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A new specimen of *Biseridens qilianicus* indicates its phylogenetic position as the most basal anomodont

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A new well-preserved basal therapsid skull from the Xidagou Formation, Middle Permian of China, is identified as *Biseridens qilianicus*. The following synapomorphies distinguish *Biseridens* as an anomodont and not an eotitanosuchian as previously described: short snout; dorsally elevated zygomatic arch and septomaxilla lacking elongated posterodorsal process between nasal and maxilla. The presence of a differentiated tooth row; denticles on vomer, palatine and pterygoid; contact between tabular and opisthotic; lateral process of transverse flange of pterygoid free of posterior ramus and absence of mandibular foramen exclude it from other anomodonts. Our cladistic analysis indicates *Biseridens* to be the most basal anomodont, highlights separate Laurasian and Gondwanan basal anomodont clades and suggests that dicynodonts had their origins in the Gondwanan clade. The co-occurrence of the most basal anomodont (*Biseridens*) together with the most basal therapsid (*Raranimus*), basal anteosaurid dinocephalians, bolosaurids and dissorophids suggests that the earliest therapsid faunas are from China.

Keywords: Anomodontia; Permian biogeography; phylogeny; Therapsida

1. INTRODUCTION

The therapsid clade Anomodontia (which includes the herbivorous Dicynodontia) is one of the most successful tetrapod taxa in terms of abundance of individuals, generic diversity and long stratigraphic range from the Middle Permian to the Triassic and possibly into the Cretaceous as well (Thulborn & Turner 2003). Anomodonts have a global distribution and are one of very few tetrapod clades known from all the continents (King 1988, 1990). The early evolution of anomodonts has been the subject of recent attention, and there has been much debate as to whether the clade had a Laurasian or Gondwanan origin (Rubidge & Hopson 1990; Modesto *et al.* 1999; Modesto & Rybczynski 2000).

Apart from *Dimacrodon hottoni* from Texas (Olson & Beerbower 1953) which is now considered to be a 'pelycosaur' rather than a therapsid (Sidor & Hopson 1995), prior to 1990, all basal anomodonts were referred to as either Dromasauria or Venyukovioidea and were known from South Africa and Russia, respectively. The poorly known former group includes the enigmatic southern African genera *Galechirus*, *Galepus* and *Galeops* (Brinkman 1981), and the Venyukovioidea comprised the Russian *Venyukovia* and *Otsheria* (Chudinov 1983). Recent discoveries from Russia (*Suminia*) (Ivakhnenko 1994; Rybczynski 2000) and South Africa (*Anomocephalus* and *Patranomodon*) (Rubidge & Hopson 1990, 1996;

Modesto *et al.* 1999; Rybczynski 2000) have greatly added to our understanding of the morphology, taxonomy and phylogeny of basal anomodonts. The description of *Patranomodon* showed this remarkably well-preserved specimen to be the most basal anomodont, and the resulting phylogenetic analysis suggested that neither Dromasauria nor Venyukovioidea is monophyletic and that early anomodonts exchanged freely between eastern Europe and southern Africa (Rubidge & Hopson 1990). *Suminia* was subsequently named for new specimens from the Late Tatarian of Russia (Ivakhnenko 1994), and most specimens previously assigned to *Venyukovia* were transferred to the genus *Ulemica* (Ivakhnenko 1996). New data showed that venyukovioids comprise a natural group of anomodonts wholly endemic to the Russian Late Permian (Rybczynski 2000). The description of *Anomocephalus* from South Africa indicated that this genus is the most basal anomodont and suggested that anomodonts had a Gondwanan origin. In addition, it was suggested that the Venyukovioidea, which includes *Otsheria*, *Venyukovia*, *Ulemica* and *Suminia*, is a monophyletic clade (Modesto *et al.* 1999; Modesto & Rubidge 2000).

In the 1990s, a diverse tetrapod fauna that includes basal therapsids was discovered in Gansu, China (Cheng *et al.* 1995; Li & Cheng 1995). This Dashankou therapsid fauna is dominated by the anteosaurid dinocephalians *Stenocybus acidentatus* and *Sinophoneus yumenensis* (Cheng & Ji 1996; Cheng & Li 1997; Li 2001) and has recently yielded the basal therapsid *Raranimus dashankouensis* (Liu *et al.* in press). This has led to the speculation that this site could host the oldest therapsids, possibly implying a Laurasian origin of Therapsida (Liu *et al.* in press). Another therapsid from the

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locality is *Biseridens qilianicus*, which was described as an eotiansuchian from two fragmentary specimens (Li & Cheng 1997). Battail (2000) later considered *Biseridens* a basal anomodont closely related to *Ulemica*, but because of the poorly preserved nature of the material, this proposal could not be verified. Recently, an additional specimen of *Biseridens* from the Dashankou locality has been prepared. Because this specimen is particularly well preserved, it provides much new information on the morphology and taxonomy of the genus and has allowed us to test the hypothesis of Battail (2000) and confirm that *Biseridens* is a basal anomodont. The presence of a basal anomodont as part of a very primitive therapsid fauna in China provides new insight into the biogeographical implications of anomodont origins.

Institution abbreviations: IGCAGS, Institute of Geology, Chinese Academy of Geological Sciences; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; PIN, Paleontological Institute, Russian Academy of Sciences.

2. MATERIAL AND METHODS

The holotype of *B. qilianicus* (IGCAGS V 632) consists of a fragmentary skull lacking the anterior end and the left ramus of a lower jaw, and the paratype (IVPP V 12009) comprises the anterior part of lower jaws with well-preserved teeth (Li & Cheng 1997). The new specimen (IVPP V 16013), which is preserved in hard mudrock, was prepared mechanically. It comprises an almost complete skull with lower jaw, but lacks the occiput. In addition, a set of 14 articulated vertebrae is preserved in the same block and is presumed to belong to the skull. Description of the vertebrae is the subject of a future paper.

To test the phylogenetic position of *Biseridens* within basal therapsids, a matrix of 75 cranial characters was set up using 15 synapsid genera (see electronic supplementary material). *Dimetrodon* was selected as the outgroup, and the ingroup included representatives from Biarmosuchia, Gorgonopsia, Dinocephalia and Anomodontia. Only three basal anomodonts (*Venjukovia prima*, *Galechirus scholtzi* and *Galepus jouberti*) were not considered in the phylogenetic analysis as they are based on incomplete cranial material. As most of the taxa examined, including *Biseridens*, are based on cranial material, only cranial characters were used in our analysis. Some of the characters are new, but most were obtained from previous studies that are referenced in the electronic supplementary material.

A phylogenetic analysis was performed using PAUP v. 4.0b10 (Swofford 2001) and resulted in two shortest trees (tree length = 176, consistency index = 0.59, retention index = 0.67). In order to determine the relative strengths of the resultant clades, a decay analysis was undertaken in addition to the phylogenetic analysis.

3. SYSTEMATIC PALAEOLOGY

Therapsida Broom 1905

Anomodontia Owen 1859

Biseridens qilianicus Li & Cheng 1997

(a) Revised diagnosis

A medium-sized basal anomodont is distinguished from other therapsids by the following combination of

primitive and derived characters: short snout; septomaxilla has a short facial exposure between nasal and maxilla; elevated zygomatic arch; lower jaw lacking a mandibular fenestra; tabular in contact with opisthotic; transverse flange of pterygoid projects laterally, free of posterior ramus; well-differentiated tooth row with three precanine dentary teeth, distinct canine and teeth with cusps arranged in two rows on both upper and lower jaws and well-developed denticles on vomer, palatine and pterygoid.

(b) Holotype

An incomplete skull with posterior portion of left ramus of lower jaw (IGCAGS V 632) (Li & Cheng 1997).

(c) Paratype

Anterior part of lower jaws with complete dentition (IVPP V 12009) (Li & Cheng 1997).

(d) Referred material

Almost complete skull with lower jaws, missing the posterior portion (figures 1–4); articulated series of 14 vertebrae (IVPP V 16013).

(e) Locality and horizon

Dashankou, Yumen, Gansu Province, China; upper part of Xidagou Formation. Li & Cheng (1995) considered the Xidagou Formation to correlate with the *Tapinocephalus* Assemblage Zone of South Africa and assigned a Late Permian age. More recently, on the basis of faunal comparison with South Africa, the Xidagou Formation has been considered to be Middle Permian (Rubidge 2005; Liu *et al.* in press).

4. DESCRIPTION

The following description is based on the recently prepared specimen IVPP V 16013, with supplementary information from the holo- and paratypes. The new specimen comprises a well-preserved and undistorted anterior portion of the skull and lower jaw. It is slightly smaller than the previously described specimens, with a skull length of approximately 17 cm from the anterior tip of the premaxilla to the posterior margin of the squamosal. The presence of a narrow and short preorbital region, interorbital area depressed with a ridge along the midline suture of the frontals, intertemporal region wider than interorbital, temporal fenestra larger than orbit, large oval pineal foramen situated on prominent boss, lateral process of postorbital that does not reach zygomatic arch, depression on posterior portion of postorbital, palatal and pterygoid tuberosities bearing teeth, low stout postcanines with grinding surfaces that are arranged in two rows, are oval in cross section and have a constricted base (Li & Cheng 1997) (figure 2) allow us to confidently assign specimen IVPP V 16013 to *B. qilianicus*. As such, it is important as it is the only specimen of *Biseridens* to have the snout and palate preserved and thus warrants description.

The relatively short preorbital region that comprises only 45 per cent of the total skull length is similar in proportion to that of *Anomocephalus* (Modesto *et al.* 1999). Apart from the tip of the snout that is weathered, the premaxilla is relatively well preserved. It extends posteriorly

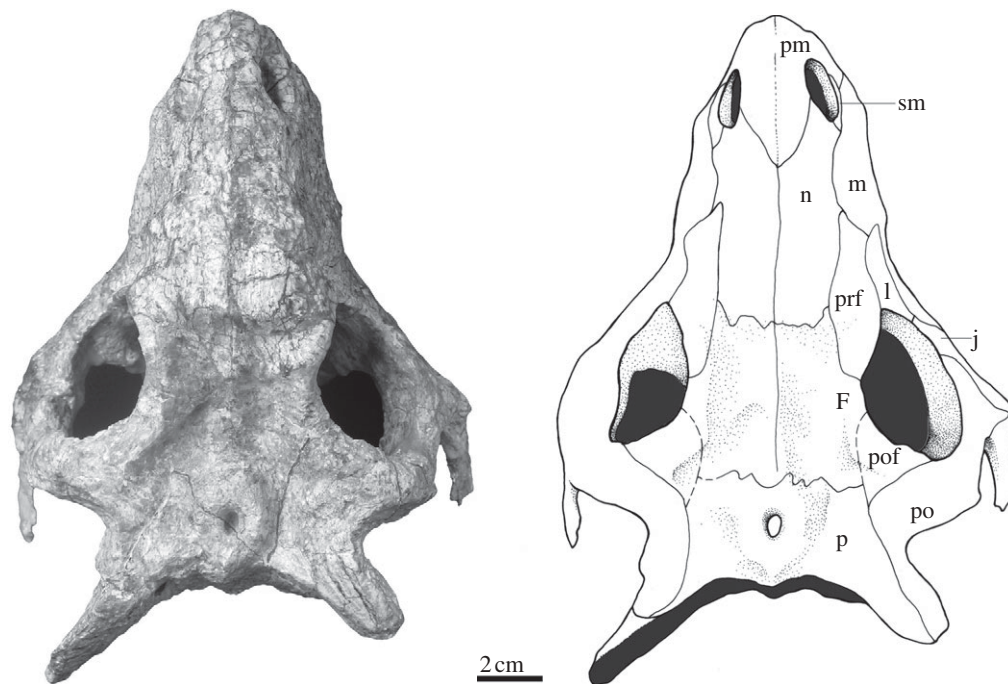


Figure 1. *Biseridens qilianicus* (IVPP V 16013): photograph and interpretative drawing of the skull in dorsal view. a, angular; c, coronoid; d, dentary; e, ectopterygoid; f, frontal; fo, fossa; i.v., interpterygoid vacuity; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pl, palate; pm, premaxilla; po, postorbital; pof, postfrontal; pra, prearticular; prf, prefrontal; pro, prootic; pt, pterygoid; rl, reflected lamina; sm, septomaxilla; sp, splenial; sq, squamosal; v, vomer.

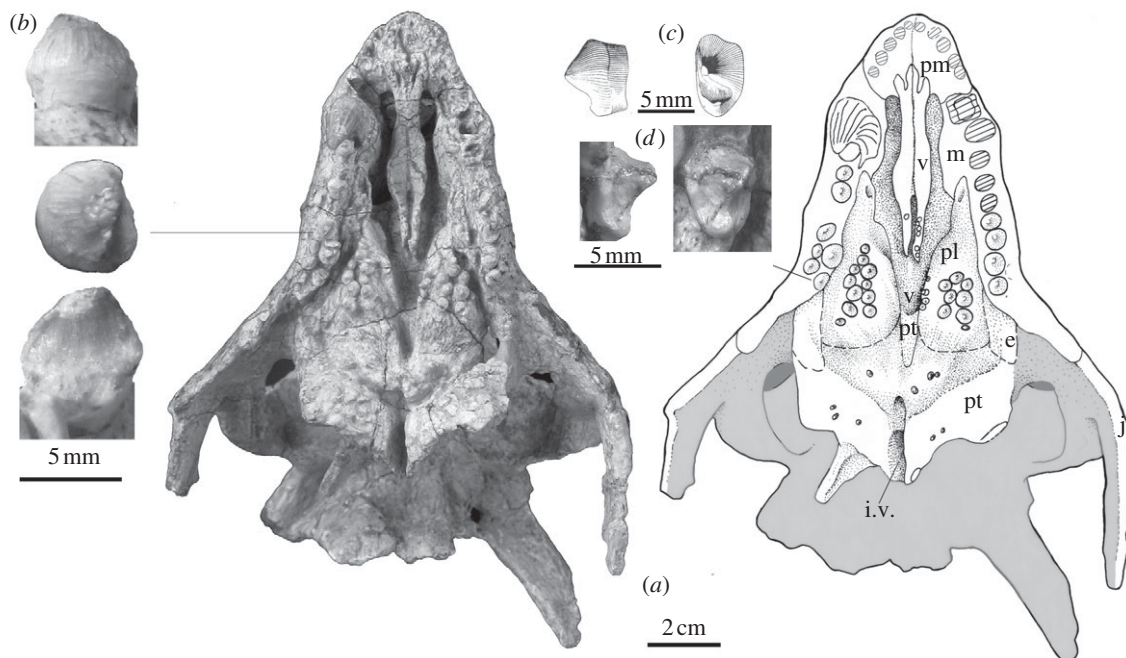


Figure 2. *Biseridens qilianicus*: (a) photograph and interpretative drawing of the skull (IVPP V 16013) in ventral view; (b) lateral, occlusal and medial views of the fourth right postcanine; (c) a left posterior postcanine of the holotype in lateral and occlusal views, anterior is on top (adapted from Li & Cheng 1997); (d) last right postcanine in lateral and occlusal views, anterior is on top. Abbreviations as in figure 1.

on the skull roof from the tip of the snout, forming the anteroventral, anterior and anterodorsal borders of the external nares and terminating posteriorly at a point on the midline between the nasals well behind the posterior margin of the external naris as in *Biarmosuchus* (Sigogneau & Tchudinov 1972), the basal anteosaurid dinocephalians *Syodon* and *Titanophoneus* (Orlov 1958)

and venyukoviids (Ivakhnenko 1996; Rybczynski 2000). In ventral view, the premaxilla is not well preserved, but it is evident that it forms only the anterior end of the palate. It is in midline contact with the vomer, makes up the anterior border of the internal naris and is in sutural contact with the maxilla anterior to the canine, but does not make contact with the palatine. Only the

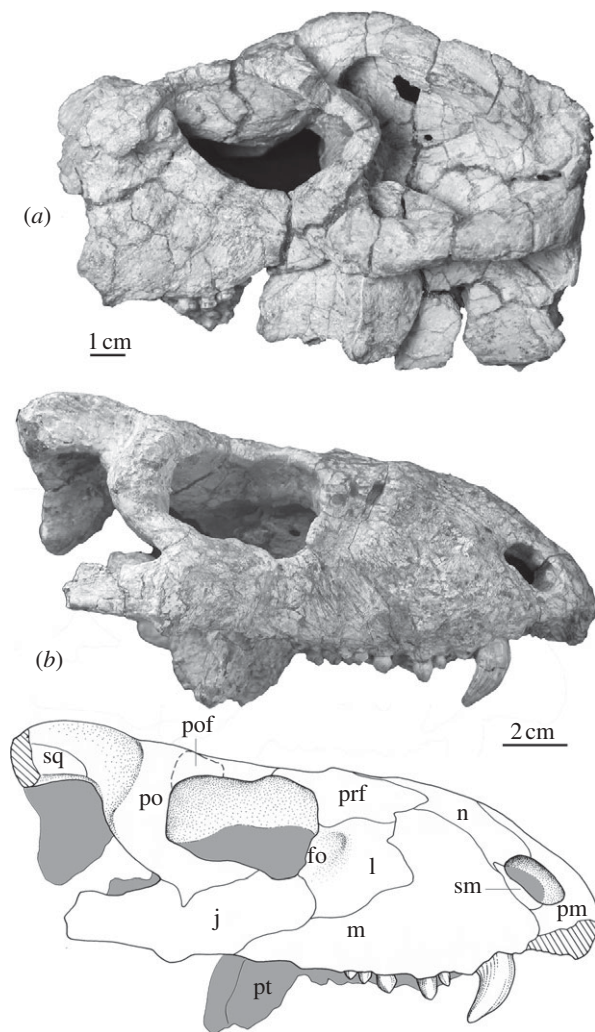


Figure 3. *Biseridens qilianicus* in lateral view. (a) Photograph of the holotype IGCAGS V 632 and (b) photograph and interpretative drawing of IVPP V 16013. Abbreviations as in figure 1.

roots of the incisors are preserved, and the exact number of incisors is uncertain, but appears to be five. The septomaxilla is a narrow elongate bone forming the ventral border of the external naris and having a narrow facial exposure on the posteroventral side of the external naris. A small spur extends posterodorsally beyond the naris.

The maxilla, as other basal therapsids, makes up most of the preorbital region of the snout and forms the entire ventral border of the skull between the external naris and the orbit. Anteroventrally, it has a short contact with the premaxilla and septomaxilla, and a relatively longer anterodorsal contact with the nasal. Dorsally, it meets the prefrontal with a short contact and has longer posterior sutural contacts with the lacrimal and jugal.

On the palate, the maxilla has a narrow exposure along the tooth row, being in contact with premaxilla anteriorly and forming most of the lateral border of the internal naris. Posteromedially, it forms a long sutural contact with the palatine, and posteriorly, it meets the ectopterygoid and jugal bones. The maxilla is anteriorly enlarged to hold the large recurved canine, which has longitudinal striations and has a basal diameter of 10 mm. Postcanines on the left maxilla are poorly preserved, but eight postcanines are present on the right maxilla, with the

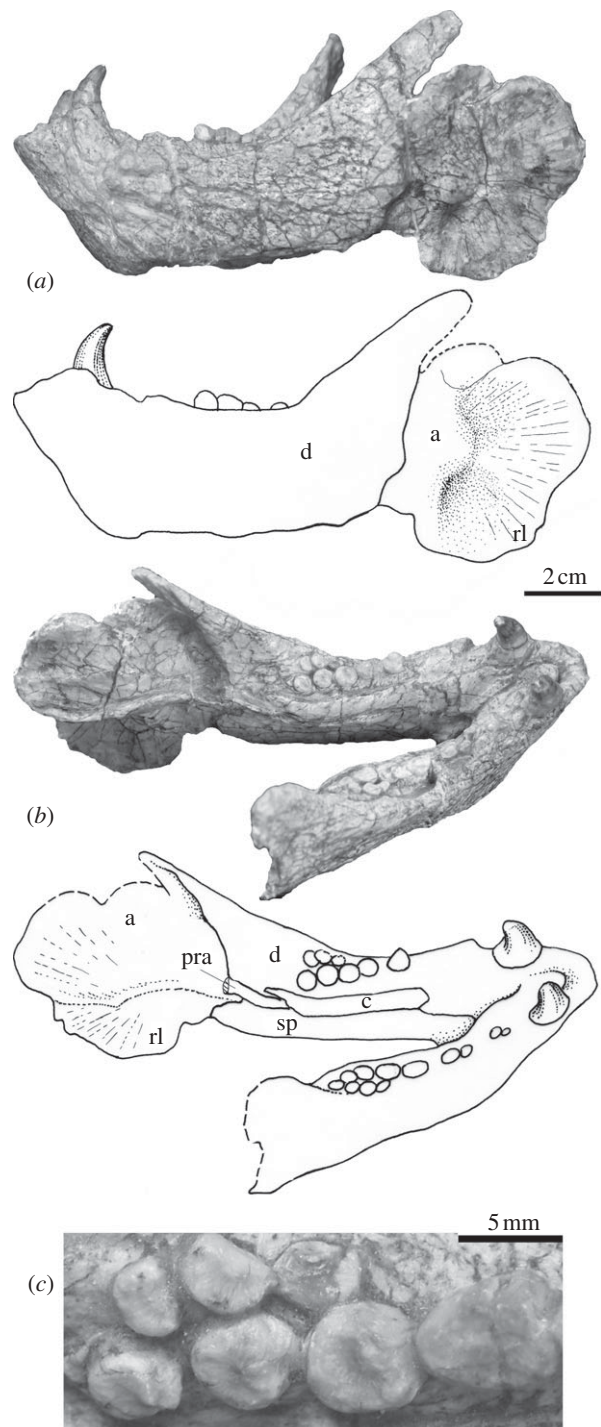


Figure 4. *Biseridens qilianicus* (IVPP V 16013): photograph and interpretative drawing of the lower jaw in (a) lateral view and (b) dorsomedial view, and (c) posterior left postcanines in dorsal view. Abbreviations as in figure 1.

posteriormost four teeth being arranged in two rows. The crown of the anteriormost postcanines is labiolingually compressed, curves lingually and has a heel-like structure on the medial side (figure 2b). Unlike the situation in *Suminia* and *Ulemica*, no cingulum is present on the labial side (Ivakhnenko 1996; Rybczynski 2000). As in the holotype (Li & Cheng 1997) (figure 2c), the lingually positioned last two postcanines have a lower crown than those of the anterior teeth. They have a short, blunt cusp on the mesial side with a concave facet developed distally and lingually to this

cuspid (figure 2*d*). The laterally positioned last two postcanines are the smallest, are strongly worn and are poorly preserved. Their worn appearance suggests that they are the unshed previous generations of teeth. Similarly, the holotype of *Ulemica invisita* (PIN no. 157/5) also has a tooth positioned lateral to the last two maxillary teeth (Ivakhnenko 1996).

The paired nasal is the longest element on the skull roof. It extends from the posterodorsal border of the external naris where it is in contact with the premaxilla medially and the maxilla and prefrontal laterally and forms a transverse interdigitating sutural contact with the frontal at the level of the anterior rim of the orbit.

An elongate prefrontal forms the anterodorsal border of the orbit; is in contact with the frontal posteriorly, the nasal medially, the maxilla anteriorly and has a long contact with the lacrimal on the ventral side. The lacrimal is a relatively large square bone forming the anteroventral border of the orbit. It is in contact with the prefrontal dorsally, has a long sutural contact with the maxilla anteriorly and ventrally and meets the jugal postroventrally below the orbit. Its lateral surface is strongly concave, forming a distinct fossa anterior to the orbit as had been reported for a number of biarmosuchid genera (Rubidge & Kitching 2003; Sidor & Welman 2003; Rubidge *et al.* 2006; Sidor & Rubidge 2006; Smith *et al.* 2006) and of which the function is unknown.

Although only the anterior part of the temporal opening is preserved, it is evident that, as in the holotype, the temporal fenestra is larger than the orbit. The jugal makes up the anteroventral border of the temporal fenestra, is in contact with the postorbital and extends anteriorly to meet the lacrimal in line with the anterior margin of the orbit. On the ventral side, the jugal has a distinct suborbital process on the right side, similar to the situation in *Endothiodon*. This process is less obvious on the left side. Although not immediately evident in specimen IVPP V16013, comparison with the holotype shows that the zygomatic arch is slightly elevated dorsally and the dorsal process of the quadratojugal is exposed laterally, a feature that is characteristic of anomodonts and is present in the biarmosuchian *Herpetoskylax* (Sidor & Rubidge 2006).

The slender postorbital forms the most part of the postorbital bar. Ventrally, it has a long sutural contact with the jugal and extends anteriorly to form the posteroventral margin of the orbit. The posterior process of the postorbital has a long dorsomedial contact with the parietal and forms the anterodorsal border of the temporal fenestra. The dorsolateral surface of the postorbital, which is slightly recessed, is the area of origin of the adductor musculature as is the situation in *Patranomodon* (Rubidge & Hopson 1996) and is in contact with the squamosal posterior to this recess. The squamosal is only partially preserved in specimen IVPP V16013, but is more complete in the holotype. It forms the posterodorsal and posterior borders of the temporal fenestra and ends anteriorly as a point on the zygomatic arch halfway along the temporal fenestra (Li & Cheng 1997; figure 1*b*). This anteroventral extension of the squamosal is shorter than in any other anomodonts. In *Anomocephalus*, the squamosal extends anteriorly to approach the postorbital bar (Modesto & Rubidge 2000); it reaches the base of the postorbital bar in *Otsheria* (J. Liu 2008,

personal observation); it extends anteriorly under the postorbital arch and contacts the postorbital in *Patranomodon* and *Suminia* (Rubidge & Hopson 1996; Rybczynski 2000); and it extends anteriorly beyond the anterior margin of the postorbital bar in *Ulemica efremovi* (PIN 2793/1, J. Liu 2008, personal observation). From the holotype of *Biseridens*, it is evident that the squamosal has a narrow oblique area on the posterodorsal margin of the temporal fenestra, which may have served as the area of origin for the medial external adductor musculature as in dicynodonts (King *et al.* 1989).

The large paired frontal exhibits a narrow midline ridge as in some other basal therapsids such as *Ulemica*, *Biarmosuchus* and *Hipposaurus* and has a short exposure on the dorsal rim of the orbit between the prefrontal anteriorly and the triangular postfrontal on the posterior side. Anteriorly and posteriorly, the frontal has a transverse interdigitating suture with nasal and parietal, respectively. The paired parietal forms the major part of the intertemporal skull roof and extends onto the dorsal border of the occipital plate. It meets the frontal in line with the anterior border of the postorbital bar and includes the pineal foramen that is positioned on a prominent chimney close to the posterior margin of the skull roof. As is the situation in *Ulemica* and *Otsheria*, no preparital could be discerned in any of the specimens, which differs from the situation in *Patranomodon* in which this bone is prominent (Rubidge & Hopson 1996).

In the palate, the internal naris is bordered by the premaxilla anteriorly, the vomer medially and posteriorly and the maxilla and palatine laterally. The paired and elongate paired vomers have a clear midline sutural contact, form a W-shaped anterior sutural contact with the premaxilla and have a long posterior contact with the palatine. The vomers are morphologically similar to those of *Patranomodon* (Rubidge & Hopson 1996). Anteriorly they are flat and posteriorly the lateral margins become progressively more ventrally oriented to form a bar with a midline trough. They flatten out further posteriorly to form a concave, triangular area between the palatine bosses. Small denticles are present on the ventral flanges of each vomer, with one on the right and at least six on the left.

The palatine is an almost triangular element in ventral view with the apex extending anteriorly as far as the second postcanine, thus failing to contact the premaxilla. Anteriorly and laterally, the palatine forms a long contact with the maxilla as in *Otsheria* (Chudinov 1960) and *Patranomodon* (Rubidge & Hopson 1990, 1996); posterolaterally, it is in contact with the ectopterygoid and posteromedially the palatine meets the posterior extension of the vomers. It forms a prominent palatine boss that merges posteriorly with a smaller pterygoid boss. The palatine boss bears numerous denticles of varying sizes, which are arranged in at least three rows. A small fossa is present posterolaterally on the palatine in the same position as the lateral palatal foramen in other anomodonts.

The paired pterygoid is the most conspicuous bone of the palate. It comprises three processes: an anterior process, a quadrate ramus and a ventromedial process. The anterior process extends forwards to meet the posterior extension of the vomers in the midline. The prominent transverse process curves posterolaterally and extends well below the level of the palate as in other basal therapsids. The right ventral surface of the process is rugose and

covered by denticles, but there are fewer denticles on the left. The lateral surface of the flange fits close to the medial surface of the mandible when it is occluded and served to brace the jaw as in *Eodicynodon* (King *et al.* 1989). In line with the transverse processes, a prominent interpterygoid vacuity is present on the ventral midline. The quadrate ramus extends posterolaterally behind the lateral flange, but only the anteriormost portion of the right ramus is preserved.

(a) Lower jaw

With the exception of the posteriormost postdentary elements, the entire lower jaw of IVPP V 16013 is preserved (figure 4). The dentary is a dorsoventrally wide and robust bone with a rugose lateral surface and an unfused symphysis. Posteriorly, the dorsal margin of the dentary extends upwards to form a prominent coronoid eminence. As the posterior margin of the coronoid eminence and the dorsal portion of the surangular are damaged, it is not possible to determine with certainty whether the coronoid process is freestanding in specimen IVPP V 16013, but comparison with the holotype shows that it is not. The angular is a large element, but most of what is preserved is reflected lamina, which has several striations that radiate from a point behind the dentary. A shallow dorsolaterally positioned fossa is separated by a slight ridge from the deeper, more ventrally positioned fossa. The anterior margin of this ventral fossa is demarcated by a distinct vertical ridge. A longitudinal ridge is present on the medial side of the angular and was probably in contact with the prearticular. The surangular is not preserved in IVPP V 16013, but is complete in the holotype. It lies above the angular in lateral view and forms the dorsal margin of the lower jaw posterior to the dentary. Posteriorly, the surangular turns ventrally to form a vertical wall that masks the articular glenoid from lateral view resembling the condition in *Patranomodon* (Rubidge & Hopson 1996). Although the jaw articulation is preserved in the holotype of *Biseridens*, the state of preservation of the quadrate and articular is not good enough for us to determine whether propalinal movement was possible.

Unlike the situation in other basal anomodonts in which the lower jaw is preserved, no mandibular fenestra is present between the dentary and the angular in *Biseridens*. Medial to the dentary, a small anterior portion, the prearticular, is present as a thin ribbon of bone above the posterior end of the splenial. The elongate flat splenial covers the lower half of the dentary and anteriorly enters into the symphysis. Above the splenial, a narrow coronoid covers the upper part of the medial surface of the dentary below the tooth series. The coronoid, which is well preserved on the right side, extends posteriorly from the level of the fourth postcanine to beyond the last postcanine. In comparison with the coronoid of *Patranomodon* (Rubidge & Hopson 1996), *Suminia* (Rybczynski 2000) and *Ulemica* (Angielczyk 2004), the coronoid of *Biseridens* is relatively long.

Several teeth are preserved in the dentary. The roots of three precanine dentary teeth are present, but no crowns are preserved in the specimens IVPP V 16013 and IVPP V 12009. A relatively large canine, which is oval in cross section, curves backwards and exhibits vertical ridges

and grooves on the surface. Morphologically, the lower postcanines are similar to those of the upper jaw and are also arranged in two rows at the posterior end, as is the situation in the upper jaw (figure 4c). Only eight (five inner and three outer) lower postcanines are preserved on the left dentary, while 12 teeth (nine inner and three outer) and one empty alveolus are present between the second and third right postcanines are present on the right side. This gives a total of 13 postcanines in the right dentary. Specimen IVPP V12009 (paratype) has 15 (11 inner and four outer) postcanines. The holotype of *U. invisus* (PIN no. 157/5) also has two rows of dentary teeth: four teeth are preserved on the outer row of the left dentary, and the anteriormost two labial teeth lie on the same level as the posteriormost two lingual teeth.

5. DISCUSSION

The two shortest trees resulting from our cladistic analysis have a tree length of 176, and these trees are shown in figure 5. The combination of the following synapomorphies clearly indicates that *Biseridens* is an anomodont: the presence of a short snout (4(1)), an elevated zygomatic arch (17(1)), the absence of a stapedial foramen (51(1)), angular reflected lamina dorsal notch close to the dentary (58(2)), and the absence of serrations on marginal teeth (75(1)). In addition, *Biseridens* exhibits several characters that are not present in described anomodonts. These are heterodont dentition comprising dentary and premaxillary precanines, canines and postcanines (63(1), 64(0)), broad distribution of teeth on the palatine and pterygoid (36(0), 37(0), 38(0)), and lack of a mandibular fenestra between the dentary, angular and surangular (56(0)).

Our analysis also shows *Biseridens* to be the most basal member of the Anomodontia. This position is relatively stable, requiring at least three steps beyond the most parsimonious resolution to move *Biseridens* out of Anomodontia. The resulting trees are similar to those obtained by previous researchers (e.g. Modesto *et al.* 1999; Modesto & Rybczynski 2000), but the surprising outcome is that *Patranomodon* is the sister taxon of Dicynodontia (figure 5) and not stem Anomodontia as proposed previously (Modesto *et al.* 1999). Synapomorphies indicating this relationship of *Patranomodon* are: having a greatly abbreviated preorbital region (4(2)), no chimney-like structure surrounding the parietal foramen 12(0), parietals contribution to skull table transversely broad as long (13(1)), and squamosal anterior extension beyond the anterior margin of the temporal fenestra (19(1)). This suggests that in the early radiation of anomodonts, there was a clade from Laurasia (Venjukovioidea) comprising *Otsheria*, *Ulemica* and *Suminia* and a separate clade from Gondwana (Chainosauria, see Kammerer & Angielczyk 2009) including *Patranomodon*, *Galeops* and *Eodicynodon*. *Biseridens* is from Laurasia and the other stem anomodont *Anomocephalus* is from Gondwana, but the only specimen representing the latter taxon comprises only the right side of a crushed skull, which hampers the coding of several skull characters. Of the 75 characters used in the analysis, 45 were coded as unknown for *Anomocephalus*.

Anomodonts are considered to have been predominantly herbivorous (King 1988), and judging by the different

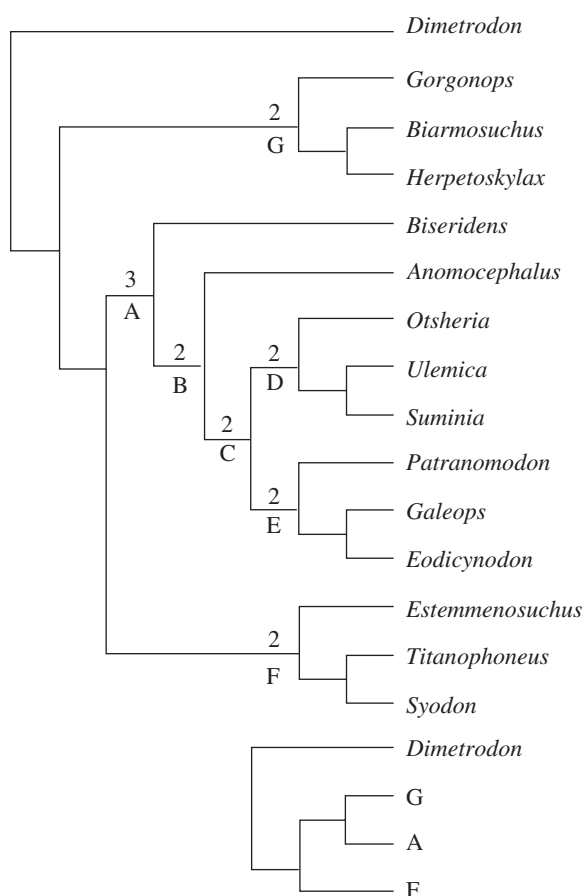


Figure 5. Phylogenetic position of *Biseridens* within basal therapsids (tree length = 176, consistency index = 0.59, retention index = 0.67). Two trees are shortest trees resulting from the PAUP analysis (branch and bound search, with unordered multistate characters) of 75 cranial and dental characters. Numbers on the tree indicate Bremer support of the respective clade. Clades are diagnosed by the following unambiguous synapomorphies in both two shortest trees, with numbers referring to characters described in the electronic supplementary material. Clade A (Anomodontia): **17(1)**, 51(1), **58(2)**, 75(1); clade B: **56(1)**, 63(2), 64(1); clade C: **20(1)**, **22(1)**; clade D (Venjukovioidea): 26(1), 28(1), 66(1); clade E (Chainosauria): 4(2), 5(0), 12(0), 13(1), 19(1). A character in bold indicates its CI is equal to 1.

cranial and dental specializations of individual anomodont genera, they experimented with processing food (mostly plant matter) using a variety of feeding mechanisms, especially in their early history. Advanced anomodonts, Dicynodontia, developed a keratinous beak rather than a complete marginal dentition. The skulls of different anomodont genera show several modifications for propalinal jaw movement. These include: modification of muscle attachment and even a new muscle mass (the lateral external adductor) (King *et al.* 1989). *Galeops* approaches a dicynodont level of organization in having a bony beak and a lateral external adductor muscle (King 1994); basal anomodonts, apart from *Biseridens*, lack a distinct canine and the incisors and postcanines display diverse morphologies in different genera; in the jaw joint propalinal sliding is not present in *Patranomodon* (Rubidge & Hopson 1996), possibly absent in *Otsheria* (Angielczyk 2004), limited in *Ulemica*, but present in *Galeops*, *Suminia* and dicynodonts

(Rybczynski & Reisz 2001; Angielczyk 2004). It thus appears likely that propaliny occurred more than once in anomodont therapsids as suggested by Angielczyk (2004).

Traditionally, the southern African therapsids are thought to have descended from the migration of basal therapsids from the Northern Hemisphere (Sigogneau & Tchudinov 1972). As a result of the discovery of *Patranomodon* in the Karoo of South Africa, Rubidge & Hopson (1990) proposed that anomodonts were dispersing freely between Europe and southern Africa in the Late Permian. Subsequent research, especially following the description of *Anomocephalus* from South Africa, supported the idea that anomodonts first evolved in African Gondwana (Modesto *et al.* 1999; Modesto & Rybczynski 2000). Our analysis now shows *Biseridens* to be the most basal anomodont. Its co-occurrence with the bolosaurid *Beleby*, the Carboniferous–Early Permian dissorophoid *Anakacops*, the basal anterosaurid dinocephalians *Stenocybus* and *Sinophoneus* (Cheng & Li 1997; Li & Cheng 1997; Li 2001), and the very basal therapsid *Raranimus* (Liu *et al.* in press) suggests that the therapsid fauna from Dashankou is the oldest (Liu *et al.* in press) and that anomodonts had a Laurasian rather than a Gondwanan origin. Our research has highlighted the existence of two separate groups of anomodonts: the Venjukovioidea in Laurasia and a separate Gondwanan one (Chainosauria) which includes *Patranomodon*, *Galeops* and *Eodicynodon*. This suggests that there may have been separate radiations of basal anomodonts from an ancestral Laurasian stock. However, as the most primitive dicynodonts are all found in Gondwana (Angielczyk 2007; Fröbisch 2009), we propose that dicynodonts had their origins from the Gondwanan clade and later dispersed across Pangaea.

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