2002), form a monophyletic taxon, the Kannemeyeriiformes. The Triassic dicynodont genus *Kombuisia* is therefore particularly interesting

because it has been suggested that it also does not belong to this monophyletic group of large Triassic dicynodonts.

Kombuisia is known from the Burgersdorp Formation (Beaufort Group) of the Karoo Basin, South Africa. The deposits are late Early to Middle Triassic in age and are assigned to the *Cynognathus* Assemblage Zone (Hancox & Rubidge, 2001). A three-fold division of this Assemblage Zone into subzones A, B and C is currently accepted with *Kombuisia* occurring in subzone B (early Anisian). *K. frerensis*, the only species of the genus, is known from only two specimens. James W. Kitching collected the holotypic specimen together with Nicholas Hotton III in 1961 about 1.6 km south of the farm Lady Frere in the Eastern Cape Province. It consists of a nearly complete skull and lower jaw, which are slightly distorted. The second

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specimen consists of a snout and dentaries only. It was temporarily lost in the collections of the National Museum, Bloemfontein, and has only recently been re-identified.

A brief description of the holotype of *Kombuisia* was published by Hotton (1974), who suggested a close relationship to *Kingoria nowacki* (von Huene) Cox and thus focused his comparison on the two genera. Since then, *Kombuisia* has not been included in a phylogenetic analysis, and the specific phylogenetic relationship of *Kingoria*, and thus *Kombuisia*, to closely related taxa such as *Emydops*, *Cistecephalus* and *Myosaurus* has been controversial. Altogether these taxa form the Emydopidae, the clade including *Emydops*, *Myosaurus* and all descendants of their most recent common ancestor. Several alternative groupings of these taxa have been suggested by various authors, briefly summarized by Angielczyk & Kurkin (2003a), with different synapomorphies supporting conflicting patterns of phylogenetic relationship. Unfortunately, the postcranial skeleton of *Kombuisia* is unknown. Knowledge about its anatomy would significantly contribute to further clarification of its interrelationship within the Emydopidae, as there are major variations in the postcranial skeleton within this clade. For example, *Kingoria* has been interpreted to be highly derived and adapted to an upright hind limb posture (King, 1985), whereas others are considered to have had a fossorial lifestyle, e.g. *Cistecephalus* and *Kawingasaurus* (Cox, 1972; Cluver, 1978).

In this study, the cranial osteology of *Kombuisia frerensis* is redescribed on the basis of new information made available by further preparation of the holotype. The hypothesis of a close relationship of *Kombuisia* and *Kingoria* is tested in a cladistic framework and a new pattern of emydopid interrelationships is presented. In addition, the survivorship of dicynodonts across the Permian–Triassic boundary is evaluated in the light of the new phylogeny.

MATERIAL

The holotype of *Kombuisia frerensis* (BP/1/430) is catalogued at the Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand in Johannesburg. The maximum length of the skull of 76.8 mm, measured from the tip of the premaxilla to the occiput. It is well preserved and consists of an almost complete cranium and lower jaws that are slightly distorted as the result of dorsoventral flattening of the specimen. Both zygomatic arches, parts of the occiput, the right maxillary process as well as a portion of the palate between the interpterygoid vacuity and the parabasisphenoid complex are missing. The anterior part of the dentaries, shortly behind the

level of the symphyseal region, is removable, which provides an unhindered view on the taxonomically important anterior part of the palate (Toerien, 1953). The original description of *Kombuisia* by Hotton (1974) illustrated a removable anterior part of the lower jaw, which was significantly larger than the currently detachable portion and comprised most of the left dentary. This additional part of the left jaw ramus has been glued back onto the palatal surface after the original publication and its dorsal surface is no longer available for study.

The second specimen (NM QR1835), which consists of a snout and dentaries, is from the same strata and housed in the National Museum of Bloemfontein, South Africa. Hotton (1974) briefly reported on the specimen in his original description, without figuring it and mentioned that he only saw the specimen as stereophotographs that were provided to him by Arthur Cruickshank. Hotton (1974) erroneously referred to this specimen with its field number 3006, which resulted in temporary difficulties to locate this specimen. It was only very recently re-identified in the collections of the National Museum (K. D. Angielczyk, pers. comm.) and was therefore not considered for this study.

SYSTEMATIC PALAEONTOLOGY

SYNAPSIDA OSBORN, 1903
THERAPSIDA BROOM, 1905
ANOMODONTIA OWEN, 1859
DICYNODONTIA OWEN, 1859
KINGORIIDAE KING, 1988

Revised diagnosis: Kingoriids are tusked or tuskless dicynodonts of small body size that are united by the following synapomorphies: a reduction of the mandibular fenestra, a narrow intertemporal region that forms a sagittal crest, the presence of a dorsolateral notch of the squamosal in occipital view, a relatively wide mid-ventral plate of the vomer, and a dorsal stapedial process.

KOMBUISIA HOTTON, 1974

Type species: Kombuisia frerensis Hotton, 1974.

Diagnosis: As for species.

KOMBUISIA FRERENSIS HOTTON, 1974

Holotype: BP/1/430, an almost complete small skull with lower jaws. The specimen was originally catalogued as USNM 22936 in the National Museum of Natural History (Smithsonian Institution) in Washington, DC, but was transferred to the Bernard Price

Institute of Palaeontological Research in Johannesburg after its designation as holotype of *Kombuisia frerensis*.

Type locality: BP/1/430 was collected about 1.6 km south of the farm Lady Frere, Eastern Cape Province, South Africa. The deposits exposed at the locality belong to the Burgersdorp Formation (Beaufort Group) of the Karoo Basin. This formation is late Early to Middle Triassic in age and corresponds to the *Cynognathus* Assemblage Zone (AZ) (Hancox & Rubidge, 2001). More specifically, BP/1/430 was found in subzone B (early Anisian) of the *Cynognathus* AZ.

Referred specimens: NM QR1835, a snout and dentaries.

Distribution: The two only known specimens (BP/1/ 430 and NM QR1835) that have been referred to *Kombuisia frerensis* are from the Burgersdorp Formation, which outcrops only in the eastern part of the South African Karoo Basin.

*Stratigraphic range:* BP/1/430 and NM QR1835 were both collected in the middle part of the Burgersdorp Formation, which corresponds to the early Anisian subzone B of the *Cynognathus* AZ.

Revised diagnosis: Edentulous kingoriid dicynodont autapomorphic in its possession of the following characters: absence of a pineal foramen, an inverted triangular shape of the interparietal bone, lack of fusion of articular and prearticular bones, and presence of an elongate, slender parietal posterolateral process that extends onto the occipital edge of the skull roof.

DESCRIPTION

SKULL ROOF

Premaxilla: The premaxillae of *Kombuisia* are fused to form a single element as in all post-*Eodicynodon* AZ dicynodonts. Forming the anterior part of the snout (Fig. 1A, B), the surface of the bone in this part of the skull is poorly preserved and reveals part of the slightly eroded internal vascular structure of the bone. The premaxilla borders the anterior quarter of the external narial opening, which is situated far anteriorly, close to the tip of the snout. The suture with the nasal bones on the dorsal surface of the skull cannot
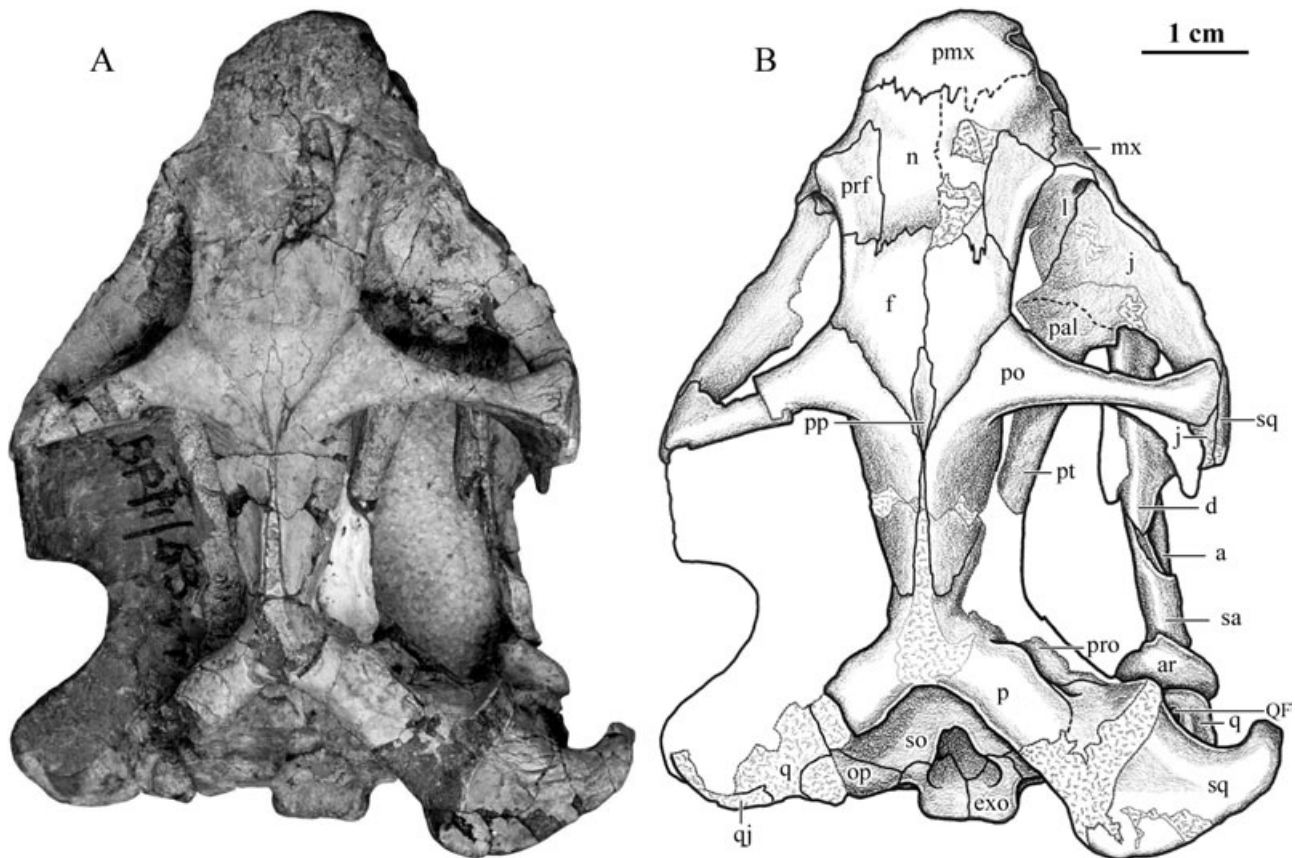
Figure 1. Photograph (A) and drawing (B) of the holotype of *Kombuisia frerensis*, specimen BP/1/430, in dorsal view.

be traced along its complete progression, but it is visible on the left side, where it runs transversely across the snout as a zigzag line. A posterodorsal process of the premaxilla is not present in *Kombuisia*. The exposure of the element on the ventral side of the skull is much larger and forms a well-developed bony secondary palate, which is typical for derived anomodonts (Fig. 2A, B). The anterior and lateral margins of the premaxilla show the remnants of sharp edges that were probably covered by a keratinous beak (Watson, 1948). On the ventral side, the bone surface is also partially damaged and slightly crushed. The premaxilla did not bear any teeth. Paired anterior ridges are not present, but a dominant median posterior ridge is well developed and reaches relatively far anteriorly. Lateral to this ridge are prominent, longitudinal depressions. These depressions show curved lateral margins. The sutures with the maxillae run laterally also in anteroposterior direction. At the level of the anterior margin of the internal narial openings, these sutures meet those connecting the premaxilla to the palatines approximately in a right angle. At the midline, the posteriormost extension of the premaxilla contacts the vomer with a short process that projects behind the level of the anterior margin of the internal narial openings.

Septomaxilla: A septomaxilla is not visible in the holotype of *Kombuisia*, although the bony elements surrounding the external naris are well preserved. This suggests that this bone, if present, was restricted to the internal narial cavity and lacked a facial exposure.

Nasal: The exposure of the nasal bone is L-shaped in dorsal view, with the bottom of the 'L' pointing anteriorly and laterally (Fig. 1A, B). A midline suture between the nasals is barely visible, but can be traced at least for parts of its course. The bone surface is badly damaged, especially on the right side of the skull, where two large holes obscure the formerly smooth surface of the nasals. Anteriorly, the zigzag suture with the premaxilla runs down to the middle of the dorsal margin of the external narial opening. Posteriorly this short bar of the nasal meets the maxilla also in a zigzag line approximately parallel to the nasal–premaxillary suture. Posterolaterally the nasal is overlapped by the prefrontal bone that, with its almost rectangular outline, gives the nasal its peculiar L-shaped configuration. The most prominent morphological feature of the nasal bone is a fairly well-developed nasal boss. It is represented by an unpaired, median swelling without a continuous posterior margin that slightly overhangs the external nares.

*Frontal:* This bone takes up most of the intraorbital region of *Kombuisia*. The suture formed between the nasal and prefrontal runs in an irregular zigzag course, but it primarily stretches transversely from one orbit to the other (Fig. 1A, B). The midline suture between the frontals is clearly visible and meanders back to the tip of the preparietal bone, which reaches forward up to nearly half of the length of the anteroposterior extent of the frontals. The posterior margin of the frontal runs diagonally across the skull roof at an angle of about 40° to the sagittal plane of the skull. Laterally, the posterior margin of the frontal is overlapped by the large postorbital, best seen in lateral view on the medial wall of the orbit.

Preparietal: The unpaired preparietal of *Kombuisia* is a narrow but long wedge between the posterior half of the frontals (Fig. 1A, B). It is 1 cm in length, about four times as long as its maximum width. The bone is widest in its central part, tapering anteriorly and posteriorly to form a narrow oval. Its dorsal surface is slightly concave and forms a shallow groove that is deepest near the posterior edge of the bone. Interestingly, the preparietal is primarily surrounded by the frontal bones and only superficially contacts the overlapping postorbitals at its posteriormost edge. Thus, contact between the preparietal and the parietal bones is not visible in dorsal view, but cannot be ruled out, as a contact beneath the postorbitals is possible.

Parietal: A large part of the parietal is overlapped anterolaterally by the postorbital and is only exposed as a narrow median ridge in dorsal view. Further posteriorly the parietal flares out laterally, which is one of the autapomorphic features of *Kombuisia*. This well-developed posterolateral wing of the parietal is at 45° to the sagittal plane, resulting in a reversed Y-shaped outline of both parietals in dorsal view, which is not found in any other dicynodont. Unfortunately, much of the dorsal surface of the bone is poorly preserved. The parietal is particularly damaged along the midline of the skull, obscuring the identification of a midline suture. The uppermost part of the median ridge has been cut off and broken bone surface is revealed. In addition, the ventral extension of the parietal is slightly damaged and obscured with plaster, partly caused by distortion of the specimen, as well as by previous overpreparation (Fig. 3). Nonetheless, it is readily discernible that posteroventrally the parietal extends back to meet the prootic as well as the squamosal further dorsally. The suture between the parietal and squamosal runs beneath a small ridge of the parietal at the anterior edge of its posterolateral wing. This suture is only visible on the right side of the specimen, as the left side of the skull is only fragmentarily preserved anterior to the level of that suture. Finally, the parietal slightly overhangs the occiput, which is probably the result of dorsoventral flattening of the specimen (Figs 3A, B, 4).
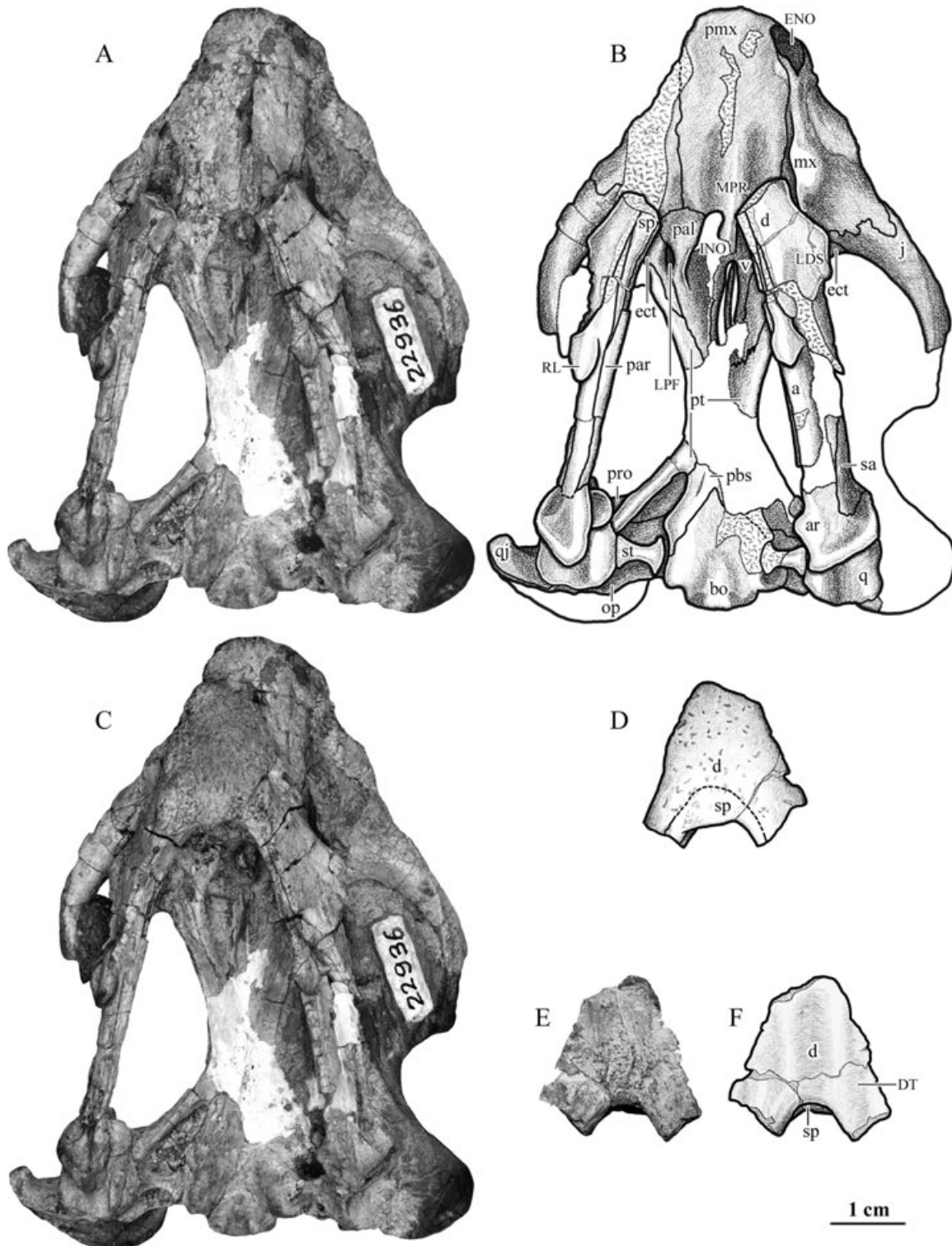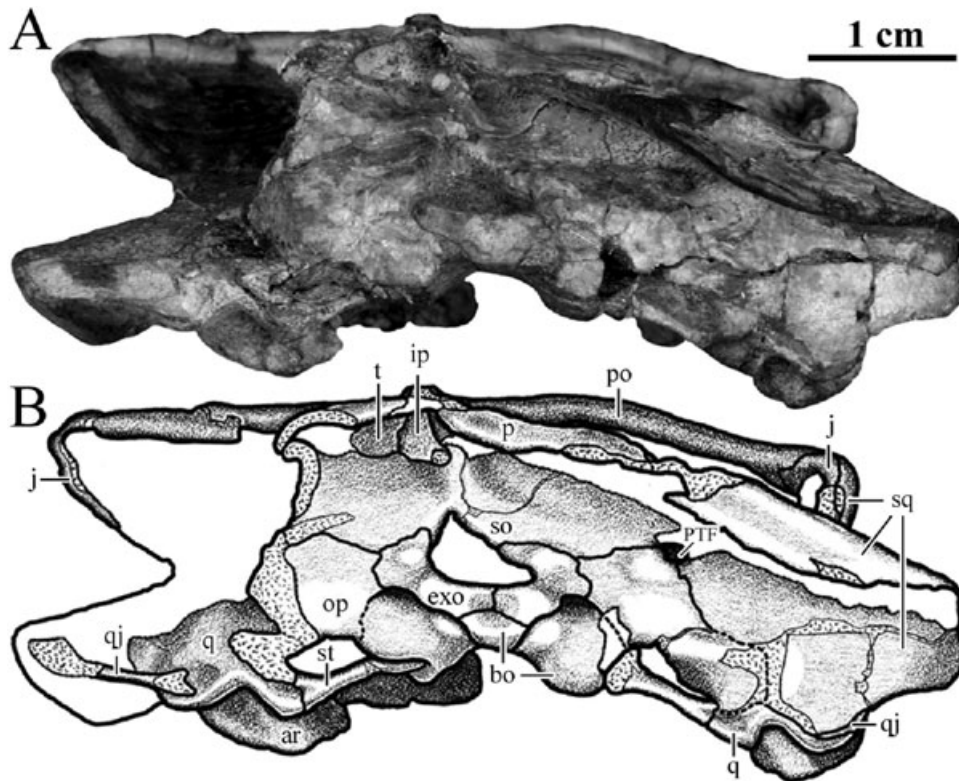
Figure 2. Photograph (A) and drawing (B) of the holotype of *Kombuisia frerensis*, specimen BP/1/430, in ventral view with the symphyseal region of the lower jaws removed to reveal the secondary palate. Photograph (C) of BP/1/430 in ventral view with the symphyseal region of the lower jaws in place, and drawing (D) of symphyseal region in ventral view. Photograph (E) and drawing (F) of symphyseal region of the lower jaws of BP/1/430 in dorsal view. The number (USNM 22936) visible in ventral view (A, C) of BP/1/430 indicates its original catalogue number at the Smithsonian Institution, before it was transferred to the collection of the Bernard Price Institute for Palaeontological Research, Johannesburg.
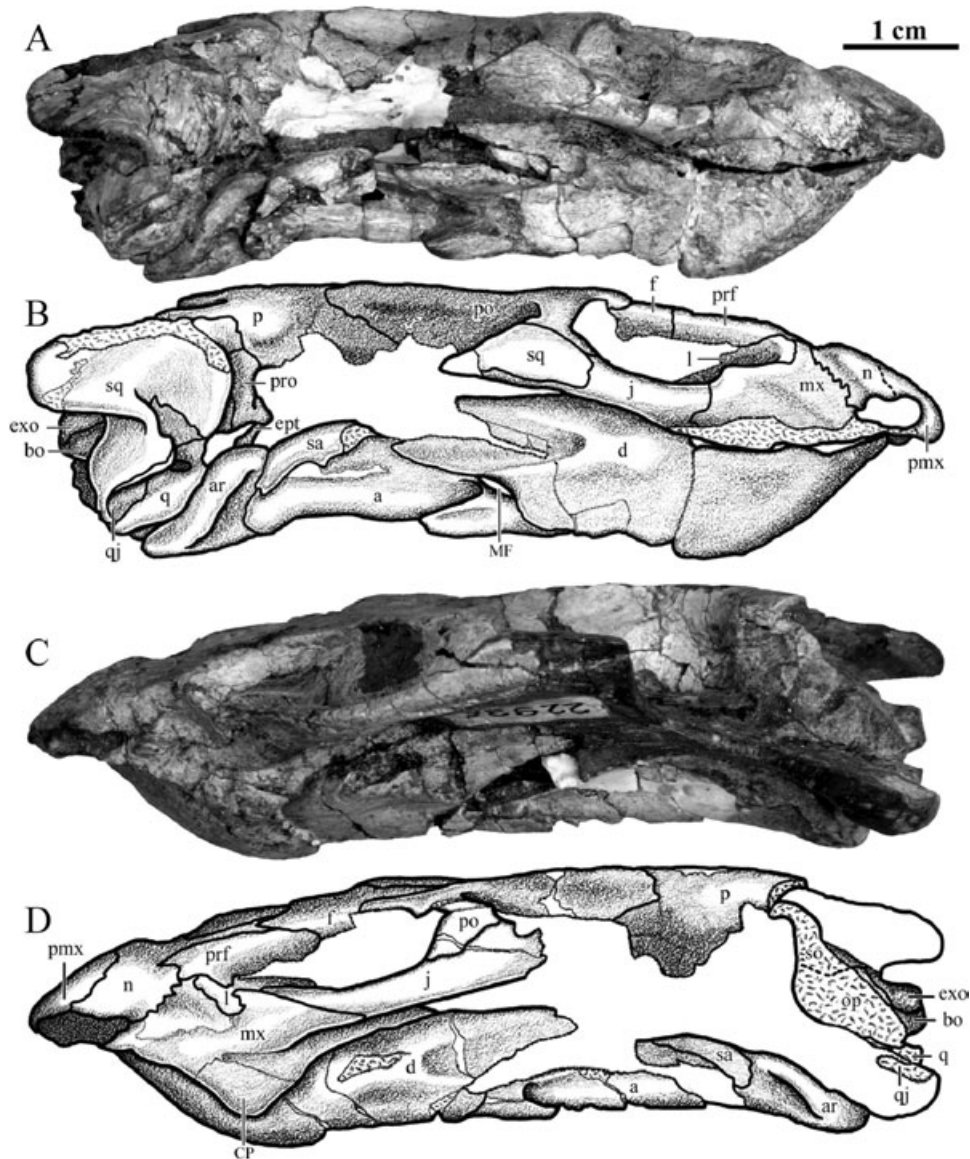
Figure 3. Photograph (A) and drawing (B) of the holotype of *Kombuisia frerensis*, specimen BP/1/430, in right lateral view, and photograph (C) and drawing (D) of BP/1/430 in left lateral view.

Maxilla: The maxilla is a dominant element on the facial exposure of *Kombuisia* (Fig. 2A, B, 3C, D). Like the premaxilla, it does not bear any teeth, but a prominent caniniform process is well developed, projecting far beyond the ventral surface of the skull. In ventral view, the lateral side of this process slopes steeply towards the lateral margin of the skull, whereas medially it overhangs the level of the secondary palate by approximately 1 cm. Ventrally, the suture with the premaxilla extends anteroposteriorly and medial to the level of the caniniform process. Thus, the maxilla is situated lateral to the premaxilla. The maxilla also forms most of the ventral margin of the external narial

opening, whereas it is excluded from the internal narial opening by the anterior flange of the palatine. The contact to the palatine runs primarily transversely as a continuation of the premaxilla–palatine suture. It is directed slightly posterolaterally, where the maxilla most likely meets the anterior tip of the ectopterygoid, but this contact is almost completely hidden beneath both jaw rami, which are still in place in the holotypic specimen. The posterior extension of the maxilla is characterized by an irregular course of the suture. It is not clear whether this irregularity is natural or caused by breakage of the very thin maxilla in this part of its exposure, which overlaps large parts of the

Figure 4. Photograph (A) and drawing (B) of the holotype of *Kombuisia frerensis*, specimen BP/1/430, in occipital view.

underlying jugal in a blade-like fashion. This condition continues laterally along the anterior part of the zygomatic arch up to the anterior margin of the orbital opening. Here, the maxilla forms a thin plate on the lateral side of the skull and runs anteromedially to contact the lacrimal along the anterior margin of the orbit. On the left side of the skull, the suture between the maxilla and lacrimal is irregular in shape and the lacrimal exhibits a transversely orientated facial exposure that projects below the rim of the orbit. However, this condition might be the result of extensive dorsoventral flattening that might have caused breakage of the blade-like overlapping maxilla. At its dorsalmost extension the maxilla also meets a small portion of the prefrontal. Anterior to that contact the maxilla meets the nasal with their suture progressing anteroventrally to terminate at the external narial opening.

Lacrimal: As noted above, the lacrimal of *Kombuisia* is asymmetrically developed (Fig. 3C, D). On the left side, it projects as an oblique process on to the facial surface, being almost completely surrounded by the maxilla and prefrontal. However, it appears to be more likely that the exposure of this bone is usually restricted to within the orbit and extends only slightly beyond its anterior rim, as typical for dicynodonts and

seen on the right side of the holotype. In dorsal view, the lacrimal contacts the jugal along an oblique suture across the suborbital plate, running anterolaterally to where it meets the anterior rim of the orbit (Fig. 1). A well-developed lacrimal foramen projects into the anterior wall of the orbit. The anterior margin of the lacrimal contacts the maxilla laterally beyond the orbital rim and meets the prefrontal medially. From there, the suture projects posteriorly across the rim onto the internal wall of the orbit. Unfortunately, the medial extension of this bone is still covered by sediment and could not be exposed by further preparation.

Prefrontal: In dorsal view, this element is roughly the shape of a parallelogram (Fig. 1). It overlaps the nasal medially along a longitudinally orientated suture. From there, its anterior margin extends posterolaterally at an angle of about 60° to the medial suture. At its lateralmost extension the prefrontal meets the maxilla with a short sutural contact, and a longer contact with the lacrimal. Thus, the prefrontal forms the anterior portion of the medial margin of the orbit, also extending ventrally onto the internal wall of this opening (Fig. 3A–D). Posteriorly, the prefrontal is bordered by the frontal, approximately at the level of nasofrontal suture. The general bone surface of this element is smooth and slightly concave, but with a slightly

elevated supraorbital rim that also extends onto the lacrimal and frontal bones (Fig. 1).

Postorbital: This bone is a dominant element on the skull roof of *Kombuisia*. Typically for dicynodonts, it consists of two processes orientated approximately perpendicular to one another. One forms the postorbital bar and the other extends posteriorly along the medial margin of the temporal fenestra (Fig. 1). The postorbital bar is a slender element that widens towards its medial and lateral ends. Ventrally, it contacts the jugal and squamosal. The anteromedial edges of the postorbitals result in a V-shaped suture that encloses the frontal bones as well as the preparietal. Along this sutural contact the postorbitals rise slightly dorsal to the level of these elements (Figs 1, 3). Both postorbitals overlap the parietals medially and meet along the midline of the skull in a short contact posterior to the preparietal. Posterior to this contact, the postorbitals diverge to reveal the parietals along a sagittal crest, which is slightly damaged in the holotype. The posterior extension of the postorbital is very short when compared with other dicynodonts, such as the closely related genus *Kingoria*, and only reaches back to about two-thirds of the length of the intertemporal bar.

Jugal: The jugal forms most of the suborbital bar and is exposed ventrally, laterally as well as dorsally, where it flares out anteriorly to contribute to the suborbital plate (Figs 1, 2A, B, 3A–D). This part is triangular in outline, being bordered by the maxilla anterolaterally and by the lacrimal medially. In dorsal view, the jugal contacts the palatine on the suborbital plate, but this suture is hardly traceable due to superficial damage of the bones in this area (Fig. 1). In ventral view, the jugal contacts the ectopterygoid posteromedially and is overlapped by the maxilla anteriorly. Laterally, the jugal forms most of the suborbital bar and extends back onto the zygoma, where it is overlapped laterally by the squamosal (Fig. 3A, B). In addition, a short process of the jugal also extends medially along the base of the ventral side of the postorbital bar (Fig. 4).

Squamosal: As in other dicynodonts the squamosal forms most of the posterolateral part of the skull roof, the lateral portion of the occiput, and the zygomatic arch. In dorsal view, the medial extension of the squamosal is overlapped by the lateral wings of the parietal. Lateral to that suture the squamosal widens where the zygomatic arch arises. In an undeformed specimen this widened exposure of the squamosal on the skull roof would be almost vertical in orientation to form the dorsolateral part of the occiput. In contrast, this portion is clearly visible in dorsal view of BP/1/430 due to the dorsoventral flattening of the specimen. Lateral to the base of the zygomatic arch, the squamosal thins and curves anteriorly to form a distinct hook (Fig. 1). The zygomatic arch itself projects anteriorly, where the squamosal eventually overlaps the jugal and postorbital bones laterally at the level of the postorbital bar. Unfortunately, the zygomatic arches are largely missing in the type specimen. In occipital view, the squamosal has a wide occipital flange. The dorsal margin of the occiput is not exposed in the holotype, as this part is only preserved on the right side, where it is bent posteriorly and still covered by matrix (Fig. 4). Nonetheless, it is reasonable to assume that the squamosal contacted the tabular and supraoccipital medially. The squamosal borders the post-temporal fenestra laterally and meets the opisthotic ventral to it in an oblique line. At its ventralmost edge, the squamosal contacts the quadrate, and laterally, the quadratojugal wedge. Thus, the squamosal nicely exhibits a long, vertical flange behind the quadrate and quadratojugal, a character that constitutes a synapomorphy of all anomodonts (Figs 3A, B, 4). Medial to the zygomatic arch, the squamosal contacts the parietal dorsally and the prootic ventrally (Fig. 1).

Quadratojugal: The quadratojugal is a thin, plate-like element that overlaps the squamosal on the anterior side of its posterolateral extension. It forms the anteroventral edge of the hook of the squamosal, contacting the quadrate further ventrally.

PALATE

Ectopterygoid: The ectopterygoid is a slender, wedge-shaped element, which is primarily exposed in ventral aspect (Fig. 2A, B). It is not shifted to a more lateral exposure on the skull, as in more derived dicynodonts like *Dicynodon*. At its anterior extension the ectopterygoid contacts the jugal laterally and the palatine medially. It is not clear whether it also meets the maxilla at its anteriormost edge, because this part is not exposed in BP/1/430. Along its medial margin, it contributes to the border of a comparably large and anteroposteriorly elongate lateral palatal foramen. Posterior to the foramen, the ectopterygoid extends for about the same length posteromedially and thins out until it is overlapped posterolaterally by the anterior ramus of the pterygoid bone.

Palatine: The palatine forms an essential part of the ventral side of the skull (Fig. 2A–C). It has a broad contact with the premaxilla at its anterior end, thereby excluding the maxilla from the margin of the choana. Anterolaterally, it meets the maxilla as well as the ectopterygoid, of which the latter borders the palatine for most of its lateral margin. Together ectopterygoid and palatine enclose the lateral palatal

foramen. Further posteriorly, the palatine meets the pterygoid with an interdigitating suture (Fig. 2A–C). The medial margin of the palatine is bordered by the vomer along its length. Anteriorly, the palatine has a sunken medial plate, which forms most of the dorsal roof of the choana, and a raised lateral plate, which underhangs the choana. This prominent lateral border of the choana disappears posteriorly, continuing in a smooth ridge along the lateral side of the anterior pterygoid ramus and enclosing an elongate groove along the medial part of the palate. In dorsal view, the palatine is exposed at the posteromedial edge of the suborbital plate, where it contacts the jugal anteriorly (Fig. 1), the ectopterygoid laterally, and the pterygoid posteriorly.

Vomer: In *Kombuisia* the vomers are fused as in most dicynodonts. The vomer extends from the posteriormost part of the premaxillary bone to the median pterygoid plate (Fig. 2A–C). Its anterior part is a posterior continuation of the median ridge on the palatal surface of the premaxilla, where the vomer projects ventrally to form a relatively wide mid-ventral vomerine plate, which is one of the shared derived characters with *Kingoria*. Anterolaterally, it forms part of the floor of the olfactory canal in front of the choana. At its posterior extension, it forms slender processes surrounding the interpterygoid vacuity.

Pterygoid: As in other dicynodonts, this element is tripartite and divided into an anterior process (palatal ramus), a medial plate, as well as a posterior process (quadrate ramus). In *Kombuisia*, the palatal ramus of the pterygoid extends far anteriorly along the lateral edge of the palate, where it overlaps the palatine as well as the ectopterygoid. This process is slightly curved and concave laterally. The median pterygoid plate is not well preserved, so that it remains unclear whether the median pterygoid plate actually forms the posteriormost margin of the interpterygoid vacuity or if the latter is entirely bordered by the vomer. As in most dicynodonts, the lateral pterygoid flange is completely reduced laterally and projects ventrally as a low keel. Unfortunately, the suture with the parabasisphenoid along the posterior edge of the pterygoid plate is also obscured by damage. Finally, the quadrate ramus of the pterygoid is distinctly set off from the median plate and projects posterolaterally, where it eventually meets the quadrate. This portion of the pterygoid is a long, slender process with parallel margins laterally and medially. This process constitutes the lateral margin of the cranioquadrate passage.

BRAINCASE AND OCCIPUT

Parabasisphenoid: The parabasispenoid is only fragmentarily preserved in the holotype, where the ante-

rior part and most of the left side of the ventral plate is damaged and has been replaced by plaster (Fig. 2A–C). Only the rostrum of the parabasisphenoid that reaches far anteriorly is preserved as thin vertical septum within the interpterygoid vacuity. As in all therapsids, the basicranial articulation is replaced by a sutural contact between the parabasisphenoid and the pterygoid. These elements meet at the anterolateral extension of the parabasispheoid in an oblique suture, which cannot be traced further medially due to lack of preservation. On its lateral side the parabasisphenoid forms the medial margin of the cranioquadrate passage. At the level of the anterior margin of the cranioquadrate passage, there is a low anteroposteriorly running ridge, approximately half way between its lateral margin and the midline. Posterolaterally, the parabasisphenoid contributes to the fenestra ovalis, where it meets the basioccipital. The suture between these two elements runs approximately from the centre of the fenestra ovalis in an oblique line anteriorly, and reverses its course in a sharp angle and runs posteriormedially to form a short posterior process along the midline.

Basioccipital: The basioccipital is almost triangular in palatal view (Fig. 2A–C), and forms the posterior half of the fenestra ovalis, where it contacts the parabasisphenoid in a long suture that extends anteromedially. This anterior process of the basioccipital is only overlain medially by the posterior projection of the parabasisphenoid. The basioccipital forms the ventral part of the occipital condyle, where it meets the exoccipitals (Fig. 4). From the condyle the suture between these two elements runs laterally towards the jugular foramen, so that, in occipital view, the basioccipital extends laterally and slightly dorsally beyond the extension of the occipital condyle. Ventral of the jugular foramen, the basioccipital contacts the opisthotic along an almost vertical suture.

Exoccipital: The wing-like exoccipitals extend far laterally from the occipital condyle, meet in a vertical suture along the midline of the condyle, and contact the basioccipital ventrally. The condyle itself projects posteriorly from the occipital plane and its posterior surface is slightly concave rather than convex. It is not circular in occipital view, but displays almost a triradiate outline with a ventral and two lateral processes. This results in a small horizontal plateau posteroventral to the foramen magnum. In dorsal view, the anterior portion of this plateau, which extends into the foramen, reveals an interfingering sutural contact with the basioccipital anteriorly. Lateral to the condyle, the exoccipitals flare out onto the occipital plane, where they contact the basioccipital ventrally, the opisthotic laterally and the supraoccipital dorsally.

Opisthotic: The opisthotic connects laterally to the basioccipital as well as the exoccipital elements (Fig. 4). Dorsally it meets the supraoccipital in an almost straight, horizontal suture that runs to the small post-temporal fenestra. Ventral to the post-temporal fenestra, the opisthotic contacts the squamosal. The suture between these two elements extends ventrolaterally, but is difficult to trace further away from the foramen due to damage. Nonetheless, it certainly meets the quadrate bone ventrally at its lateralmost extension. In ventral view, it becomes apparent that the opisthotic forms the dorsal roof of the cranioquadrate passage, where it meets the prootic in an oblique suture (Fig. 2A–C). Thus, the opisthotic and prootic elements do not seem to be fused to form a periotic element as in other dicynodonts.

Prootic: This element contributes to the lateral wall of the braincase, meets the parietal bone in a short contact on its dorsomedial extension, and contacts the squamosal dorsally and laterally (Fig. 3A, B). In palatal view, the prootic has a long sutural contact with the opisthotic, which together form the otic capsule (Fig. 2A–C). In addition, a small foramen for the facial nerve is visible on the anterior surface of the prootic.

Supraoccipital: The supraoccipital is the largest element of the occipital plate (Fig. 4). It forms the dorsal margin of the foramen magnum and contacts the exoccipitals ventrally. Laterally, the supraoccipital has a straight suture with the opisthotic until it reaches the post-temporal fenestra. Lateral to the post-temporal fenestra the supraoccipital certainly contacts the squamosal bone. However, this portion of the occipital plate is not preserved on the left side of the specimen, and it is not visible on the right side because the matrix beneath the strongly overhanging dorsal edge of the occiput could not be removed. Dorsally, the supraoccipital contacts the interparietal bone at the midline of the skull and meets the tabular elements further laterally. Two shallow grooves below these sutural contacts run parallel to the midline of the occiput; however, their origin may be the result of the distortion of the skull.

Tabular: The tabular bones are sheet-like elements at the dorsal edge of the occiput that cover the occipital side of the parietals. They contact the interparietal medially and the supraoccipital ventrally. The lateral extent of the tabular is unknown as it is also covered by matrix.

Interparietal: The interparietal is a small and robust element in the centre of the dorsal part of the occiput and has the outline of an inverted triangle (Fig. 4). It does not extend onto the skull roof. Its ventralmost extension has been cut off and reveals a circular cross-section. The interparietal overlaps the supraoccipital ventrally and on its lateral sides it is overlapped by the tabulars.

PALATOQUADRATE AND STAPES

Quadrate: The quadrate has the typical dicynodontian shape. The most striking feature is the structure of the articulation surface for the lower jaw. It consists of well-defined, anteroposteriorly elongated lateral and medial condyles that are separated by a median groove (Fig. 2A–C, 4). The medial condyle is slightly larger and exhibits a sharp lateral border towards the median groove. In general, the articular surface of the quadrate is approximately as wide as it is long and allows for propalinal movement of the lower jaw. In occipital view, the quadrate reveals its bicondylar morphology at the base of posterolateral edge of the skull. It is a rather flat element, which is, together with the quadratojugal, strongly overlapped by the squamosal posteriorly, as is diagnostic for anomodonts. Dorsally, the quadrate contacts the opisthotic medially and the squamosal as well the quadratojugal further laterally. The dorsal sutural surface of the quadrate is exposed on the left side of the skull and reveals an irregular surface, where the usually contacting opisthotic, squamosal and quadratojugal bones are only partially preserved (Fig. 4). Anteriorly, the quadrate extends dorsally and encloses a small quadrate foramen (Fig. 3A, B). At its anteromedial edge, the quadrate contacts the quadrate ramus of the pterygoid. Finally, the quadrate articulates with the stapes medially to form part of the auditory apparatus.

Epipterygoid: The epipterygoid of *Kombuisia* is only fragmentarily preserved. It is only visible in right lateral view and seems to have shifted ventrally and posteriorly from its original position (Fig. 3A, B). The epipterygoid contacts the pterygoid element with a slightly expanded base. From there, it extends anterodorsally and seems to contact the prootic. However, this contact most certainly is the result of the dorsoventral flattening of the skull. The dorsalmost part of the epipterygoid, which typically contacts the parietal on the ventral side of the skull roof in dicynodonts, is not preserved, as this area was damaged and obscured by plaster.

Stapes: The stapes of *Kombuisia* is a solid, rod-like element that lacks a foramen for the stapedial artery (Fig. 2A–C, 4). In ventral view, it exhibits a short, robust shaft and flares out anteroposteriorly at its medial and lateral ends. In occipital view, the stapes is more slender and shows approximately the same diameter for most of the shaft. In contrast, the footplate at the medial end of the stapes is quite broad and articulates with the fenestra ovalis of the braincase. The distal end is also slightly expanded into a distinct

ventral and dorsal process (Fig. 4). In posterior view, these processes are separated by a shallow groove, which has previously been termed the extrastapedial facet (Cox, 1959). The ventral process is approximately in line with the shaft and contacts the quadrate bone. The dorsal process projects dorsally from the stapedial axis with an angle of about 45° to contact the paroccipital process of the opisthotic. Based on its position and morphology, the dorsal process of the stapes in *Kombuisia* is probably homologous with the dorsal stapedial process of 'pelycosaurs' and other non-anomodont early synapsids (Reisz, 1986; Sigogneau, 1989).

MANDIBLE

Dentary: The dentary is the dominant element of the lower jaw. Both dentaries are fused across the midline to form a strong mandibular symphysis, as is typical for dicynodonts and some basal anomodonts (Hopson & Barghusen, 1986; Modesto, Rubidge & Welman, 1999; Sidor, 2003; Fig. 2C–F). The symphyseal region itself is long and not parallel-sided in dorsal view, but tapers rostrally to a squared-off anterior tip, which was slightly damaged after the original description of the specimen (Hotton, 1974). A comparatively shallow median groove extends along the dorsal surface of the jaw symphysis. This groove is bounded laterally by low, but sharp ridges that extend anteroposteriorly from the corners of the squared-off tip and separate the median groove from the dentary tables laterally. Hotton (1974) reported the presence of an additional ridge lateral and parallel to each of these ridges, but the complete course of these ridges is no longer visible due to additional preparation since the first description of the holotype. In lateral aspect, the jaw symphysis is drawn into a dorsally projecting, sharp beak that is spatulate in shape (Fig. 3). The dentary does not bear any teeth, but the symphyseal region exhibits sharp anterior and lateral margins. Although the bone surface is slightly damaged, a number of small pits and foramina are visible, which indicates that this part of the lower jaw was certainly covered by a keratinous beak and provided an effective cutting tool in life. Along the ventral margin of the lower jaw the dentary extends back approximately to the middle of the jaw ramus. Here, it curves dorsally to form a notch and extends further back along the dorsal margin of the jaw. However, the posterior end of the dentary is not preserved dorsally. At its posterior margin the dentary overlaps the angular bone ventrally and the surangular element further dorsally (Fig. 1). Approximately in the centre of the lower jaw, at the level of the notch, the dentary and the angular enclose the remnant of a reduced external mandibular fenestra (Fig. 3A, B). Anteriorly and dorsally to this fenestra,

the dentary has a well-developed lateral dentary shelf that projects horizontally. From this shelf two ridges diverge posteriorly and enclose a shallow embayment right above the mandibular fenestra. Ventromedially, the splenial bone overlaps the dentary and extends far anteriorly to the level of the jaw symphysis. Further medially and at its posteriormost extension, the dentary is overlapped by the prearticular.

Splenial: The splenial bones of *Kombuisia* are fused across the midline. The splenial bone forms the ventromedial edge of the anterior part of the lower jaw. It is a very thin and slender element that is fused to its counterpart from the opposing jaw ramus at the posteroventral edge of the symphysis (Fig. 2C–F). The splenial contacts the dentary along most of its length and meets the angular and prearticular bones posteriorly. Furthermore, the splenial is fused to the dentary near the jaw symphysis (Fig. 2C, D).

Angular: The angular constitutes the ventral portion of the central part of the lower jaw (Fig. 2). The most striking feature of the angular bone is its well-defined reflected lamina. Nonetheless, the angular wing of the reflected lamina is quite small and positioned far anteriorly right behind the mandibular fenestra, which results in a very long angular cleft (*sensu* Allin & Hopson, 1992). Anteriorly, the angular contacts the overlapping posterior part of the dentary in an undulating suture, where it forms the ventral rim of the strongly reduced external mandibular fenestra. Dorsally, the angular is overlapped by the surangular and posteriorly it itself overlaps the articular. Finally, it has a long contact with the slender prearticular on its medial side.

Surangular: The surangular is best preserved in the right jaw ramus of the holotype, where it forms the dorsal margin of the lower jaw between the posteriormost extension of the dentary anteriorly and the articular posteriorly (Fig. 1, 2A, B). Ventrally it overlaps the angular bone.

Articular: As in other dicynodonts, the articular is at the posteriormost edge of the jaw ramus and contacts the angular anteroventrally, the surangular anterodorsally and the prearticular medially. Its articulation surface faces mainly dorsally, but descends slightly posteriorly (Fig. 3). The articulation surface is anteroposteriorly elongated, but is also broad mediolaterally to form an overhang laterally. In ventral aspect, the articular displays a dorsoventrally flattened projection with rounded edges on its medial side (Fig. 2A–C). This medial flange is positioned slightly below the level of the main articular surface and fits to the medial condyle of the quadrate. Overall, the articular surfaces of the articular are more extensive than that of the quadrate element, which allows for extensive

propalinal movement of the lower jaw (Crompton & Hotton, 1967). A fusion of the articular to the prearticular, as described for most anomodonts (Sidor, 2001, 2003), was not observed in *Kombuisia*. Therefore, the lack of fusion of these two elements represents one of the autapomorphies of this taxon.

Prearticular: The prearticular bone is a slender, sheet-like element at the medial side of the lower jaw, which extends about two-thirds of the length of the jaw ramus (Fig. 2A–C). It contacts the articular bone at the back of the jaw and extends anteriorly by overlapping the angular and surangular elements to finally meet the dentary and splenial bones at its anteriormost extension.

A PHYLOGENY OF THE ANOMODONTIA

ANALYSIS

The cladistic analysis includes 39 anomodont taxa from primarily Permian strata and 100 morphological characters. The gorgonopsian *Gorgonops*, the basal dinocephalian *Titanophoneus*, and a composite coding for basal therocephalians, the Lycosuchidae, were used for outgroup comparison to determine character polarities. The ingroup consists of six non-dicynodont anomodont taxa as well as 33 dicynodont taxa. Some of the ingroup taxa, such as *Anomocephalus*, *Lanthanostegus* and *Colobodectes* (Modesto *et al.*, 1999, 2002, 2003b; Modesto, Rubidge & Welman, 2003c), were not considered in phylogenetic analyses after their original description. The main arguments for the exclusion of these taxa were the poor preservation and therefore large number of missing data when coded for analysis. Most recently, however, empirical studies have showed that it is not the proportion of missing data, but rather too few complete characters that cause reduced accuracy associated with incomplete taxa (Wiens, 2003). Therefore, even taxa with a large amount of missing data were included in the present analysis. The analysis also includes a Russian dicynodont that has not been formally described. Angielczyk & Kurkin (2003a) figured photographs of PIN 156/114 and referred to this specimen as 'New Taxon 1' and cited 'A. A. Kurkin, unpubl. data' as reference. Ivakhnenko (2003) figured a reconstruction of this taxon based on PIN 156/4 and referred to it as '*Idelisaurus tatarica* Kurkin, in press' without designating it as a new genus and species or providing a description and diagnosis. As this description does not comply with the rules of the International Code of Zoological Nomenclature, the taxon will be referred to as '*Idelisaurus*', but it will be kept in quotation marks to indicate its status as a *nomen nudum*.

The characters used in this study include 74 cranial, 13 mandibular and 13 postcranial features.

Most characters were used in previous cladistic analyses of anomodont therapsids (Cluver & King, 1983; Hopson & Barghusen, 1986; King, 1988; Rubidge & Hopson, 1996; Modesto *et al.*, 1999, 2003b; Modesto & Rybczynski, 2000; Rybczynski, 2000; Angielczyk, 2001, 2004; Sidor, 2001, 2003; Maisch, 2002; Angielczyk & Kurkin, 2003a; Maisch & Gebauer, 2005; Surkov, Kalandadze & Benton, 2005), but are combined in this study for the first time in a total evidence approach. For this, the most recent morphological data sets for reconstructing anomodont relationships using cladistics were considered (see Appendix 1). All available characters were evaluated and included. The best suited character definitions were adopted or, where regarded as necessary, modified. Characters were only discarded from the analysis if they were parsimony uninformative when applied to this set of taxa. Codings of previous authors were scrutinized and in most cases could be corroborated via personal observation of relevant specimens. Data on taxa that could not be studied in person was obtained from the literature. A list of all characters and their sources is provided in Appendix 1. The codings for each taxon can be obtained from the data matrix in Appendix 2.

A parsimony analysis was carried out on the resulting data matrix using the heuristic search algorithm of PAUP 4.0b10 (Swofford, 2001), and 10 000 random addition sequence replicates were performed to avoid the analyses being trapped in a local minimum. All characters were equally weighted and treated as unordered. Multistate taxa were interpreted as polymorphism, and missing data as well as inapplicable characters were coded as '?'. Node support was measured by performing a decay analysis (Bremer, 1988) and bootstrap analysis with 1000 bootstrap replicates and ten random addition sequence replicates (Felsenstein, 1985).

RESULTS AND DISCUSSION

The parsimony analysis resulted in six most parsimonious trees with a tree length of 332 steps, the strict consensus of which is presented in Figure 5. The consistency index (CI) is 0.494, its retention index (RI) is 0.764 and its rescaled consistency index (RC) is 0.377. These values indicate that the amount of homoplasy in this tree is relatively high. This is probably related to the fairly large size of the data matrix (Archie, 1989), and comparable values have also been calculated in previous analyses. The nodal support, which has been measured by decay analysis and bootstrapping, is also displayed in Figure 5.

Phylogenetic relationships within the Anomodontia are well resolved and the support values of the individual nodes show a comparably stable general
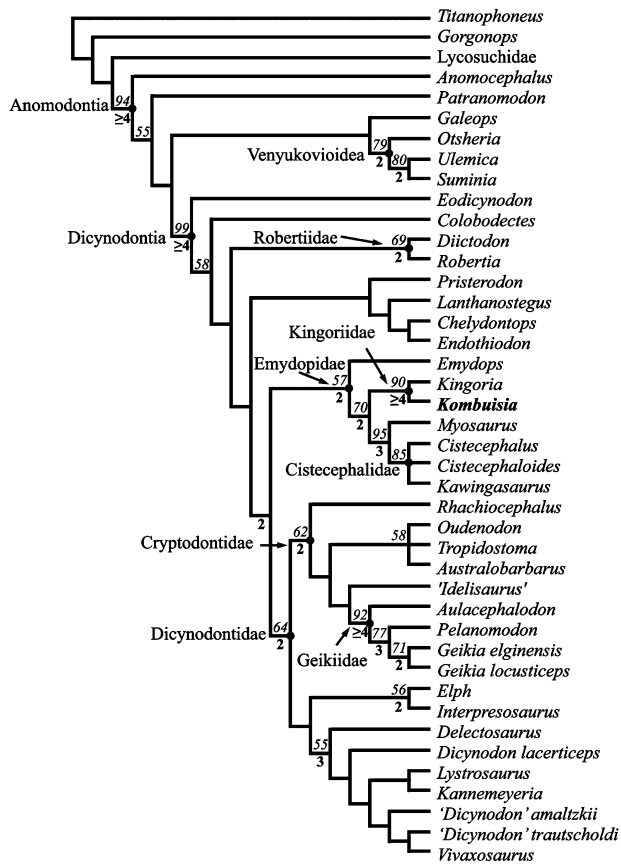
Figure 5. Strict consensus cladogram of the six most parsimonious trees (332 steps; CI: 0.494; RI: 0.764; RC: 0.377). Italic numbers indicate bootstrap values above 50% and bold numbers indicate Bremer decay values. No Bremer decay values are shown for nodes that collapse at one extra step. Selected clade names are labelled and discussed in the text.

topology. In general, this new phylogeny supports the major nodes and relationships of recent hypotheses. However, a number of significant modifications in tree topology are suggested and provide new insights into anomodont relationships. These results also raise additional questions for future research.

Anomodontia: It is important to note that this phylogeny corroborates the hypothesis that the recently described South African species *Anomocephalus africanus* Modesto, Rubidge and Welman constitutes the most basal known member of the Anomodontia. This position was suggested in the original description of this taxon (Modesto *et al.*, 1999; Modesto & Rubidge, 2000). However, subsequent papers that discussed basal anomodont relationships (Modesto & Rybczynski, 2000; Rybczynski, 2000; Modesto *et al.*, 2003b; Angielczyk, 2004) either excluded *Anomocephalus* or

the taxon was not yet available for study, such that this hypothesis has not been tested again. The present study supports the proposed phylogenetic position of *Anomocephalus* as the most basal anomodont, immediately basal to the comparably well-known South African taxon *Patranomodon nyaphulii* Rubidge and Hopson.

In addition, the monophyletic status of the Russian Venyukovioidea (*sensu* Modesto *et al.*, 1999; Modesto & Rybczynski, 2000; Rybczynski, 2000; *contra* Rubidge & Hopson, 1990), i.e. *Otsheria*, *Ulemica* and *Suminia*, is also supported by this analysis. Within the Venyukovioidea, *Otsheria* represents the most basal form, and *Suminia* and *Ulemica* are sister taxa, supporting the results of previous phylogenetic analysis (Modesto *et al.*, 1999; Rybczynski, 2000). The Russian venyokovioids belong to a larger monophylum that also includes the South African genus *Galeops*. This clade forms the sister taxon of the dicynodont anomodonts, but whether it is equivalent with what was originally known as the Dromasauria (*sensu* Broom, 1907, 1910, 1912), including the Venyukovioidea, remains unclear. To solve this, a more detailed consideration of the genera *Galepus* and *Galechirus* in a phylogenetic framework must be completed, even though a thorough anatomical desciption by Brinkman (1981) already exists. Regardless, the present topology conflicts with results of previous analyses (Modesto *et al.*, 1999; Modesto & Rybczynski, 2000; Rybczynski, 2000; Angielczyk, 2004) that indicated a sister-taxon relationship of *Galeops* to the Dicynodontia.

Dicynodontia: Within dicynodonts, *Eodicynodon* represents the earliest known and most basal genus, being followed by the slightly more derived and only recently described genus *Colobodectes* (Modesto *et al.*, 2003b). Higher up on the tree there are a number of taxa, *Robertia* + *Diictodon*, *Endothiodon* + *Chelydontops*, and *Pristerodon*, whose phylogenetic relationships have been unresolved in the strict consensus cladogram of the most recent phylogenetic analysis of Permian dicynodonts (Angielczyk & Kurkin, 2003a). However, the authors favoured the tree topology ((*Robertia*, *Diictodon*)((*Endothiodon*, *Chelydontops*) (*Pristerodon*, other advanced dicynodonts))), which was supported by stratigraphic data as well as its similarity to a previous analysis (Angielczyk, 2001). Here, I suggest a slightly different relationship of these taxa.

As in the previous studies, the basal most clade recovered in the present analysis is the Robertiidae, including *Robertia* and *Diictodon*, of which particularly the latter has recently received increased attention (Ray & Chinsamy, 2003, 2004; Sullivan, Reisz & Smith, 2003; Sullivan & Reisz, 2005). In contrast to

Angielczyk & Kurkin's (2003a) topology, however, *Pristerodon* does not form the sister taxon to all other advanced dicynodonts, but represents the basal most taxon within a clade that includes *Endothiodon* + *Chelydontops*, and *Lanthanostegus* (Modesto *et al*., 2002, 2003c). This position of *Pristerodon* was also suggested by one of the six equally parsimonious topologies in Angielczyk & Kurkin (2003a: 175). In any case, the phylogenetic position of *Lanthanostegus* differs slightly from that in Modesto *et al*. (2002), who suggested its sister-taxon relationship to *Endothiodon* rather than to *Endothiodon* + *Chelydontops* as proposed here. Overall, the relative basal position of these taxa within the Dicynodontia in this analysis agrees with recent studies (Angielczyk, 2001; Angielczyk & Kurkin, 2003a), but contrasts a deeper nested placement of the robertiids and *Pristerodon* proposed by other authors (Cluver & King, 1983; King, 1988, 1990a).

Emydopidae: The more advanced dicynodonts fall within two groups, the Emydopidae and Dicynodontidae (*sensu* Angielczyk & Kurkin, 2003a), that have a sister-taxon relationship. The Emydopidae, the clade including *Emydops*, *Myosaurus* and all descendants of their most recent common ancestor, is of particular interest to this investigation, because the results of the phylogenetic analysis confirm that the taxon under study, *Kombuisia frerensis*, indeed belongs to this clade. Previous analyses included *Emydops*, *Cistecephalus*, *Kingoria* and *Myosaurus* and resulted in conflicting relationships within this clade. The most recent topology (*Emydops*(*Cistecephalus*(*Kingoria*, *Myosaurus*))) as well as a detailed discussion of the characters involved in this relationship assessment was presented by Angielczyk & Kurkin (2003a). However, as the current topology differs from the latter, this point necessitates some further discussion. Overall, the placement of *Emydops* as the basal-most member of this clade is supported by this study. But the current topology suggests a basal split into the Kingoriidae, i.e. *Kingoria* and *Kombuisia*, as well as a clade that includes *Myosaurus* and the Cistecephalidae. Besides *Cistecephalus*, the latter comprises two closely related taxa, *Kawingasaurus* and *Cistecephaloides*, which were for the first time included into a phylogenetic analysis, but whose relationships within the cistecephalids could not be resolved beyond a trichotomy.

Dicynodontidae, clade I – Cryptodontidae: The Dicynodontidae can be subdivided into two major groups, the Cryptodontidae and a clade that includes the genera *Dicynodon* and *Lystrosaurus* as well as the Triassic Kannemeyeriiformes. Originally, the Cryptodontidae (Owen, 1859; *sensu* Toerien, 1953) only included the four genera *Oudenodon*, *Kitchingia* (a

junior subjective synonym of *Rhachiocephalus*), *Platycyclops* and *Pelanomodon*. Rowe (1980) discussed the taxonomic status of *Geikia elginensis* and assigned this taxon, as well as a number of other taxa whose taxonomic validity are pending, to this clade. Therefore, the Cryptodontidae are defined here as *Rhachiocephalus*, *Oudenodon* and all descendants of their most recent common ancestor, which is regarded as closest to the original definition. The internal relationships of the cryptodontids correspond to those suggested by Angielczyk & Kurkin (2003a) and Maisch & Gebauer (2005). *Rhachiocephalus* is the most basal cryptodontid. The remaining cryptodontids split into a clade comprising *Oudenodon*, *Tropidostoma* and *Australobarbarus* on the one hand, and a clade including *Geikia locusticeps*, *Geikia elginensis*, *Pelanomodon*, *Aulacephalodon*, and '*Idelisaurus*' on the other. *Oudenodon*, *Tropidostoma* and *Australobarbarus* are not further resolved and form a trichotomy. This underlines the necessity for a clarification of their taxonomic status, which is currently addressed by Angielczyk & Botha (2005). One aspect in this taxonomic question is that *Oudenodon* and *Tropidostoma* might represent sexual dimorphic morphotypes of the same taxon, rather than two different genera. Another aspect is the taxonomic validity of the Russian genus *Australobarbarus*, which might be a junior synonym of *Tropidostoma*. However, these questions will be considered elsewhere and are beyond the scope of this study.

In contrast, the phylogenetic relationships within the other branch of derived cryptodontids are comparatively robust. Thereby, the topology ('*Idelisaurus*' (*Aulacephalodon* (*Pelanomodon* (*Geikia locusticeps*, *Geikia elginensis*)))) corresponds to that presented by Maisch & Gebauer (2005), with the inclusion of the Russian taxon '*Idelisaurus*'. In their paper, Maisch & Gebauer (2005) concluded that the correct name for this clade, excluding '*Idelisaurus*', should be Geikiidae (*sensu* von Huene, 1948), which has priority over Aulacephalodontinae (*sensu* Cluver & King, 1983). The correct synonym of Geikiidae (*sensu* Maisch & Gebauer, 2005), however, is Aulacephalodontidae (Keyser, 1969; *sensu* Cluver & King, 1983) rather than Cluver & King's Aulacephalodontinae, of which the latter only comprises the genus *Aulacephalodon*. To grant stability of nomenclature this issue necessitates some further discussion, since it is not clear whether both suggested clade-names refer to the same clade under the topology presented in this study. Moreover, von Huene (1948: 80) used a character-based definition for Geikiidae to describe all Upper Permian anomodonts with the following features: 'parietal region narrow, frontal region broad; short pointed snout; large prefrontal corners'. In contrast, Maisch & Gebauer (2005) used a taxon-based definition, which is much more restricted than it was originally

approached by von Huene (1948). Thus, for reasons of nomenclatural stability, it is hereby suggested to retain the clade-name Aulacephalodontidae (Keyser, 1969; Kitching, 1977; *sensu* Cluver & King, 1983) for the most recent common ancestor of *Aulacephalodon bainii* and *Geikia elginensis* and all of their descendants. In addition, the clade-name Geikiidae (*sensu* von Huene, 1948) should be used for all dicynodonts that are more closely related to *Geikia elginensis* than to *Oudenodon bainii*, which also includes the genus '*Idelisaurus*'.

Dicynodontidae, clade II: The sister group of the cryptodontids within the Dicynodontidae includes two Russian dicynodonts at the base, *Elph* and *Interpresosaurus*, and a clade comprising *Delectosaurus*, several *Dicynodon*-like taxa, *Lystrosaurus*, *Vivaxosaurus* and the Kannemeyeriiformes, exemplified by *Kannemeyeria*. A name for this clade has yet to be proposed. Although Angielczyk & Kurkin's (2003a) strict consensus tree did not fully resolve the base of this clade, the basal placement of *Elph* and *Interpresosaurus* was also recovered in their favoured tree out of 54 most parsimonious cladograms. Thus, the fully resolved cladogram of the present analysis further corroborates the previous placement of the two taxa. Moreover, the topology within their sister group is identical to the phylogenetic hypothesis of Angielczyk & Kurkin (2003a), with the exception of the placement of *Kannemeyeria*. This results in a different hypothesis for the sister-taxon relationship of the Kannemeyeriiformes. *Vivaxosaurus*, which has been suggested to represent the sister taxon to this large Triassic monophylum, as exemplified by *Kannemeyeria*, falls within the Russian '*Dicynodon*' species, whereas *Kannemeyeria* clusters with *Lystrosaurus*. Although this topology is not very robust and collapses when an additional step is added to the most parsimonious tree, this hypothesis justifies doubt about the proposed phylogenetic position of *Vivaxosaurus* as the sister taxon to all kannemeyeriiforms (Kalandadze & Kurkin, 2000; Angielczyk & Kurkin, 2003a). Finally, the taxonomic status of the genus *Dicynodon* should be addressed. It has already been discussed by Angielczyk & Kurkin (2003a,b) that a taxonomic re-evaluation of this taxon is necessary and that the two Russian species assigned to this genus probably should be assigned to a different genus, instead of forming a clade with the genotype *Dicynodon lacerticeps*. Although it has been argued otherwise by Lucas (2005), this conclusion is also supported by the present phylogeny. Furthermore, the recognition of *Vivaxosaurus permirus* (Kalandadze & Kurkin, 2000; Surkov, 2004) as a distinct taxon appears to be doubtful based on its striking similarity with '*Dicynodon*' trautscholdi, as noted by previous authors (Angielczyk &

Kurkin, 2003a). Independent of the possible synonymy of *V. permirus* and '*D.' trautscholdi*, the clustering of *V. permirus*, '*D.' trautscholdi* and '*D.' amaltzkii* may justify their inclusion into a single genus, possibly *Vivaxosaurus* itself.

Support values: The Bremer decay and bootstrap values (Fig. 5) indicate strong nodal support (Bremer decay ≥4; bootstrap ≥90) for the monophyly of the Anomodontia, Dicynodontia, Geikiidae (excluding '*Idelisaurus*'), and the sister-taxon relationship of *Kombuisia* and *Kingoria*. Moderate to strong support values (Bremer decay 2–3; bootstrap 50–95) were obtained for the Venyokovioidea, Robertiidae, Emydopidae and Geikiidae, as well as at the nodes uniting all dicynodontids, cryptodontids, *Elph* and *Interpresosaurus*, and the clade comprising *Delectosaurus*, *Vivaxosaurus* and all descendants of their most recent common ancestor. Weaker support of a number of nodes at the base of anomodonts, dicynodonts and higher up the tree is indicated by their collapse with one additional step added to the most parsimonious cladogram, and bootstrap values between 25 and 60.

In summary, the present analysis corroborates the general topologies of recent hypotheses (Modesto *et al.*, 1999, 2003b; Rybczynski, 2000; Angielczyk, 2001, 2004; Angielczyk & Kurkin, 2003a; Maisch & Gebauer, 2005). Moreover, it provides further resolution and suggests a number of new relationships.

SURVIVORSHIP OF DICYNODONTS ACROSS THE PERMIAN–TRIASSIC BOUNDARY

It is widely accepted that the most severe extinction event of the Earth's history at the end of the Permian had a major impact on the taxonomic diversity of life, especially in the marine realm (Erwin, 1993, 1994; Erwin, Bowring & Yugan, 2002). The evidence for a similar effect on terrestrial ecosystems, and in particular on the vertebrate fauna, was for most of the 19th and 20th centuries regarded as weak (for a review see Benton, 2003). In contrast, recent studies on boundary beds in South Africa and Russia support a major effect on terrestrial vertebrates (Smith & Ward, 2001; Benton, Tverdokhlebov & Surkov, 2004). Most recently, Ward *et al.* (2005) documented both a gradual and an abrupt extinction among Late Permian land vertebrates in the South African Karoo Basin.

These studies, however, are solely based on stratigraphic occurrence data of the fossil taxa on a local scale and they either do not consider a phylogenetic context at all, or use higher taxonomic levels to evaluate extinction rates. The main argument for the use of higher taxonomic levels for the investigation of extinction rate is that the fossil record for species is

not complete enough and that higher taxa, in particular the family level, provide a more accurate picture of a general pattern (Valentine, 1974). In the meantime, mathematical approaches such as the rarefaction method (Raup, 1979; McKinney, 1995) are used to extrapolate species extinction rates, without actually considering existing data about species. An estimated rarefaction value for the extinction rate of tetrapod species at the Permian–Triassic boundary has been suggested to be 95% (Benton, 2003: 220) scaled up from a family extinction rate of 75% (Maxwell, 1992).

The extinction rate naturally varies among tetrapod groups, which leads to the complete extinction of some clades and only a decrease of taxonomic diversity in others. For example, of all dominant terrestrial amniote clades of the Late Permian, the pareiasaurs, biarmosuchians and gorgonopsians became extinct at or near the Permian–Triassic boundary (Maxwell, 1992; Rubidge, 1995; Smith & Ward, 2001; Benton, Tverdokhlebov & Surkov, 2004). In contrast, procolophonoids, diapsids, cynodonts, therocephalians and dicynodonts all survived the end-Permian extinction with varying numbers of surviving genera and species (Dilkes, 1998; Modesto, Sues & Damiani, 2001; Modesto *et al.*, 2003a; Sidor & Smith, 2004; Smith & Botha, 2005).

As the dominant element of Upper Permian terrestrial ecosystems, it has often been stated that dicynodonts suffered from a substantial decrease in taxonomic diversity (King, 1990b, 1991; Maxwell, 1992; Smith & Botha, 2005), before they successfully diversified again in the Triassic period. It is important to note that there is only a single dicynodont species, *Lystrosaurus curvatus*, which is known from below as well as above the Permian–Triassic boundary (King & Jenkins, 1997; Smith & Botha, 2005). As a result, it has often been stated that *Lystrosaurus* was the only dicynodont that survived the end-Permian extinction (Benton, 2003; Retallack, Smith & Ward, 2003). However, a complete picture of dicynodont survivorship across the Permian–Triassic boundary can be developed only if both stratigraphic occurrence data and phylogenetic relationships are taken into account.

The Triassic dicynodont genus *Kombuisia* is of particular interest for a phylogenetic evaluation of the survivorship of dicynodonts across the Permian–Triassic boundary. *Kombuisia* is Early to Middle Triassic in age, but the present phylogenetic analysis supports the previously proposed hypothesis that this taxon does not belong to the monophyletic Triassic Kannemeyeriiformes. The evaluation of its phylogenetic position has implications for the survivorship of the Dicynodontia across the Permian–Triassic boundary within a phylogenetic context and with special consideration of ghost lineages (Fig. 6).

The present phylogeny suggests a survival of multiple dicynodont lineages across the Permo-Triassic boundary. There are at least four surviving dicynodont lineages with *Kombuisia*, *Myosaurus*, *Lystrosaurus* and the monophyletic Kannemeyeriiformes extending beyond the end-Permian extinction event. This pattern is paralleled by various other groups of Permian–Triassic tetrapods, such as diapsids (Dilkes, 1998) and procolophonoids (Modesto *et al.*, 2001, 2003a), supporting a higher estimation of survivorship across the Permian–Triassic boundary than previously suggested. Smith & Ward (2001) proposed an ecologically stepped extinction pattern, characterized by the disappearance of small forms first, being followed by larger taxa. While *Lystrosaurus* and the lineage of the Kannemeyeriiformes represent large forms, two of the surviving lineages are the small, but non-burrowing emydopids *Kombuisia* and *Myosaurus*. This indicates a survivorship also of these ecological forms. This pattern seems to contradict the previously proposed scenario of an ecologically stepped extinction and could be the result of an incomplete fossil record. However, the early extinction of small forms could also be a real local phenomenon in the South African Karoo Basin, and the survivorship and re-appearance of *Kombuisia* and *Myosaurus* in the Lower and Middle Triassic reflect environmentally driven biogeographical migrations of these taxa. Further research will be necessary to gain a more complete picture of the effect of the end-Permian extinction on the diversity of anomodonts.

CONCLUSION

The cranial anatomy of the Middle Triassic diynodont *Kombuisia frerensis* provides insights not only into its phylogenetic position, but also into the interrelationships of the other Emydopidae. The previous hypothesis of a close relationship of *Kombuisia* to the Permian genus *Kingoria* is corroborated by this study. Their sister-taxon relationship is supported by a number of newly recognized synapomorphies, including a reduction of the mandibular fenestra, a narrow intertemporal region that forms a sagittal crest, the presence of a dorsolateral notch in occipital view of the squamosal, a relatively wide mid-ventral plate of the vomer, and a dorsal stapedial process. Furthermore, *Kombuisia* is easily recognizable and distinguishable form *Kingoria* on the basis of its autapomorphies, which are the absence of a pineal foramen, an inverted triangular shape of the interparietal bone, the lack of fusion of the articular and prearticular bones, and the presence of parietal posterolateral processes that are elongate, slender and extend onto the occipital edge of the skull roof.
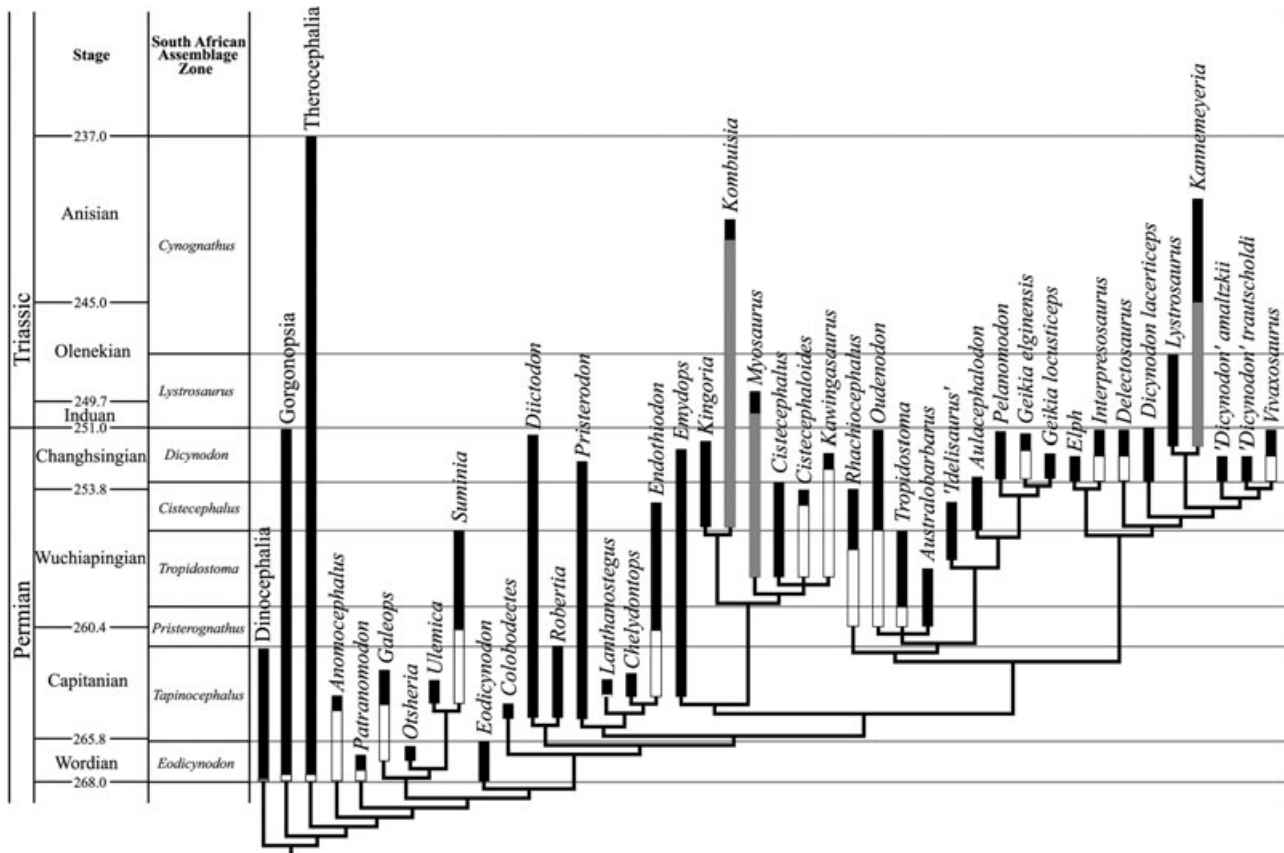
Figure 6. Time-calibrated strict consensus cladogram, depicting the survivorship of multiple anomodont lineages across the Permian–Triassic boundary. The stratigraphic ranges of the included anomodont species are plotted on a stratigraphic column that uses the well-established Permian–Triassic assemblage zones from the South African Karoo Basin (Rubidge, 1995) and the international marine stages (Gradstein *et al*., 2004) as basis. Stratigraphic ranges of the South African taxa are taken from Rubidge (1995) and Angielczyk & Kurkin (2003a), with the addition of *Lanthanostegus* (Modesto *et al*., 2002, 2003c) and *Colobodectes* (Modesto *et al*., 2003b). The stratigraphic range of *Emydops* is extended to fit the maximal range as proposed by Angielczyk, Fröbisch & Smith (2005). The stratigraphic position of the holotypic and only specimen of *Cistecephaloides boonstrai* (Cluver, 1974) is here considered to be in the upper part of the *Cistecephalus* AZ (Kitching, 1977). Correlation and stratigraphic ranges of the non-South African anomodont taxa from Russia, Scotland and Tanzania are based on Benton & Walker (1985), Gay & Cruickshank (1999), Angielczyk & Kurkin (2003a), Angielczyk (2004), Golubev (2005) and Rubidge (2005). Solid bars represent the known stratigraphic ranges, whereas open and grey bars indicate ghost lineages. Grey bars indicate the ghost lineages of survivors that cross the Permian–Triassic boundary.

The phylogenetic hypothesis for anomodont relationships presented here supports a number of previously proposed higher-level phylogenetic relationships within the Anomodontia, such as the nodes Anomodontia, Venyukovioidea, Dicynodontia, Dicynodontidae and Emydopidae. Furthermore, the consensus tree of the six most parsimonious trees resolves nodes that remained unresolved in previous phylogenetic analyses, such as the position of the Robertiidae, Endothiodontidae and *Pristerodon* at the base of the Dicynodontia. In addition, the topology suggests a basal split into two large clades within the Dicynodontidae, which are represented by the Cryptodontidae on the one hand,

and a clade comprising *Elph*, *Dicynodon* and all descendants of their most recent common ancestor on the other.

However, the proposed topology also conflicts with previously suggested hypotheses, including the phylogenetic placement of *Galeops*, *Pristerodon*, *Lanthanostegus* and *Kannemeyeria*. The latter is associated with the question of the origin of the large monophylum of Triassic dicynodonts, the Kannemeyeriiformes. To resolve this issue further it will be necessary to expand the existing morphological data set to include more kannemeyeriiform dicynodonts in a comprehensive phylogenetic analysis of Permian and Triassic anomodonts.

Finally, the present phylogeny can be used to evaluate the survivorship of anomodonts across the Permian–Triassic boundary in a phylogenetic context. The topology documents that at least four distinct dicynodont lineages survived the end-Permian extinction event. These are *Kombuisia*, *Myosaurus*, *Lystrosaurus* and the Kannemeyeriiformes, all of which represent different ecological forms.

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APPENDIX 1

CHARACTER LIST

Most of the following characters have been used in previous phylogenetic analyses of anomodont therapsids, but some character states and character 72 are new. The most inclusive anomodont phylogeny to date is that of Angielczyk & Kurkin (2003a) and was used as the starting point for the present study. Sources are listed behind the character definition and include Cluver & King (1983), Hopson & Barghusen (1986), King (1988), Rubidge & Hopson (1996), Modesto *et al.* (1999, 2003b), Modesto & Rybczynski (2000), Rybczynski (2000), Angielczyk (2001, 2004), Sidor (2001, 2003), Maisch (2002), Angielczyk & Kurkin (2003a), Maisch & Gebauer (2005) and Surkov *et al.* (2005). Modifications of character state codings from the original publications are discussed.

CRANIAL CHARACTERS

1. Antorbital region long (0), short (1), or greatly abbreviated (2). (From Modesto *et al.*, 1999: #6)
Modified versions of this character have been used in previous phylogenetic analyses of basal anomodonts (e.g. Modesto *et al.*, 1999; Angielczyk, 2004). Quantitative as well as qualitative definitions of character states were attempted by the various authors. The inclusion of a larger number of dicynodont taxa increased the spectrum of interspecific variation and hampers a clear delimitation of character states in form of quantitative values. I adapt the qualitative character definition of Modesto *et al.* (1999) following the modified codings for *Ulemica*, *Otsheria* and *Suminia* made by Angielczyk (2004). Modesto *et al.* (1999) regarded Gorgonopsia to be polymorphic ('0 + 1') for this character. Angielczyk (2004) discussed this issue and concluded in the text that '1' is the preferable character state for *Gorgonops*, but in his data matrix *Gorgonops* was coded as '0'. The latter is also considered to be the accurate coding in this study.
2. Premaxillae unfused (0) or fused (1). (From Angielczyk & Kurkin, 2003a: #3)
3. Paired anterior ridges on palatal surface of premaxilla absent (0), present and converge posteriorly (1), or present and do not converge (2). (From Angielczyk & Kurkin, 2003a: #7)
4. Posterior median ridge on palatal surface of premaxilla absent (0), present with a flattened, expanded anterior area (1), or present without a flattened, expanded anterior area (2). (From Angielczyk & Kurkin, 2003a: #8)
5. Palatal surface of premaxilla with well-defined depressions with curved sides lateral to median ridge (0), with groove-like depressions that have straight sides and a rounded anterior end (1), or relatively flat with poorly defined or no depressions present (2). (From Angielczyk & Kurkin, 2003a: #9)
6. Location of premaxillary teeth lateral (0), medial (1) or absent (2). (From Angielczyk & Kurkin, 2003a: #2)
7. Internal narial shelf absent (0), narrow and formed by premaxilla, maxilla, and palatine (1), or well developed and formed primarily by premaxilla (2). (Modified from Modesto *et al.*, 1999: #22)
Modesto *et al.* (1999) and Modesto & Rybczynski (2000) considered their therocephalian outgroups to possess a narrow internal narial shelf that is formed by maxilla and palatine only (their character state '1'). In contrast, Rybczynski (2000) and Angielczyk (2004) argued that this character state is only present in more derived therocephalians and not in the basal lycosuchid therocephalians, which are therefore rather coded as '0'. I agree with this conclusion and omitted their character state '1' from this analysis. In addition, I changed the wording of character state '2' (previously state '3'), which is the general dicynodont condition. The well-developed internal narial shelf primarily consists of the premaxilla. There is only minor lateral contribution of the maxilla, which is sometimes even excluded from the internal narial opening, e.g. in *Kombuisia*. However, these variations are considered to be independent and are included in character #58 of this study.
8. Median ridge on anterior surface of the snout absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #47)
9. Anterior tip of snout rounded (0) or squared off (1). (From Maisch & Gebauer, 2005: #11)
10. Snout transversely narrow (0) or broadened (1). (From Maisch & Gebauer, 2005: #2)
11. Snout open to back of the skull (0) or anterior margin of orbit extended posteromedially to partly close off the snout from the rest of the skull (1). (From Angielczyk & Kurkin, 2003a: #25)
12. Septomaxilla posterodorsal spur present (0), absent and septomaxilla recessed within naris (1), or absent but septomaxilla with broad facial exposure (2). (Modified from Modesto *et al.*, 1999: #8)
The original character definition by Modesto *et al.* (1999) was complemented by character state '2', which corresponds to character state '1' of character 13 from Maisch & Gebauer (2005). This differentiation is made, because there is a clear difference between the very slender posterodorsal spur of the septomaxilla in basal taxa and the broad exposure in more derived forms.
13. Maxillary alveolar region short, occupying less than 53% of the ventral length of the bone (0) or tooth bearing region long, occupying 72% or more of the ventral length of the bone (1). (From Modesto *et al.*, 1999: #9)

14. Maxillary canine present as large member of tooth series (0), absent (1), or present as tusk (2). (From Modesto *et al.*, 2003b: #6)

15. Maxillary non-caniniform teeth located near lateral margin of maxilla (0), located more medially, but with more posterior teeth often approaching the lateral margin of maxilla (1), located medially and with teeth a constant distance from the margin of the maxilla (2), or absent (3). (From Angielczyk & Kurkin, 2003a: #4)

16. Shelf-like area lateral to the maxillary non-caniniform teeth absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #5)

17. Fine serrations on marginal teeth present (0), serrations absent (1), or coarse serrations present (2). (From Modesto *et al.*, 1999: #3)

18. Denticulated cingulum on marginal teeth absent (0) or present (1). (From Modesto *et al.*, 1999: #4)

19. Sutural contact of maxilla and prefrontal present (0) or absent (1). (From Modesto *et al.*, 2003b: #10)

20. Caniniform process absent (0) or present (1). (Modified from Angielczyk & Kurkin, 2003a: #6)

The original character definition by Angielczyk & Kurkin (2003a) was modified and character state '2' of their study was excluded from this character to represent a new character (#22 of this study).

21. Embayment of palatal rim anterior to caniniform process or tusk absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #14)

22. Notch in palatal rim anterior to caniniform process absent (0) or present (1). (Modified from Angielczyk & Kurkin, 2003a: #6)

23. Keel-like extension of the palatal rim posterior to the caniniform process absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #1)

24. Postcaniniform crest absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #28)

25. Ventral edge of the caniniform process or dorsal edge of the erupted portion of the canine tusk anterior (0), at the same level (1), or posterior to (2) the level of the anterior orbital margin. (From Angielczyk & Kurkin, 2003a: #44)

26. Nasal bosses absent (0), present as a median swelling with a continuous posterior margin (1), present as paired swellings near the dorsal or posterodorsal margin of external nares (2), present as paired swellings that meet in the midline to form a swollen anterodorsal surface on the snout (3). (From Angielczyk & Kurkin, 2003a: #23)

27. Crest on naso-frontal suture absent (0) or present (1). (From Maisch, 2002: #18)

28. Postfrontal bone present (0) or absent (1). (From Maisch, 2002: #8)

29. Postorbital sharply tipped ventrally (0) or anteroposteriorly expanded upon zygoma in lateral aspect (1). (From Angielczyk, 2004: #10)

This character was first introduced by Modesto *et al.* (1999) and was subsequently used by Modesto & Rybczynski (2000), Rybczynski (2000), Modesto *et al.* (2003b) and Angielczyk (2004). The latter reanalysed the codings for a number of basal anomodonts and restricted the use of character state '1' to *Gorgonops*, *Patranomodon* and *Galeops*, which is agreed upon in this study.

30. Postorbital bar without (0) or with thickenings and rugosities (1). (From Maisch & Gebauer, 2005: #5)

31. Preparietal bone absent (0), present and its dorsal surface relatively flat and flush with the skull roof (1), or present and with a depressed dorsal surface relative to the surrounding skull roof (2). (From Angielczyk & Kurkin, 2003a: #45)

The order of the original character states by Angielczyk & Kurkin (2003a) was changed, such that state '0' (character state '2' therein) reflects the plesiomorphic condition for the Anomodontia.

32. Parietals' contribution to skull table transversely as broad as long (0), longer anteroposteriorly than broad (1), or shorter anteroposteriorly than broad (2). (From Modesto & Rybczynski, 2000: #16)

33. Parietal posterolateral process slender and elongate (0), or short (1). (From Modesto & Rybczynski, 2000: #17)

I coded *Kombuisia* for this character as state '0', because a slender and elongate posterolateral process of the parietal, similar in shape to that of *Titanophoneus* and *Gorgonops*, is present. A short posterolateral process of the parietal is a shared derived character of the Anomodontia. Thus, the condition in *Kombuisia* represents an autapomorphy of this taxon.

34. Parietals widely exposed on the skull roof (0), postorbitals partially overlap parietals on skull roof, but parietals are exposed in a central groove or depression (1), parietals exposed on skull roof and postorbitals steeply placed on the lateral sides of the skull and concave laterally (2), postorbitals slope ventrolaterally and overlap parietals nearly completely (3), parietals exposed on dorsal skull roof between postorbitals that are nearly vertically placed on the side of the skull, with flat lateral surfaces (4), or postorbitals slope slightly ventrolaterally for most of their width and partially overlap the parietals, which form a slight crest along the midline of the skull (5). (From Angielczyk & Kurkin, 2003a: #20)

35. Fossa on the ventral surface of the intertemporal bar formed by the postorbital and parietal large (0), reduced (1), or absent (2). (From Angielczyk & Kurkin, 2003: #53)

36. Pineal foramen surrounded by a thin, smooth, chimney-like boss (0), flush or nearly flush with dorsal surface of skull (1), surrounded by a strong, often rugose boss (2), or absent (3). (Modified from Angielczyk & Kurkin, 2003a: #26)

The order of the original character states by Angielczyk & Kurkin (2003a) was changed and the original definition was complemented by character state '3', which represents the lack of a pineal foramen in *Kombuisia* & *Kawingasaurus*. Modesto *et al.* (1999) coded Gorgonopsia as '1', whereas Angielczyk (2004) changed the coding for *Gorgonops* to '0', which is adapted in this publication. In addition, Angielczyk (2004) coded *Suminia* for this character as state '1'. I disagree with this coding and coded Suminia as '0', in agreement with Modesto *et al.* (1999), Modesto & Rybczynski (2000), and Rybczynski (2000). Furthermore, in all previous analyses *Patranomodon* was coded as state '1' for this character. However, in this paper '?' is considered to be the appropriate coding for *Patranomodon*, because the thin, chimney-like boss that surrounds the pineal foramen in all other nondicynodont anomodonts is a very delicate structure and the imperfect preservation of the skull roof of the only specimen of *Patranomodon* justifies to question the previous codings.

37. Interparietal does contribute to intertemporal skull roof (0) or does not contribute to intertemporal skull roof (1). (From Angielczyk & Kurkin, 2003a: #48)

38. Squamosal without (0) or with (1) lateral fossa for the origin of the lateral branch of the M. adductor mandibulae externus. (From Angielczyk & Kurkin, 2003a: #21)

39. Squamosal with a relatively straight contour in occipital view (0) or with a distinct dorsolateral notch in occipital view (1). (From Angielczyk & Kurkin, 2003a: #32)

40. Squamosal posteroventral process behind quadrate and quadratojugal absent (0) or present (1). (From Modesto *et al.*, 1999: #15)

A posteroventral process of the squamosal that reaches behind the quadrate and quadratojugal has previously been described to represent an unambiguous autapomorphy of the Anomodontia (Rubidge & Hopson, 1996; Modesto *et al.*, 1999, 2003b; Modesto & Rybczynski, 2000; Rybczynski, 2000; Angielczyk, 2004). However, van den Heever (1994: p. 27) mentioned that in basal therocephalians the squamosal also extends laterally to cover the quadrate and quadratojugal posteriorly. Therefore, in this study the Lycosuchidae are coded as state '1' for this character.

41. Zygomatic portion of the squamosal of nearly constant thickness and lacking a distinctly downturned section near its posterior end (0) or posterior portion thickened and/or downturned (1). (From Angielczyk & Kurkin, 2003a: #51)

42. Zygomatic process of squamosal parasagittally deep (0), narrow and rod-like (1), or transversely expanded (2). (From Modesto *et al.*, 1999: #12)

43. Squamosal zygomatic process narrowly based and in line with occiput (0) or widely based and flares posteriorly beyond occiput (1). (From Modesto *et al.*, 2003b: #15)

44. Sigmoid curvature of zygomatic portion of squamosal absent (0) or present (1). (From Maisch & Gebauer, 2005: #4)

45. Sutural contact of squamosal and maxilla absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #34)

46. Squamosal separated from (0) or contacts (1) postorbital on zygoma. (From Modesto *et al.*, 2003b: #14)

47. Squamosal separated by tabular bone from supraoccipital (0) or contacts supraoccipital (1). (From Modesto *et al.*, 1999: #20)

48. Zygomatic arch approximately at one level with tooth row, basicranium, and jaw articulation (0) or displaced dorsally well above those features (1). (From Rubidge & Hopson, 1996: #1)

49. Quadratojugal narrow and rod-like (0) or plate-like distally (1). (From Modesto *et al.*, 1999: #17)

50. Vomers unfused (0) or fused (1). (From Angielczyk & Kurkin, 2003a: #11)

51. Mid-ventral plate of vomers with an expanded, oval-shaped area posterior to junction with premaxilla (0) or without a notable expanded area posterior to junction with premaxilla (1). (From Angielczyk & Kurkin, 2003a: #12)

52. Mid-ventral plate of vomers relatively wide in ventral view (0) or more narrow and blade-like in ventral view (1). (From Angielczyk & Kurkin, 2003a: #13)

53. Palatine dentition present (0) or absent (1). (From Modesto *et al.*, 1999: #25)

This character is discussed in detail by Angielczyk (2004: #27 of his study) and his proposed coding for *Suminia* as '?' is adopted here in agreement with the description of Rybczynski (2000).

54. Palatal surface of the palatine without evidence of a keratinized covering (0), with a rounded, bulbous surface texture that may have had a keratinized covering (1), relatively smooth and flat, but with fine pitting and texturing suggestive of a keratinized covering (2), highly rugose and textured, suggesting a keratinized covering, with a raised posterior section and an anterior section that is flush with the secondary palate (3), or moderately rugose with pitting suggesting a keratinized covering and flush with the secondary palate (4). (From Angielczyk & Kurkin, 2003a: #22)

The evidence for a keratinized covering of the palatine and its possible confusion with small denticle-bearing alveoli in basal anomodonts has been discussed in detail by Angielczyk (2001, 2004). van den Heever (1994: p.24) described a distinctly rugose and foveate surface of the palatine medial to the postcanine tooth row, which he thought was covered by a layer of keratinized integument in life. This condition appears to be similar to that seen in *Eodicynodon* an is therefore

coded as state '1' in this paper. In addition, the relative flat but pitted palatine surfaces in *Suminia* and *Ulemica* are coded as state '2'. The palatines of *Patranomdon*, *Otsheria*, and *Galeops* do not show evidence of a keratinized covering and are therefore coded as state '0'. The palate of *Anomocephalus* is not known and accordingly this taxon is coded as '?'.

55. Palatine widest at its approximate midpoint of length (0), widens anteriorly (1), or width relatively constant for entire length (2). (Modified from Rybczynski, 2000: #23; and Angielczyk, 2004: #30)

Rybczynski (2000) and Angielczyk (2004) coded *Galeops* for this character as a condition where the palatine widens posteriorly (character state '1' therein), representing an autapomorphy of this taxon. This morphology of the palatine is also visible in Brinkman's (1981, fig. 5b) skull reconstruction in palatal view, but it contradicts the morphology of this element in the original specimen drawing that was used to produce the reconstruction. The specimen drawing (Brinkman, 1981: fig. 5a) clearly shows the plesiomorphic morphology in that the palatine is widest at its approximate midpoint of length (character state '0' in all studies). Therefore, *Galeops* is coded as '0' in this paper and character state '1' of Rybczynski (2000) and Angielczyk (2004) is excluded from this study.

56. Foramen on the palatal surface of the palatine absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #24)

57. Lateral palatal foramen absent (0), present at level of the anterior, expanded palatal exposure of the palatines (1), present posterior and dorsal to the level of the anterior, expanded palatal exposure of the palatines (2). (From Angielczyk & Kurkin, 2003a: #35)

58. Sutural contact of palatine and premaxilla absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #27)

59. Labial fossa absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #19)

60. Ectopterygoid extends further posteriorly than palatine (0) or vice versa (1) in palatal aspect. (From Modesto *et al*., 1999: #24)

61. Pterygoids contact anteriorly (0) or separated by vomers at pterygoid vacuity (1). (From Modesto *et al*., 1999: #29)

62. Transverse flange of pterygoid projects laterally, free of posterior ramus (0), projects laterally, bound by posterior ramus (1), ventrally directed and relatively large, wing-like (2), or ventrally directed and low, keel-like (3). (Modified from Modesto *et al*., 2003b: #31; and Rybczynski, 2000: #27)

Modesto *et al*. (1999), Modesto & Rybczynski (2000), Angielczyk (2001), and Angielczyk & Kurkin (2003a) treated this character as a binary character. In contrast, Rybczynski (2000) recognized three character states, which were also adapted by Angielczyk (2004),

and Modesto *et al*. (2003b) used four states to define this character. The codings among basal anomodont taxa varied significantly in the different analyses. Here, I use a character definition that is modified from Modesto *et al*. (2003b) and Rybczynski (2000). Modesto *et al*. (2003b) coded *Colobodectes* and *Pristerodon* as state '3', exhibiting a low, keel-like transverse flange of the pterygoid that projects ventrally. In contrast, they emphasize in the text that these taxa possess pterygoid flanges that are, although not as angled as in *Eodicynodon*, deep and conspicuous, whereas '[i]n later dicynodonts the flange is reduced to a low, slightly rounded keel' (Modesto *et al*., 2003b: 216). Therefore, *Colobodectes* and *Pristerodon* as well as *Chelydontops* and *Lanthanostegus*, two taxa, which were not considered by Modesto *et al*. (2003b), are coded as state '2' in this analysis.

63. Ventral surface of the median pterygoid plate depressed (0), smooth and flat (1), with a thin median ridge (2), or with a wide, boss-like median ridge (3). (From Angielczyk & Kurkin, 2003a: #43)

64. Pterygoid dentition present (0) or absent (1). (From Modesto *et al*., 1999: #26)

65. Contact of pterygoid and maxilla absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #46)

66. Interpterygoid vacuity relatively short and does not reach the level of the palatal exposure of the palatines (0), relatively long but does not reach the level of palatal exposure of the palatines (1), long and reaches the level of palatal exposure of the palatines (2), or absent (3). (From Angielczyk & Kurkin, 2003a: #33)

67. Parasphenoid excluded from (0) or reaches (1) interpterygoid vacuity. (From Modesto *et al*., 1999: #32)

68. Stapedial facet of basisphenoid-basioccipital tuber exposed laterally (0) or exposed ventrolaterally (1). (From Angielczyk & Kurkin, 2003a: #42)

69. Intertuberal ridge absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #49)

70. Epipterygoid separate from (0) or contacts (1) parietal. (From Modesto *et al*., 1999: #31)

71. Stapedial foramen present (0) or absent (1). (From Angielczyk & Kurkin, 2003a: #29)

72. Dorsal process of the stapes present (0) or absent (1).

The distribution of this character within anomodonts has previously not received much attention. Cox (1959) was the first one to describe and figure a dorsal process at the lateral end of the stapes of *Kingoria* that articulates with the ventrolateral edge of the paroccipital process. A dorsal process is also present in *Kombuisia* and has been described for *Lystrosaurus* and *Patranomdon* (Cluver, 1971; Rubidge & Hopson, 1996). Ewer (1961) identified an additional ossification at the stapes of '*Daptocephalus*' (*Dicynodon*) that

she termed extrastapes. This structure is different in position and shape and is therefore not considered to be homologous to the dorsal process of *Patranomodon*, *Kingoria*, *Kombuisia*, and *Lystrosaurus*. The dorsal process of the stapes in the latter taxa is regarded here as homologous with the dorsal stapedial process that is present in some 'pelycosaurs' (Reisz, 1986). A dorsal process of the stapes is also present in *Titanophoneus* (King, 1988). Although the process is poorly developed in *Gorgonops* (Sigogneau, 1970), it is common and usually well developed in other gorgonopsians (Sigogneau-Russell, 1989). van den Heever (1994) stated that a dorsal stapedial process was probably present in lycosuchids, but its occurrence could not yet be unequivocally demonstrated. Therefore, this taxon is coded as '?' in this analysis.

73. Tabular contacts opisthotic (0) or separated from opisthotic by squamosal (1). (From Modesto *et al.*, 1999: #21)

74. Floccular fossa present (0) or absent (1). (From Angielczyk & Kurkin, 2003a: #41)

MANDIBULAR CHARACTERS

1. Mandibular fenestra absent (0), present and well developed (1), or present, but significantly reduced (2). (Modified from Rubidge & Hopson, 1996: #5; and Modesto *et al.*, 1999: #36)

The original character definition by Modesto *et al.* (1999) was complemented by character state '2', which describes the strongly reduced size of the mandibular fenestra in *Kombuisia* as well as *Kingoria* and represents a synapomorphy that unites both taxa.

2. Dentaries sutured (0) or fused (1) at symphysis. (From Modesto *et al.*, 1999: #33)

The character codings of this character for *Patranomodon*, *Ulemica*, and *Galeops* varied among the different analyses. Here, I coded *Patranomodon* as '?' and *Ulemica* and *Galeops* as state '1', following Angielczyk (2004).

3. Lower teeth present on dorsal surface of dentaries (0), present on a medial swelling or shelf (1), or absent (2). (From Angielczyk & Kurkin, 2003a: #10)

4. Symphyseal region of lower jaw smoothly rounded and bearing teeth (0), with an upturned margin that is raised above the level of the dorsal surface of the jaw rami and has a scooped-out depression on its posterior surface (1), drawn into a sharp, spiky beak (2), shovel-shaped with a rounded or squared-off edge and a weak depression on its posterior surface (3), with a wedge-shaped margin that does not extend much above the dorsal surface of the jaw rami and has a groove-like depression on its posterior surface (4). (From Angielczyk & Kurkin, 2003a: #18)

5. Dentary table absent (0), present as a small rounded expansion of the dorsal surface of the dentary located near symphysis (1), present as an elongate grooved surface on the dorsal surface of the dentary bounded laterally by a low ridge and medially by a tall, thin, dorsally convex blade (2), or present as an elongate grooved surface on the dorsal surface of the dentary bounded by low ridges (3). (From Angielczyk & Kurkin, 2003a: #15)

6. Posterior dentary sulcus absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #16)

7. Lateral dentary shelf absent (0), present but relatively small (1), present as a boss-like swelling that is located near ventral margin of jaw ramus (2) or present and well-developed (3). (From Angielczyk & Kurkin, 2003a: #17)

8. Splenial symphysis unfused (0) or fused (1). (From Sidor, 2001: #26) Sidor (2001) originally coded *Ulemica* as state '0' (state '2' therein), but later (Sidor, 2003: #24) modified its coding to a polymorphism of '0' and '1'. The latter coding is also adopted for this analysis.

9. Coronoid bone present (0), or absent (1). (From Modesto *et al.*, 1999: #38)

10. Prearticular with (0) or without (1) lateral exposure posteriorly. (From Modesto *et al.*, 1999: #39)

11. Articular distinct (0) or at least partially fused to prearticular (1). (From Sidor, 2003: #48)

This character was first introduced in a modified form by Sidor (2001: #30). At least a partial fusion of the articular to the prearticular is a shared derived character of the Dicynodontia. However, a fusion of the two elements was not observed in *Kombuisia*, which therefore represents an autapomorphy of this taxon.

12. Surangular vertical lamina present and lateral to articular (0) or absent (1). (From Modesto *et al.*, 1999: #37)

13. Jaw articulation permits strictly orthal closure (0), permits extensive parasagittal movement (1), or permits very little parasagittal movement (2). (From Rybczynski, 2000: #37; and Angielczyk, 2004: #41)

POSTCRANIAL CHARACTERS

1. Number of sacral vertebrae three (0), four (1), five (2), or six (3). (From Angielczyk & Kurkin, 2003a: #36)

2. Cleithrum absent (0) or present (1). (From Angielczyk & Kurkin, 2003a: #39)

3. Proximal articular surface of humerus formed by a slightly convex area on proximal surface of the bone without much expansion onto the dorsal surface (0), somewhat expanded with some encroachment onto the dorsal surface (1), or strongly developed and set off from rest of humerus by a weak neck (2). (From Angielczyk & Kurkin, 2003a: #30)

4. Insertion of M. latissimus dorsi at rugose tuberosity on the posteroventral surface of the humerus (0) or extended into a dorsoventrally flattened pinna-like process (1). (From Angielczyk & Kurkin, 2003a: #50)

5. Ectepicondylar foramen on humerus present (0) or absent (1). (From Angielczyk & Kurkin, 2003a: #38)

6. Proximal articular surface of the femur present as a weak swelling that is mostly limited to the proximal surface of the bone (0), present as a more rounded, hemispherical swelling that has some encroachment on the anterior surface of the femur (1), or present as a rounded, hemispherical to subspherical swelling that is set off from the proximal surface by a neck (2). (From Angielczyk & Kurkin, 2003a: #31)

7. Insertion of M. iliofemoralis present as a low rugosity on the dorsolateral portion of the femur (0) or developed into a distinct crest that extends down part of the lateral surface of the femur (1). (From Angielczyk & Kurkin, 2003a: #52)

8. Posterodorsal corner of the scapular blade poorly (0) or well (1) ossified. (From Surkov et al., 2005: #5) *Myosaurus* has in previous analyses been coded as '?', but a newly prepared specimen of this taxon (BP/1/4269) comprises a completely preserved pectoral girdle and shows a well ossified posterodorsal corner of the scapular blade, so that *Myosaurus* is coded as '1' for this character in the present anaylsis.

9. Olecranon process poorly ossified and presumably cartilaginous (0) or high and well ossified (1). (From Surkov et al., 2005: #11)

10. Radial and ulnar condyle on distal end of humerus continuous (0) or well ossified and separate (1). (From Surkov et al., 2005: #12)

11. Supraacetabular crest present (0) or absent (1). (Modified from Surkov et al., 2005: #13) Orlov, 1958) figures of the pelvic girdle of *Titanophoneus* show a pronounced thickening of the iliac rim dorsal to the acetabulum. In addition, Broili & Schröder (1935) decribed a pronounced supraacetabular crest for *Gorgonops whaitsi*. Therefore both of these taxa are coded as state'1' for this character. However, the plesiomorphic state for the Anomdontia is not resolved, since the pelvic girdle of nondicynodont anomodonts is only poorly known.

12. Pubic plate is significantly expanded ventrally (0) or reduced ventrally (1). (From Surkov et al., 2005: #14)

13. Pubic tubercle present (0) or absent (1). (From Surkov et al., 2005: #15)

APPENDIX 2

DATA MATRIX

Missing and inapplicable data are coded as '?'. Polymorphisms for states 0 and 1 are coded as 'A', polymorphisms for states 1 and 2 are coded as 'B', and polymorphisms for states 1 and 3 are coded as 'C'. In species of the genus *Dicynodon*, the genus name is abbreviated as '*D.*'.

Taxon	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890
Titanophoneus	0000?00000	0000000000	????000000	0000000000	0000000000
Gorgonops	0000?00000	0000000000	????000010	1000001000	0000000001
Lycosuchidae	1000?00000	0000000000	????000000	0100?11001	0000000000
Anomocephalus	1????0????	??010?1000	?????0??0?	?????0?0?0	01?000?11?
Patranomodon	2000??0?00	0101001000	????00010	10100?1001	0100010100
Otsheria	1000?010??	?01100??00	?????00?0?	0210?01001	01??0011?1
Suminia	1000?01000	0011002100	?????00000	0210001101	010001110?
Ulemica	1000?01000	?010002100	?????00000	0210?0?1?1	01?0001101
Galeops	2000?01??0	?101001000	?????0?010	0??0???101	01?001?100
Eodicynodon	2001022000	0?0B0010?1	0000010?00	1010011111	02A0011110
Colobodectes	2011022000	0102001001	0000010???	11???11???	?????????0
Robertia	?111022100	0?021010?1	0100110??0	1110011111	0210111111
Diictodon	2111022100	010B3???11	0100110??0	1113011111	0210111111
Pristerodon	2111222000	010B102011	0000010000	1110010111	0210111111
Endothiodon	2100212100	010121?000	?????20??0	1114121111	0?100??111
Chelydontops	?101222100	0101112011	0000010??0	1110021111	?210???111
Emydops	2101122000	0?0B001011	1010110000	1110011101	0210111111
Kingoria	2102022000	110B3???11	1010010100	1115011111	0?10011111
Cistecephalus	2102122000	1?013???11	1010010100	0210010101	02?0001111
Myosaurus	2102122000	1?013???11	1010100100	1210011101	0210001111
Tropidostoma	?122222100	0?02101 0?1	0001020??0	111101011?	0??01???11

APPENDIX 2 *Continued*

Taxon	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890
Oudenodon	2122222100	01013???11	0001020000	1111010111	0210101111
Rhachiocephalus	?122222100	0?0?3???11	00010200?0	1113021111	0?1011?111
Pelanomodon	2122222101	02013???11	00010211?1	1112021111	12111?1111
Aulacephalodon	2122222101	01023????1	0000021101	1112021111	1211101111
D. lacerticeps	?122222000	02023???11	0000010000	1113111111	0210111111
Lystrosaurus	?122222110	02023???11	00000B0100	1110111111	0?10111111
Kannemeyeria	?122222100	02023???11	0000301?0	2114210111	0?10111111
'Idelisaurus'	?122222100	01023???11	0001020000	111101111?	121011?1?1
Interpresosaurus	?12??2?000	02023????1	000010000??	1??3??????	?????????1
Elph	?1?222?000	0?023???11	0000100?0	1115?1111?	0210???1??
'D.' trautscholdi	?122222000	01023???11	0000010000	2114110111	021011?111
Delectosaurus	?122222000	02023???11	0000010000	1113111111	0210111111
Vivaxosaurus	?122222000	01023???11	0000030000	2114110111	021011?1?1
'D.' amalitzkii	?1?????000	0102????11	?000110000	2114?1111?	021011?11?
Australobarbarus	?122222100	0101201011	0001020000	111C01A11?	021011?1?1
Geikia elginensis	?122?22111	02013????1	000122211??	???2??1?1?	021????1?1
Geikia locusticeps	?122?22011	02013???11	0001021101	B112?21??1	0211101111
Kombuisia	2102122000	??013???01	1?10110100	1105231111	?2??01?111
Kawingasaurus	2102122000	11013???01	1?10000100	02?003?101	02?010?111
Cistecephaloides	2102122000	11013???01	10100101?0	0210010101	02?0001111
Lanthanostegus	??????????	0??2??????	??????00??	11?2?21???	????0??1?0

Taxon	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890	8888888889 1234567890	1 9999999990 1234567890
Titanophoneus	0000000000	0000000000	000?000000	0000000?0	0000?00000
Gorgonops	0000000000	0000000001	0000000000	0000100?0	?010?100??
Lycosuchidae	1011010000	0000001001	1??1000000	0001000???	??????????
Anomocephalus	??????????	??????????	????1?00??	0??0?????	??????????
Patranomodon	00?0000001	000100000?	101?1?0000	0?000000??	??00??????
Otsheria	1?10000101	000100?00?	??1?1?????	??????????	??????????
Suminia	10?2201101	01?100100?	1?1?100000	1000001???	?1????????
Ulemica	1012200101	0101001???	??1?1100??	1A01002???	??????????
Galeops	001000?001	00?1001???	????110??0	10?0001?00	01???10???
Eodicynodon	0011101001	1231010001	0110110310	3111111000	0100011101
Colobodectes	1012101001	1221010?01	??????????	??????????	??????????
Robertia	0012101001	132101000?	1?10111120	111??11010	0000000100
Diictodon	1112101001	1321010001	1110112120	1111111110	0000000101
Pristerodon	0012102101	1221010001	1110111111	3111111200	0100000110
Endothiodon	001200210?	??3?01?00?	1??0111211	21??1??100	0100??????
Chelydontops	1012101001	123101?A0?	1???1?1111	1?11?11???	??????????
Emydops	1112101101	132101010?	1?10111301	3111111??0	00????????
Kingoria	1012201A01	132101010?	1010212300	3111111101	??11101110
Cistecephalus	1112111101	?32103?10?	011?1?2301	3111111012	1020111101
Myosaurus	1110111101	13210B0101	1?10?12300	3?11111???	1???1?????
Tropidostoma	1013101101	?32?02?10?	1??0111131	1??????201	1111?000??
Oudenodon	1113101101	132102010?	1?10112131	1011111201	11111?00??
Rhachiocephalus	1113101101	?32101010?	1??01?2131	1?11?11201	11????????
Pelanomodon	1113101111	132110011?	1?1?1?2131	1111111?0?	????100010
Aulacephalodon	1013101111	13210101 A?	1?101?2131	1011?11201	11111??0??
D. lacerticeps	1114101111	1321000111	1111112131	1111111???	??????????
Lystrosaurus	111410101?	132110011?	1011112431	1111111301	1111100011

APPENDIX 2   *Continued*

| | | | | | 1 |
Taxon	5555555556 1234567890	6666666667 1234567890	7777777778 1234567890	8888888889 1234567890	9999999990 1234567890
Kannemeyeria	1114101111	131110010?	1?11112431	1111111301	1111100010
'*Idelisaurus*'	1013101111	132101010?	????1?2131	1?11?11???	??????????
Interpresosaurus	??1????00?	??????????	??????????	??????????	??????????
Elph	??13?01101	?31?0?010?	????1?2131	1?????????	??????????
'*D.' trautscholdi*	1113101111	?32110011?	1???1?2131	1?11?11???	??????????
Delectosaurus	111410111?	132111011?	??10??2???	??????????	??????????
Vivaxosaurus	101310111?	132110010?	??1??????	???????01	11??1?00??
'*D.' amalitzkii*	??????????	?32????11?	1???11?1??	1?11?1131?	??????????
Australobarbarus	1113101001	132112010?	1?????1131	1?????????	??????????
Geikia elginensis	111?10?10?	1321?10???	??????2?31	1?????????	11????????
Geikia locusticeps	111310?111	1321110?0?	??1???????	??????1???	??????????
Kombuisia	?012101110?	13?101?10?	101?212310	31?1011???	??????????
Kawingasaurus	1112111101	?31103?10?	0??0112?00	1?11??1?12	10??111???
Cistecephaloides	111?1?1101	?3?113?10?	1?1?112301	3?11111???	??????????
Lanthanostegus	??1?102?01	1231010???	??????????	??????????	??????????

APPENDIX 3

INSTITUTIONAL ABBREVIATIONS

BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; NM, National Museum, Bloemfontein, South Africa; PIN, Palaeontological Institute, Moscow, Russia; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

ANATOMICAL ABBREVIATIONS

a, angular; ar, articular; bo, basioccipital; CP, caniniform process of maxilla; d, dentary; DT, dentary table; ect, ectopterygoid; ENO, external narial opening; exo, exoccipital; f, frontal; INO, internal narial opening; ip, interparietal; j, jugal; l, lacrimal; LDS, lateral dentary shelf; LPF, lateral palatal foramen; MF, mandibular fenestra; MPR, median posterior ridge of premaxilla; mx, maxilla; n, nasal; op, opisthotic; p, parietal; pal, palatine; par, prearticular; pbs, parabasisphenoid; pmx, premaxilla; po, postorbital; pp, preparietal; prf, prefrontal; pro, prootic; pt, pterygoid; PTF, post-temporal fenestra; q, quadrate; QF, quadrate foramen; qj, quadratojugal; RL, reflected lamina; sa, surangular; so, supraoccipital; sp, splenial; sq, squamosal; st, stapes; t, tabular; v, vomer.