

HEAD KINEMATICS AND FEEDING ADAPTATIONS OF THE PERMIAN AND TRIASSIC  
DICYNODONTS

MIKHAIL V. SURKOV<sup>1</sup> and MICHAEL J. BENTON<sup>2</sup>

<sup>1</sup>Geology Institute of Saratov University, Astrakhanskaya 83 st., 410075 Saratov, Russia, e-mail

SurkovMV@info.sgu.ru

<sup>2</sup>Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, U.K., e-mail

mike.benton@bris.ac.uk

ABSTRACT -- Dicynodont head kinematics, the distribution of neck muscles and the shape of the skull, shows that the Permian and Triassic forms may be classified into three categories which probably reflect feeding on low, medium and high vegetation. The basicranium is relatively shortened in Triassic forms, except in *Vinceria*, *Shansiodon*, *Tetragonias*, and *Jachalera*, as has been noted before. Data on skull proportions indicates that the height of the parietal crest may be of little taxonomic use, and that the genus *Tetragonias* is not a clade. Dicynodonts that fed at an intermediate level correspond to the main branching points in dicynodont phylogeny. High-level feeding among dicynodonts arose by the middle of the Tatarian and lasted until the Late Triassic. Specialised ground-level feeders existed only in the Mid Triassic.

## INTRODUCTION

Dicynodonts were a clade of non-mammalian synsids that arose in the Late Permian and spread widely over the world. Dicynodonts had a superficially turtle-like toothless beak and a jaw joint that allowed a sliding motion of the lower jaw, a mechanism that was evidently important in permitting them to process vegetation highly efficiently and so become dominant herbivores worldwide during the Late Permian and much of the Triassic (Keyser and Cruickshank, 1979; King, 1981, 1988; Benton, 1983). In such a diverse group, feeding style may determine skull morphology, and yet skull proportion characters are often used in systematics. It is important to distinguish the feeding adaptations within the group, and to determine whether such characters evolved convergently to suit particular dietary preferences, or whether they are phylogenetically informative.

Lehman (1961) identified two subfamilies of Middle Triassic dicynodonts, based on the presence or absence of a high parietal crest and the different relative widths of the occiput. Later, Cox (1965) elaborated the idea that the mode of feeding and shape of the skull might be correlated. For example, he proposed that kannemeyeriid dicynodonts, with a pointed snout and a high, oblique occiput, must have had a different mode of feeding from the stahleckeriids with their blunt snout and low, vertical occiput. He made an analogy with the different shapes of the lips in living rhinoceroses, where the black rhinoceros has pointed lips and a diet mainly of leaves, and the white rhinoceros has square lips and a diet mainly of grass.

Subsequent investigations of the skull proportions of Triassic dicynodonts (Cruickshank, 1968; Keyser and Cruickshank, 1979; Cox and Li, 1983) focused on finding trends in skull measurements. About a dozen proportions were estimated, including the ratio between occipital width and height, the relative length of the interpterygoid space to the length of the internal naris, the ratio of preorbital length to the whole skull length, and others. However, no clear trend in

skull shape was revealed, except that Triassic dicynodonts are generally characterised by a short interpterygoid vacuity relative to the length of the internal naris and a more elongated preorbital length than in Permian forms (Cruickshank, 1968; Keyser and Cruickshank, 1979). The latter feature was also considered as a reliable character for distinguishing shansiodontids from other Triassic dicynodonts (Cox and Li, 1983).

Our aim is to analyse dicynodont head kinematics with a view to determining whether head shape is related to dietary preferences, to phylogeny, or to both.

**Institutional Abbreviations** -- **BMNH**, British Museum of Natural History, London, England; **CAMZM**, University Museum of Zoology, Cambridge, England; **CGP**, Council for Geosciences, Pretoria, South Africa; **ISI**, Indian Statistical Institute, Calcutta, India; **IVPP**, Institute for Vertebrate Paleontology and Anthropology, Beijing, China; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, USA; **PIN**, Paleontological Institute, Moscow, Russia; **PMNH**, Muséum National d'Histoire Naturelle, Paris, France; **SAM**, South African Museum, Cape Town, South Africa; **SGU**, Saratov University geological collection, Russia; **UT**, Museum und Institut für Geologie und Paläontologie, Universität Tübingen, Germany.

## MATERIALS AND METHODS

**Taxa, Specimens, and Literature Examined** -- During this research we investigated cranial material from Tanzania: *Angonisaurus cruickshanki* (BMNH, R9732), Manda Formation, Middle Triassic; *Kannemeyeria* sp. (CAMZM 1037), *Cynognathus* Assemblage Zone, Lower Triassic; *Dicynodon leoniceps* (CAMZM 1089), Kawinga Formation, Upper Permian; *Tetragonias njalilus* (CAMZM T 750-T756, T1140; UT 292), Manda Formation, Middle Triassic; Morocco: *Moghreberia nachouensis* (PMNH ALM 281), Argana Formation, Upper Triassic; South Africa: *Dicynodon* sp. (SAM PK K7011), *Dicynodon* Assemblage zone, Upper

Permian; Russia: *Rhadiodromus maria* (PIN 1579/14; SGU 161/236), Donguz Gorizont, Middle Triassic; *Rhinodicynodon gracilis* (PIN 1579/50), Donguz Gorizont, Middle Triassic; Brazil: *Stahleckeria potens* (UT n1, n2, n3), lower member of Santa Maria Formation, Middle Triassic.

Additional measurements has also been retrieved from descriptions by Case (1934), Yeh (1959), Sun (1963), Cox (1965), Araujo and Gonsaga (1980), Brink (1982), Cluver and Hotton (1981), King (1981), and Bandyopadhyay (1988).

**The main measurements** -- In their study of skull proportions among Triassic dicynodonts, Cox and Li (1983) used five measurements: length at the dorsal midline, length over the squamosal wings (total skull length), length of the midline of the palate, height of the occiput, and width over the squamosals. Here, we use only three of their measurements, and we include more Permian and Triassic taxa in the sample.

Only two areas of the occiput may be defined confidently as muscle attachment sites, marked by rough and ridged patterns on the bone surface for ligament-bone incorporation (Hildebrand, 1982). The first is located dorsally in the area of the interparietal, the second at the lateral termination of the paraoccipital condyle. The first area is characterised by an elongated, rough, and sometimes ridged, surface along the midline of the interparietal and rough areas along the dorso-posterior edge of the parietals/squamosal, the posterior edge of the interparietal. This area may mark the insertion of the *m. rectus capitis major* and *m. semispinalis capitis medialis/trapezius* (Cox 1959, Ewer 1961). These muscles are responsible for upward head movements, and their main tension corresponded with the uppermost part of the occiput that is clearly defined among large-headed dicynodonts, especially in Triassic forms, by posterior outgrowth of the interparietal and parietals for attachment of the ligamentum nuchae which was formed primarily from the aponeurotic attachments of the adjacent and subjacent musculature. Therefore, the uppermost part of the occiput has been chosen as a landmark, and the height of the

occiput from the level of the occipital condyle was measured.

We rejected two of the five measurements used by Cox and Li (1983) because they are closely correlated with others. The measure of skull length over the squamosal wings is questionable because there are no obvious landmarks for muscle insertion (e.g. *m. cleido-occipitalis*; Cox 1959; Ewer 1961). Further, this measure is strongly correlated with the length along the dorsal midline ( $r = 0.99$ ) and palatal midline ( $r = 0.98$ ), when estimated from the measurements of Cox and Li (1983). We also reject their measure of the width of the skull over the squamosals. We sampled 11 digitised photographs of dicynodont occiputs and found a strong correlation ( $r = 0.99$ ) between the distances between attachments (centres of muscle scars) for the lateral neck muscles and the width of the occiput across the squamosals (Table 1). Therefore general measurements of the occiput such as its height and width may be correlated confidently with the relative positions of visible attachments for the main neck muscles (e.g., *m. rectus captis* and *m. obliquus capitis* (Cox 1959; Ewer 1961).

In this study, we used three main measurements of skull proportions: cranial length ( $L_{Cr}$ ) – distance along the ventral side of the skull from the level of the occipital condyle to the tip of the premaxillae; width across the occiput ( $W_{Sq}$ ), and height of the occiput ( $H$ ), which was measured at a right angle to the plane of the basicranium (Fig. 1A, B). We also checked King's (1988) statement that the Triassic forms are characterised by a visually shorter basicranium by estimating the ratio of basicranial length ( $L_{Bs}$ , Fig. 1A) to the length of the skull.

Measurements were taken from uncompressed material, but in the case of the obviously slightly squashed specimen of *Dicynodon* sp. (SAM PK K7011), we restored vertical measurements on the basis of the orbit shape of an uncompressed *Dicynodon leonceps* (CAMZM 1089), assuming that there are no pronounced allometric differences between SAM PK K7011 and CAMZM 1089, which is much larger.

Recent phylogenetic analysis of Permian dicynodonts (Angielczyk and Kurkin 2003) suggests that the genus *Dicynodon* is paraphyletic, but the result was not unequivocal. For the present we consider all *Dicynodon* specimens to belong to one group because all measurements are comparable, but we refer to all Laurasian '*Dicynodon*' material with apostrophes.

#### ANALYSIS OF HEAD KINEMATICS

**Muscles and forces** -- The main function of the occipital plate, in addition to being the posterior wall of the braincase, is as a site for attachment of neck muscles that operate the head in three dimensions during feeding, attack, and defense. Cox (1959) and Ewer (1961) thoroughly investigated the position of the occipital muscles by comparison with recent reptiles (*Varanus*, *Alligator*, *Sphenodon*) and mammals. Reconstructions of the occipital musculature by these researchers were generally the same with a few minor differences – the presence of the *m. obliquus capitis magnus*, which was rejected by Ewer (1961) and a different position of the *m. depressor mandibulae* (Ewer 1961:398). Apart from this, in both reconstructions of the occipital muscles, the attachment sites for the *m. rectus capitis lateralis*, *m. obliquus capitis* and *m. cleido-occipitalis* (Ewer 1961; Fig. 1C) or these muscles and *m. obliquus capitis magnus* (Cox 1959), are placed at the lateral termination of the paroccipital processes. The insertions of the *m. rectus capitis* and *m. semispinalis* are placed in the area of the interparietal and the posterior termination of the parietals, where there are obvious muscle scars. This distribution of muscle insertions on the occipital plate indicates a rough division into lateral (*m. cleido-occipitalis*, *m. obliquus capitis*, *m. rectus capitis lateralis*) and dorsal (*m. rectus capitis posterior*, *m. semispinalis*, *m. longissimus capitis*) portions. Judging from the muscle scars, contraction of the first group initiates lateral movements of the head, while the second group produces movements in the vertical plane. More complicated movements of the head were effected by the combined action

of all sets of neck muscles.

Since the insertions of the main occipital muscles corresponded to three areas, muscle work and initiated forces may be represented by a simplified scheme of vectors (Fig. 1D). The vertical ( $F_v$ ) and lateral ( $F_l$ ) components of the resultant forces indicate forces applied to the occiput by the dorsal ( $F_{dors}$ ) and lateral ( $F_{lat}$ ) portions of the neck muscles. The forces applied by the two muscle blocks are inversely proportional to the distance from the occipital condyle (swing point) to the point of muscle attachment, and to the distance between the occiput and the point of application of the resultant forces,  $F_v$  and  $F_l$ . The latter distance is equivalent to cranial length, because dicynodonts undoubtedly used the tip of the snout to tear off vegetation or foliage. The distances between the occipital condyle and the points of application of  $F_{dors}$  and  $F_{lat}$  are the best positions for muscle attachments on the occipital plate to move the head with least effort, and they are proportional to occiput height and width. Therefore, according to the lever rule, the relationships between the forces  $F_{dors}$  and  $F_{lat}$  generated by the neck muscles and the resultant forces can be represented as:

$$\frac{F_v}{F_{dors}} = \frac{H}{L_{Cr}} \quad \text{or} \quad F_v = F_{dors} \frac{H}{L_{bs}}$$

and

$$\frac{F_l}{F_{lat}} = \frac{W_{Sq}}{2L_{Cr}} \quad \text{or} \quad F_l = F_{lat} \frac{W_{Sq}}{2L_{cr}}$$

The ratios  $\frac{H}{L_{Cr}}$  and  $\frac{W_{Sq}}{2L_{Cr}}$ , termed the occipital indices, reflect relative efficiency of the lateral and dorsal portions of the neck muscles, and differences between these values might indicate which muscle block dominated: if the value of the index for the dorsal muscles is more than for the laterals, it is possible to assume that the dorsal muscles are more advantageously and effectively located on the occipital plate than the laterals and vice versa. Therefore, the difference between

$\frac{W_{Sq}}{2L_{Cr}}$  ( $I_{Lat}$ ) and  $\frac{H}{L_{Cr}}$  ( $I_{Dors}$ ) reflects the relative effectiveness of lateral and dorsal portions of the neck muscles and might indicate the preferred plane of head movement.

**Results and interpretation** -- Differences between lateral and dorsal occipital indices for Late Permian and Triassic dicynodonts ( $I_{Lat}$ - $I_{Dors}$ ; Table 2-3 Fig. 2) indicate a wide range of values, suggesting extreme biomechanical differences from end to end of the distribution. The standard deviation of values for the occipital index of different specimens of a species does not exceed 0.1 for most taxa. When all dicynodont genera are pooled, the histogram of occipital indices is bimodally distributed, suggesting two categories of dietary preferences. For the Permian taxa, most values fall in the modal intervals  $-0.08/0.06$  and  $<-0.08$ ; for Triassic taxa  $-0.3/-0.1$  and  $0.05/0.3$ . Plants were almost certainly the main component of the dicynodont diet and movements of the head were presumably mainly to tear foliage. Thus, dicynodonts that fed on low plants, below or at the level of the head, used lateral movements of the head more than vertical (values  $> 0.05$ ; Fig. 2), since they did not have to reach for high vegetation. The cluster of values less than  $-0.1$  (Fig. 2) reflects the more advantageous position of the dorsal portion of the neck muscles, which would have been strengthened in dicynodonts that fed on high foliage and which had to keep the head up all the time during feeding. Values in the bin  $-0.1/0.05$  (Fig. 2) reflect no particular advantage for either the lateral or dorsal neck muscle blocks, and these dicynodonts probably fed equally on low and high vegetation, or at the middle level.

Frequency histograms show different distributions among Permian and Triassic taxa. Permian taxa are generally characterised by values closer to zero (Fig. 2A-B) than in the Triassic forms, and this suggests generalised dietary preferences among most Permian dicynodonts, including the ancestral forms *Otscheria* and *Ulemica* whose indices are nearly zero (Table 2). Dicynodonts with generalised feeding adaptations (values  $-0.1/0.6$ ) were distributed worldwide

and belong to forms that were most likely ancestral to the Triassic taxa (Fig. 3). Only a few genera show a preference for vertical head movements – *Eodicynodon* and the clade *Emydops-Myosaurus* (sensu Angielczyk and Kurkin 2003; Fig. 3). Even though this feature appeared twice in Permian forms, the longevity and geographical distribution of taxa with this feature suggests that stable ecological niches, where strengthening of the dorsal neck muscles was advantageous, appeared only by the middle of the Tatarian and were restricted to Africa. This confirms that the clade *Emydops-Myosaurus* was endemic, and raises a question about what obstacles prevented a wider geographic distribution of this clade.

The occipital indices of Triassic taxa (Fig. 2B-C) show a clear division into ground-level feeders, with estimated values greater than 0.05, high-level feeders with values less than  $-0.1$ , and intermediates with indices in the range  $-0.1/0.5$ . Plotting these values on the cladogram of Triassic dicynodonts (Fig. 3) by Vega-Dias et al. (2004) shows that certain clades are characterised by similar indices. Even though Vega-Dias' cladogram does not include many taxa, this correspondence is likely the case for most Triassic clades because some taxa are represented by a single node, e.g. *Placerias* which may be related to *Moghreberia* ( $I_{\text{Lat}}-I_{\text{Dors}}=-0,29$ ) according to Vega-Dias et. al. (2004), or have not been included in their analysis, e.g. *Rechnisaurus* ( $I_{\text{Lat}}-I_{\text{Dors}}=0,08$ ), *Uralokannemeyeria* ( $I_{\text{Lat}}-I_{\text{Dors}}=0,08$ ) and *Radiodromus* ( $I_{\text{Lat}}-I_{\text{Dors}}=0,122$ ). The latter group has been referred earlier to the subfamily Rechnisaurinae (Maisch 2001).

The matching of the occipital index and feeding adaptation is also reflected in the paleogeographic distribution of dicynodonts (Fig. 4). All areas were equally inhabited with forms which fed at low level ( $I_{\text{Lat}}-I_{\text{Dors}} \geq 0.06$ ) and at middle - high levels ( $I_{\text{Lat}}-I_{\text{Dors}} -0.1/0.06$  and less  $-0.1$ ).

This study confirms King's (1988) observation that most Triassic dicynodonts show

shortening of the basicranium (Table 4), although *Vinceria*, *Tetragonias*, *Shansiodon*, and *Jachalera* retained a basicranium as long as in Permian forms.

## DISCUSSION

This study raises an important issue concerning the coding of cranial characters of Triassic dicynodonts, most notably the parietal crest. Traditionally (Lehman, 1961; Keyser and Cruickshank, 1979; King, 1988; Renault and Hancox, 2001), this character was assumed to be a key feature of *Kannemeyeria* and its relatives, and it was widely used in systematic works. However, nobody described the character in detail, and usually the parietal crest was coded simply as relatively pronounced or unpronounced. Indeed, this structure, really the level of the interparietal bar, may simply reflect feeding adaptations and the development of dorsal neck tendons to hold up the heavy head. Therefore we measured the angle of the intertemporal bar to the plane of the basicranium (Table 4) and plotted these estimates on the Triassic cladogram (Fig. 3). The phylogenetic distribution of these values, and the occurrence of pronounced angles only in large animals (Fig. 5A), suggests that the raised intertemporal bar is controlled by two factors, the massive head (e.g., *Stahleckeria*) and feeding at high level (*Tetragonias* UT 292). In both cases, the interparietal bar is substantially raised, so it is hard to assess the height of the interparietal bar unequivocally, except in its extreme autapomorphic development in *Moghreberia*, *Rabidosaurus*, and possibly *Placerias*. This is then a poor character for taxonomic purposes.

This study revealed a further problem, concerning the taxonomic integrity of *Tetragonias*. Cruickshank (1967) erected this genus for cranial and postcranial material (CAMZM T 750-T756, T1140), and he selected as holotype a specimen of *Dicynodon njalilus* (UT 292; Huene, 1942). He interpreted all differences as the result of sexual dimorphism. However, the occipital

indices and measurements of the steepness of the parietal crest revealed significant differences between the Cambridge and Tübingen specimens, and the closeness of *Tetragonias njalilus* (UT 292;  $I_{\text{Lat}}-I_{\text{Dors}}=-0,21$ ) to *Shansiodon* (IVPP V2416;  $I_{\text{Lat}}-I_{\text{Dors}}=-0,260$ ). The skulls have not undergone visible compression, and differences in size and skull proportions probably do not reflect sexual dimorphism, but rather differences in feeding adaptations. Additional differences are the less anterior extent of the maxillae in UT 292 and a pronounced reduction in the ventral maxillary process in CAMZM T 750-T756, T1140. Besides, the skull of the Tübingen specimen is very like that of *Shansiodon* (Fig. 5B), as also noted by Michael Maisch (pers. comm., 2001). Unfortunately, we lack sufficient descriptive data and cannot provide a detailed comparison of the Chinese and African specimens to conclude definitively that the Tübingen specimen is *Shansiodon*. *Shansiodon* is currently known only from China, but there is evidence that it might also occur in Africa (Hancox and Rubidge, 2001; MVS, observation of BMNH R12710 from the Manda formation, Tanzania, tentatively considered as *Shansiodon* sp.).

## CONCLUSION

The matching of the occipital index and main clades of Permian and Triassic dicynodonts as well as paleogeographic distribution of taxa suggest that this feature is a good phylogenetic character which is corresponded with preferable head movement in vertical or horizontal plane and likely reflects various feeding adaptations. However, we should point out that in some cases preferable plane of head movement may be corresponded with other peculiarities of lifestyle. For example strengthening of dorsal neck muscles for presumably fossorial *Cistecephalus* (Cluver 1978) may be explained by "headlift" digging to displace and compact the soil similar to recent spalacid mole-rats or using upwards thrusts of the head in combination with forelimbs to move the soil as marsupial mole (Hildebrand 1985). From other hand, this feature indeed may reflect

dietary preferences of *Cistecephalus* because unlike to obviously digging *Diictodon*, which complete skeletons are commonly available in borrows (Smith 1993) *Cistecephalus* remains are mostly known by skulls (King and Cluver 1991) which, judging from usually fractured bone surface, were exposed to weathering for a long period before burring (Surkov's pers. observ.). Another example – presumably more advantageous position for dorsal neck muscles in *Lystrosaurus*, which may reflect necessity to keep head upward if we assume sub aquatic lifestyle for this animal. This point of view is also corresponded to apparent absence of well developed terrestrial vegetation after Upper Permian crisis. However, we are reluctant to discuss here possible aquatic or non-aquatic adaptations of *Lystrosaurus* (Broom 1902, King and Cluver 1991), until thorough comparative investigation of lystrosaur postcranial morphology will be done and wider range of skull proportions will be collected.

Distribution of different occipital indices along dicynodont's phylogeny shows that main branching points are corresponded with taxa which had no particular preferences in head movement. Specialization for vertical head movement appeared first, but steadily existed only from middle of the Tatarian. Pronounced specialisation for lateral head movement appeared only in the Anisian, but existed until the end of the Middle Triassic, when they were probably competed off by herbivorous gomphodonts which unlike to clumsy dicynodonts had more chances to escape advanced archosaurs, especially on open spaces. Late Triassic is characterized only by specialised high-level feeders (*Moghreberia*, *Ishigualastia*, *Jachaleria*, *Placerias*) which fed on higher then gomphodonts level and therefore presumably may inhabited forestry areas, there archosaur's speed advantage was less obvious.

#### ACKNOWLEDGEMENTS

MVS acknowledges a grant from the Russian Ministry of Education \_02-9.0-25, an INTAS

fellowship award for 2002, and a Royal Society/NATO Postdoctoral Fellowship allowing him to work in Bristol during 2001 and collect data for this paper. We are grateful to Ray Symons (University Museum of Zoology, Cambridge), Sandra Chapman (Natural History Museum, London), Michael Maisch (Tübingen University), Sheena Kaal (South African Museum, Cape Town) and especially Bernard Battail (Muséum National d'Histoire Naturelle, Paris), for their hospitality, guidance in fossil collections and access to specimens. MJB thanks the Leverhulme Trust (Grant F/182/BK) for support of his work on Triassic tetrapods.

#### LITERATURE CITED

- Angielczyk, K. D. 2001. Preliminary phylogenetic analysis and stratigraphic congruence of the dicynodonts (Synapsida: Therapsida). *Palaeontologia africana* 37:53-79.
- Araujo, D. C. and T. G. Gonzaga. 1980. Uma nova especie de *Jachaleria* (Therapsida, Dicynodonta) do Triassico do Brasil. *Actas II Congreso Argentino de Paleontologia y Biostratigraphia y I Congreso Latinoamericano de Paleontologia*, Buenos Aires 1978 2:159-174.
- Bandyopadhyay, S. 1988. A kannemeyeriid dicynodont from the Middle Triassic Yerrapalli Formation. *Philosophical Transactions of the Royal Society of London, Series B* 320:185-233.
- Benton, M. J. 1983. Dinosaur success in the Triassic: a noncompetitive ecological model. *Quarterly Review of Biology* 58:29-55.
- Brink, A. S. 1982. *Illustrated Bibliographical Catalogue of the Synapsida. Part 1.* Government Printer, Pretoria.
- Broom, R. 1902. On the leg and toe bones of *Ptychosiafum*. *Transactions of the South African Philosophical Society* 11:233-235.

- Case, E.C. 1934. Description of a skull of *Kannemeyeria erithrea* Haughton. Contributions from the Museum of Paleontology, University of Michigan 4:115-127.
- Cluver, M. A. 1987. The skeleton of the mammal-like reptile *Cistecephalus* with evidence for a fossorial mode of life. Annals of the South African Museum. 83:99-146.
- Cluver, M. A. and N. N. Hotton, III. 1981. The genera *Dicynodon* and *Diictodon* and their bearing on the classification of Dicynodontia. Annals of the South African Museum 83:99-146.
- Cox, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. Proceedings of the Zoological Society of London 132:321-367.
- Cox, C. B. 1965. New Triassic dicynodonts from South America; their origins and relationships. Philosophical Transactions of the Royal Society of London, Series B 248:457-516.
- Cox, C. B. 1991. The Pangaea dicynodont *Rechnisaurus* and the comparative biostratigraphy of Triassic dicynodont fauna. Palaeontology 34:767-784.
- Cox, C. B. and J.-L. Li. 1983. A new genus of Triassic dicynodont from East Africa and its classification. Palaeontology 26:389-406.
- Cruickshank, A. R. I. 1967. A new dicynodont genus from the Manda Formation of Tanzania (Tanganyika). Journal of Zoology 153:163-208.
- Cruickshank, A. R. I. 1968. A comparison of the palates of Permian and Triassic dicynodonts. Palaeontologia Africana 11:23-31.
- Ewer, R. F. 1961. The anatomy of dicynodont *Daptocephalus leoniceps* (Owen). Proceedings of the Zoological Society of London 136:375-402.
- Hancox, P. J. and B. C. Rubidge. 2001. Breakthroughs in the biodiversity, biogeography, biostratigraphy, and basin analysis of the Beaufort group. Journal of African Earth Sciences 33:563-577.

- Hildebrand, M. 1982 *Analysis of Vertebrate Structure*. Wiley, New York.
- Hildebrand, M. 1985. Digging of quadrupeds; pp. 89-109 in M. Hildebrand, D. M. Bramble, K. E. Liem, and D. B. Wake (eds.), *Functional Vertebrate Morphology*. Belknap Press, London.
- Huene, F. von 1942. Die Dicynodontier des Ruhuhu-Gebietes in der Tübinger Sammlung. *Neues Jahrbuch für Geologie, Mineralogie, und Paläontologie, Abhandlungen* 92:47-136.
- Kalandadze N. N. 1970 [New Triassic kannemeyeriids from the South Ural region;] pp. 51-57 in *Materials on Evolution of Terrestrial Vertebrates*. Moscow, Nauka Press. [Russian]
- Keyser, A. W. and A. R. I. Cruickshank. 1979. The origins and classification of Triassic dicynodonts. *Transactions of the Geological Society of South Africa* 82:81-108.
- King, G. M. 1981. The functional anatomy of a Permian dicynodont. *Philosophical Transactions of the Royal Society of London, Series B* 291:243-322.
- King, G. M. 1988. Dicynodontia. *Handbuch der Paläoherpetologie*. Teil 17. Gustav Fischer, Stuttgart.
- King, G. M. and Cluver, M. 1991. The aquatic *Lystrosaurus*: an alternative lifestyle. *Historical Biology* 4:323-341.
- Lehman, J. P. 1961. Dicynodontia; pp. 287-351 in J. Piveteau (ed.), *Mammifères, Origène Reptilienne, Evolution*. *Traité de Paléontologie*, 6. Masson et Cie, Paris.
- Maisch, M. 2001. Observations on Karroo and Gondwana vertebrates. Part 2: A new skull reconstruction of *Stahleckeria potens* von Huene, 1935 (Dicynodontia, Middle Triassic) and reconsideration of kannemeyeriiform phylogeny. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 220:127-152.
- Maisch, M. W., and Gebauer, E. V. I. 2005. Reappraisal of *Geikia loucusticeps* (Therapsida: Dicynodontia) from the Upper Permian of Tanzania. *Palaeontology* 48:309-324.

- Renaut A. J. and P. J. Hancox P.J. 2001. Cranial description and taxonomic re-evaluation of *Kannemeyeria argentinensis* (Therapsida: Dicynodontia). *Palaeontologia Africana* 37:81-91.
- Smith, R. M. H. 1993. Vertebrate taphonomy of Late Permian floodplain deposits in the Southwestern Karoo basin of South Africa. *Palaios* 8:45-67.
- Sun, A. L. 1963. Chinese kannemeyeriids. *Paleontologia Sinica* 17:1-109.
- Vega-Dias, C., M. W. Maisch and C. L. Schultz. 2004. A new phylogenetic analysis of Triassic dicynodonts (Therapsida) and the systematic position of *Jachaleria candelariensis* from the Upper Triassic of Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 231:145-166.
- Yeh, H. K. 1959. A new dicynodont from the *Sinokannemeyeria* Fauna of Shansi. *Vertebrata Palasiatica* 3:187-204.

TABLE 1. Measurements between areas for attachments of lateral occipital muscles and width of the occiput. Values represents pixels.

Taxa	Distance between attachments for lateral occipital muscles	Width over squamosal
1. <i>Rachiocephalus</i> UT 100	442	778
2. <i>Pelanomodon</i> UT K114	393	751
3. <i>Dicynodon huenei</i> UT K101	383	658
4. <i>Tetragonias njalilus</i> UT 292	609	1056
5. <i>Stahleckeria potens</i> UT no2	476	937
6. <i>Dicynodon leoniceps</i> CAMZM 1089	7988	15060
7. <i>Diictodon testidirostris</i> BMNH R11184	560	884
8. <i>Kingoria nowacki</i> CAMZM 747	6080	9537
9. <i>Angonisaurus cruickshanki</i> BMNH R9732	277	595
10. <i>Kannemeyeria latifrons</i> CAMZM 1037	5248	10288
11. <i>Tetragonias njalilus</i> CAMZM T754	4422	10370

TABLE 2. Estimates of occipital indices of Permian dicynodonts. Explanations in the text.

**Abbreviations:** \* measurements taken from photographs; \*\* measurements taken from reconstructions.

Permian Taxa	ILat-Idors	Mean	Standard deviation		
1 <i>Aulacephalodon tigriceps</i> BMNH 36235	0.041	0.03	0.011		
2 <i>Aulacephalodon</i> SAM PK K6064	0.025				
3 <i>Cistecephalus</i> SAM PK K7667	-0.368	-0.291	0.11		
4 <i>Cistecephalus</i> SAM PK K8584	-0.342				
5 <i>Cistecephalus</i> SAM PK 10664	-0.162				
6 <i>Dicynodon leoniceps</i> CAMZM 1089	-0.060				
7 ' <i>Dicynodon</i> '(?) sp. PIN no number	-0.067	-0.08	0.010		
8 <i>Dicynodon huenei</i> UT K101	-0.070				
9 <i>Dicynodon lacerticeps</i> BMNH 36233	-0.071				
10 <i>Dicynodon lacerticeps</i> SAM-PK-K7011	-0.072				
11 <i>Dicynodon pardiceps</i> BMNH 47045	-0.078				
12 <i>Dicynodon</i> sp. SAM-B88*	-0.080				
13 ' <i>Dicynodon</i> ' <i>amaltzkii</i> PIN 2005/38a	-0.088				
14 <i>Dicynodon trigonocephalus</i> TSK 14	-0.090				
15 <i>Diictodon testudirostris</i> BMNH R11184	0.083			0.03	0.056
16 <i>Diictodon</i> sp. BMNH R3744	0.042				
17 <i>Diictodon</i> sp. BMNH 47052	-0.029				
18 <i>Emydops</i> sp. SAM PK K1517	-0.130	-0.19	0.087		
19 <i>Emydops</i> sp. SAM PK 3721	-0.144				
20 <i>Emydops</i> sp. SAM PK 11060	-0.287				
21 <i>Eodicynodon</i> SAM PK 11879	-0.190				
22 <i>Eodicynodon</i> SAM PK 117569	-0.199	0.00	0.11		
23 <i>Geikia locusticeps</i> UT K114	0.080				
24 <i>Geikia elginensis</i> (cast) BMNH R2112	-0.078	-0.04			
25 <i>Idelisaurus tatarika</i> PIN 156/4	-0.037				
26 <i>Kingoria</i> CAMZM 749	-0.120	0.00			
27 <i>Otscheria netzvetayevi</i> PIN 1758/5	0.000				
28 <i>Oudenodon halli</i> BMNH R4067	0.159	0.05	0.090		
29 <i>Oudenodon baini</i> BMNH 36232	0.074				
30 <i>Oudenodon</i> SAM PK 10066	0.025				
31 <i>Oudenodon</i> SAM PK K5227	-0.056				
32 <i>Pristerodon</i> sp. SAM PK 1658	0.001	-0.02	0.029		
33 <i>Pristerodon</i> sp. SAM PK 10153	-0.040				
34 <i>Rachiocephalus</i> UT 100*	-0.033	0.00			
35 <i>Robertia</i> SAM PK 11761	-0.002				
36 <i>Tropidostoma microtrema</i> BMNH R1662	0.039	0.03	0.018		
37 <i>Tropidostoma</i> SAM PK K8633	0.014				
38 <i>Vivaxosaurus permirus</i>	-0.020	0.02			
39 <i>Ulemica efremovi</i> PIN 2793/1	0.019				

TABLE 3. Estimates of occipital indices of Triassic dicynodonts. Explanations in the text.

**Abbreviations:** \* measurements taken from photographs; \*\* measurements taken from reconstructions.

Taxa	$I_{\text{Lat}}-I_{\text{Dors}}$	Mean	Standard deviation
1 <i>Angonisaurus</i> BMNH R9732	0.123	0.123	
2 <i>Dinodontosaurus turpior</i> MZC 1670	0.070	0.070	
3 <i>Ischigualastia</i> MCZ 318-19	-0.190	-0.190	
4 <i>Jachaleria candelariensis</i> PVL 3841	-0.220	-0.220	
5 <i>Kannemeyeria lophorhinus</i> CGP R313	0.140		
6 <i>Kannemeyeria latifrons</i> CAMZM 1037	0.130	0.132	0.008
7 <i>Kannemeyeria simocephalus</i> UMMP 14530*	0.125		
8 <i>Lystrosaurus curvatus</i> BMNH R3597	-0.122	-0.122	
9 <i>Moghreberia</i> PMNH ALM 281	-0.290	-0.290	
10 <i>Parakannemeyeria dolichocephala</i> IVPP 973	-0.155		
11 <i>Parakannemeyeria youngi</i> IVPP 979	-0.170		
12 <i>Parakannemeyeria youngi</i> IVPP 978	-0.174	-0.121	0.077
13 <i>Parakannemeyeria ningwuensis</i> IVPP 983	-0.115		
14 <i>Parakannemeyeria dolichocephala</i> IVPP V984	0.010		
15 <i>Placerias</i> **	-0.240	-0.240	
16 <i>Rechnisaurus</i> **	0.080	0.080	
17 <i>Rhadiodromus</i> SGU 161/236	0.124	0.122	0.003
18 <i>Rhadiodromus</i> PIN 1579/14	0.120		
19 <i>Rhinodicynodon gracilis</i> PIN 1579/50	-0.026	-0.026	
20 <i>Shansiodon wangi</i> IVPP 2415	-0.083	-0.172	0.125
21 <i>Shansiodon</i> IVPP V2416	-0.260		
22 <i>Sinokannemeyeria yingchiaoensis</i> IVPP 974	0.078	0.039	0.055
23 <i>Sinokannemeyeria pearsoni</i> IVPP 976	0.000		
24 <i>Stahleckeria</i> UT n2	0.260	0.260	
25 <i>Tetragonias njalilus</i> CAMZM T754	0.060		0.191
26 <i>Tetragonias njalilus</i> UT 292	-0.210		
27 <i>Uralokannemeyeria</i> SGU D-104/1	0.080	0.080	
28 <i>Vinceria</i> **	-0.120	-0.120	
29 <i>Wadisasaurus</i> ISI R38	0.000	0.000	

TABLE 4. Estimates of occipital index ( $L_{Bs}/L_{Cr}$ ) and angle of the intertemporal bar ('angle of temporal crest') in Late Permian - Triassic dicynodonts. Explanations in the text.

**Abbreviations:** \* measurements taken from photographs; \*\* measurements taken from reconstructions.

Taxa	Angle of temporal crest	$L_{Bs}/L_{Cr}$
1. <i>Angonisaurus</i> BMNH R9732	<10	21.3
2. <i>Dicynodon</i> sp. SAM-PK-K07011	<10	29
3. <i>Dicynodon</i> SAM-B88*	<10	28.9
4. <i>Dicynodon leoniceps</i> CAMZM 1089	<10	29.9
5. <i>Dicynodon trigonocephalus</i>	<10	29.2
6. <i>Dinodontosaurus turpior</i> MZC 1670	<10	17.6
7. <i>Ischigualastia</i> MCZ 318-19	40	23.5
8. <i>Jachaleria candelariensis</i> PVL 3841	40	29
9. <i>Kannemeyeria lophorhinus</i> CGP R313	26	19.4
10. <i>Kannemeyeria simocephalus</i> UMMP 14530*	40	20
11. <i>Kannemeyeria latifrons</i> CAMZM 1037	26	19.3
12. <i>Moghreberia</i> PMNH ALM 281	70	?
13. <i>Parakannemeyeria</i> IVPP V984	~10	22.5
14. <i>Placerias</i> **	70	21.2
15. <i>Rechnisaurus</i> **	35	20
16. <i>Rhadiodromus</i> PIN 1579/14	<10	21.2
17. <i>Rhinodicynodon</i> PIN 1579/50	<10	?
18. <i>Shansiodon</i> IVPP V2416	~10	29.1
19. <i>Sinokannemeyeria</i> IVPP V 974*	38	18.9
20. <i>Stahleckeria</i> UT n2	~30	21.1
21. <i>Tetragonias njalilus</i> CAMZM T754	<10	30.0
22. <i>Tetragonias njalilus</i> UT 292	38	27.6
23. <i>Uralokannemeyeria</i> SGU D-104/1	38	19.1
24. <i>Vinceria</i> **	~35	27
25. <i>Wadiasaurus</i> ISI R38	~30	23.6

## [FIGURE CAPTIONS]

FIGURE. 1. Main skull measurements and simplified scheme of skull movements in Triassic dicynodonts; **A, B**, scheme of skull measurements in ventral (**A**) and posterior (**B**) views; **C**, scheme of attachments for the main neck muscles (modified from Ewer, 1961); **D**, simplified scheme of forces applied by neck muscles; not to scale. **Abbreviations:**  $F_{\text{dors}}$ , force applied by the dorsal portion of the neck muscles;  $F_l$ , lateral component of the force applied to an object;  $F_{\text{lat}}$ , force applied by the lateral portion of the neck muscles;  $F_v$ , vertical component of the force applied to an object; **H**, height of the skull;  $L_{\text{Bs}}$ , length of basicranium;  $L_{\text{Cr}}$ , skull length along palatal midline; **mcloc**, attachment for m. cleidoocipitalis; **mlc**, attachment for m. longus capitis; **mocs**, attachment for m. obliquus capitis; **mrcl**, attachment for m. rectus capitis lateralis; **mrcp**, attachment for m. rectus capitis posterior; **msmp**, attachment for m. semispinalis;  $W_{\text{sq}}$ , width of the skull across squamosal wings.

FIGURE. 2. Distribution of values of occipital indices and frequency histograms for Permian taxa (**A, B**), and for Triassic taxa (**C, D**).

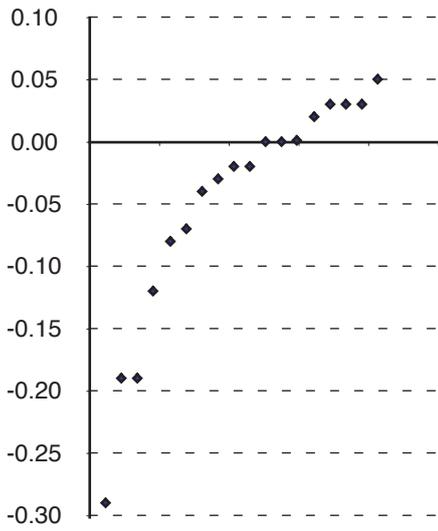
FIGURE. 3. Distribution of occipital indices among main clades of the Permian and Triassic dicynodonts. Composite phylogeny based on Angielczyk and Kurkin (2003), Vega-Dias et al. (2004), and Maisch and Gebauer (2005).

FIGURE. 4. Paleogeographic and stratigraphic distribution of Middle and Late Triassic dicynodont high-level and ground-level feeders. **1.** *Kannemeyeria*; **2.** *Vinceria*; **3.** *Rechnisaurus*; **4.** *Parakannemeyeria*; **5.** *Sinokannemeyeria*; **6.** *Rhadiodromus*; **7.** *Uralokannemeyeria*; **8.** *Stahleckeria*; **9.** *Ischigualastia*; **10.** *Dinodontosaurus*; **11.** *Jachaleria*; **12.** *Placerias*; **13.** *Moghreberia*; **14.** *Wadiazaurus*; **15.** *Shansiodon*; **16.** *Rhinodicynodon*; **17.** *Angonisaurus*; **18.** *Tetragonias* (CAMZM T754); **19.** *Tetragonias* (UT 292).

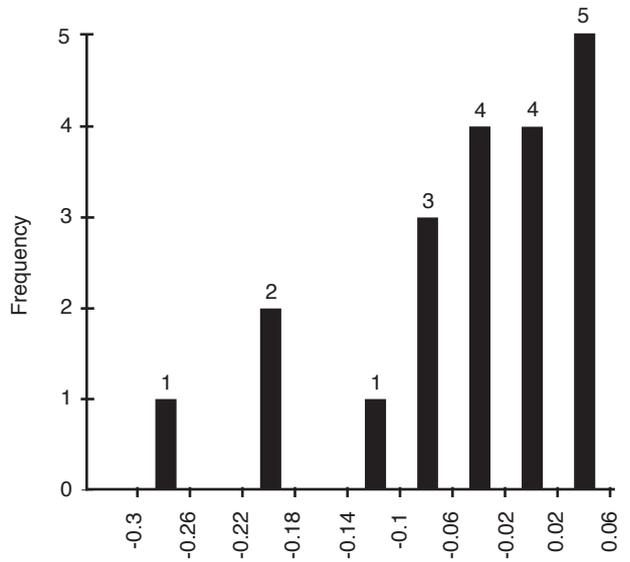
FIGURE. 5. Skull outlines of the Middle-Late Triassic dicynodonts **A**, large taxa with a skull length greater than 350 mm in adult individuals. Not in scale. **B**, skull outlines of *Shansiodon*, *Tetragonias* (UT 292), *Tetragonias* (CAMZM T754), from left to right; Scale bar represents 5

(Sun 1963); **5.** *Sinokannemeyeria* (Sun 1963); **6.** *Rhadiodromus*; **7.** *Uralokannemeyeria*; **8.** *Rabidosaurus* (Kalandadze 1970); **9.** *Wadiasaurus* (Bandyopadhyay 1988); **10.** *Stahleckeria*; **11.** *Ischigualastia* (Cox 1965); **12.** *Jachaleria* (Araujo and Gonsaga 1980); **14.** *Placerias* (Cox 1965); **15.** *Moghreberia*.

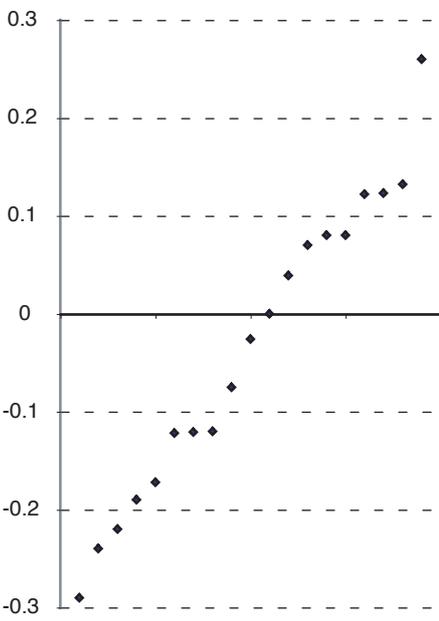




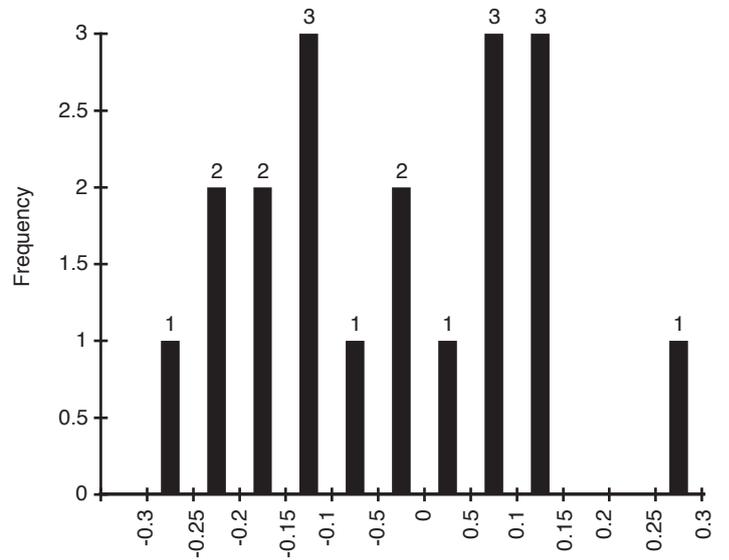
A



B

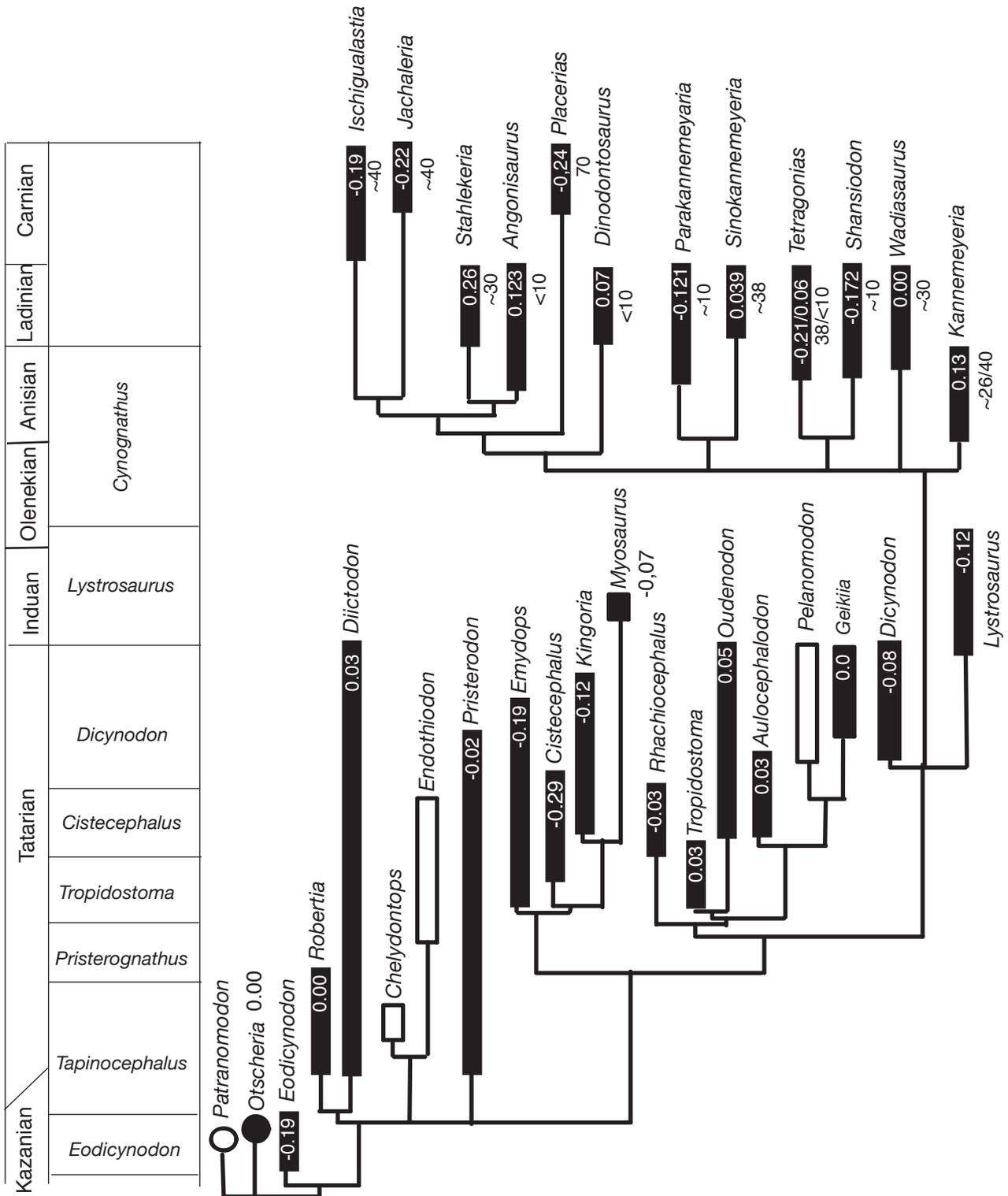


C



D

Surkov and Benton Figure 2



Surkov and Benton Figure 3

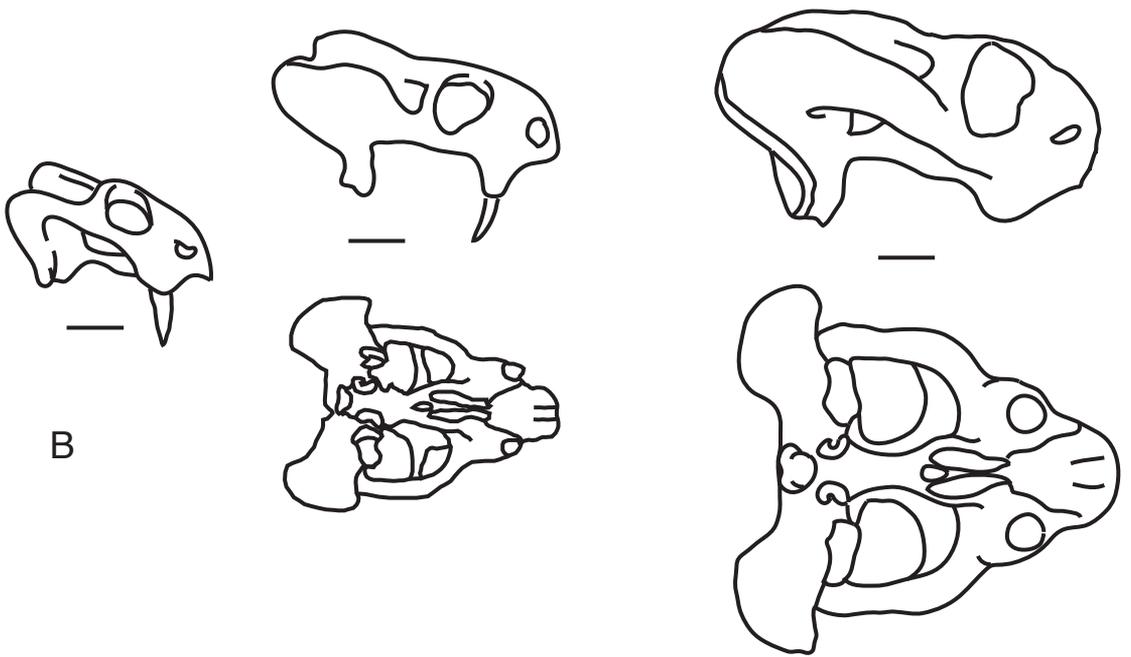
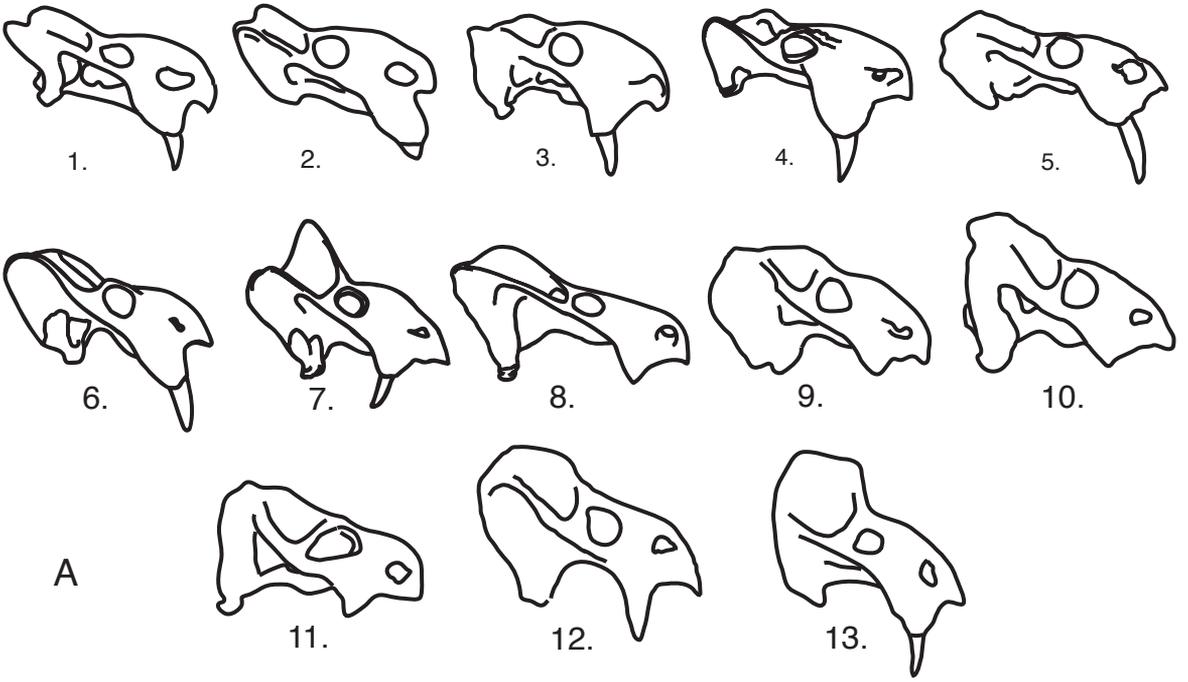
			S.America	N.America	Africa	India	China	Eastern Europe			
TRIASSIC	Upper	Carnian	 9, 11.	 12.	 13.						
	Middle	Ladinian	 8, 10.		 3, 18.	 17, 19.	 3.  14.	 5.	 4, 15.	 6, 7.	 16.
		Anisian	 2.		 1.						



Low-level feeders ( $L_{Lat} - L_{Dors} > 0.05$ )



High-level feeders ( $L_{Lat} - L_{Dors} < -0.1$  and  $-0.1/0.05$ )



Surkov and Benton Figure 5