THE BASICRANIUM OF DICYNODONTS (SYNAPSIDA) AND ITS USE IN PHYLOGENETIC ANALYSIS

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ABSTRACT. Current phylogenetic hypotheses for the dicynodonts conflict, probably because the characters used, especially those of the jaws and facial region, show considerable convergence. Characters of the braincase and basipterygoid articulation of the Late Permian–Middle Triassic dicynodonts *Diictodon*, *Dicynodon*, *Kingoria, Lystrosaurus*, *Rechnisaurus*, and 14 other genera, may have phylogenetic value. Parsimony analysis and the character compatability permutation test suggest, at the highest possible confidence level, that the data set contains significant hierarchical structure, interpreted as a result of phylogeny. The most parsimonious tree broadly agrees with all recent hypotheses on the relationships among dicynodonts. However, it conflicts with the recent suggestion that *Lystrosaurus* is part of a clade of Middle–Late Triassic dicynodonts, but supports the basal position of *Kingoria*. The use of *Eodicynodon* as an outgroup does not perturb the parsimonious relationship of the included taxa. Topological constraints reveal that phylogenetic hypotheses based only on basicranial characters are not robust. Characters of the basipterygoid articulation and inner braincase have high consistency and retention indices, which suggests that the main evolutionary transformations in the dicynodont basicranium occurred within these structures.

KEY WORDS: Dicynodontia, Synapsida, Therapsida, braincase, phylogeny, cladistics.

DICYNODONTS arose in the Late Permian, spread widely over the world, and occupied almost all terrestrial herbivorous niches. This success may be related to their turtle-like toothless snout and specialized masticatory apparatus, which allowed them to chop vegetation much more effectively than other competitors, and they remained the major herbivores during the Late Permian and most of the Triassic (Benton 1983; Sennikov 1995).

The specialized masticatory apparatus gives dicynodonts a distinctive appearance, but it also contributes to many convergences and obscures evolutionary trends in the group. This is probably one of the reasons why no consensus has been reached on their relationships in over 150 years of research. In previous phylogenetic studies (Keyser and Cruickshank 1979; Cluver and King 1983; Cox and Li 1983; King 1988; Angelczyk 2001; Maisch 2002), mostly superficial cranial characters were used, and there was little reference to inner cranial structures such as the basipterygoid articulation and the braincase.

The aim of this paper is to provide descriptions of the basicranial morphology of major derived dicynodonts and to investigate the phylogenetic usefulness of this region. We were able to re-examine the basicranium of representatives of the main dicynodont superfamilies (*sensu* King 1988): *Kingoria nowacki* (Superfamily Kingorioidea), *Diictodon* (Superfamily Diictodontoidea), as well as *Dicynodon*, *Lystrosaurus*, and *Rechnisaurus* (Superfamily Pristerodontoidea). In addition, we considered material of other Middle and Late Triassic genera from South and North America, South Africa, Tanzania, and Eastern Europe (listed in Appendix). Additional morphological data for phylogenetic analysis were taken from original descriptions by Camp and Welles (1956) and Barry (1967).

Institutional abbreviations. BMNH, The Natural History Museum, London, England; CAMZM, University Museum of Zoology, Cambridge, England; PIN, Paleontological Institute, Moscow, Russia; SAM, South African Museum, Cape Town, South Africa; SGU, collection of Saratov University, Russia; UT, Universität Tübingen, Museum und Institut für Geologie und Paläontologie, Tübingen, Germany.

[Palaeontology, Vol. 47, Part 3, 2004, pp. 619–638]

DESCRIPTION

Braincase and basipterygoid articulation of Kingoria nowacki

Kingoria nowacki was described by Cox (1959) on the basis of several specimens from the Kawinga Formation (Upper Permian), and later the Superfamily Kingorioidea was established by Cluver and King (1983). Cox (1959) described the skull and the braincase region, but only the appearance of the dorsum sellae was mentioned as peculiar for *Kingoria*. Additional investigation of the *Kingoria* specimens (CAMZM T747–9, T792) has revealed new information on the construction of the braincase and basipterygoid articulation.

Parabasisphenoid. The parabasisphenoid is an elongate and rather massive bone that forms the anterior part of the braincase floor (pbs, Text-fig. 1A). The processus basitrabecularis is narrow and fused, without noticeable sutures with the presphenoid, and forms the ascending processus cultriformis that supported the anterior part of the brain. Posteriorly this bone makes a straight ventral contact with the basioccipital, forming the anterior surface of the tuber fenestra ovalis.

There are two longitudinal ridges on the antero-ventral side of the tuber fenestra ovalis that extend anteriorly, but their anatomical significance is not clear. They may be homologous to the parabasisphenoidal crista ventrolateralis of basal synapsids (including basal dicynodonts; Rybczynski 2000), indicating the presence of the m. protractor pterygoidei (rpbs, mpp, Text-fig. 1A), which helped to keep the parabasisphenoid and pterygoids in a proper position despite the weak basipterygoid joint. These ridges meet anteriorly at the level of the foramina for the carotid canals, forming a pronounced ridge along the ventral midline of the parabasisphenoid and pterygoids forwards to the posterior edge of the interpterygoid vacuity (r, Text-fig. 1A). This ridge might divide the attachments for the m. pterygoidei posterior which were on the medial part of the pterygoids in dicynodonts (King 1981) or might have been involved in attachment of the hyoid apparatus (Cluver 1971).

The foramina for the carotid arteries enter separately on the ventral side of the parabasisphenoid at the contact with the pterygoids (cc, Text-fig. 1A), and they exit in the anterior half of the sella turcica through a single foramen (cc, Text-fig. 1B). The palatal branches of cranial nerve VII passed anteriorly through a separate channel, the canalis vidii (cv, Text-fig. 1A–B) between the pterygoid and the parasphenoidal wing (Olson 1944) or processus basitrabecularis (Tatarinov 1966). They accompanied the carotid arteries in the anterior wall of the carotid canals, and exited dorsally well forward on the processus basitrabecularis.

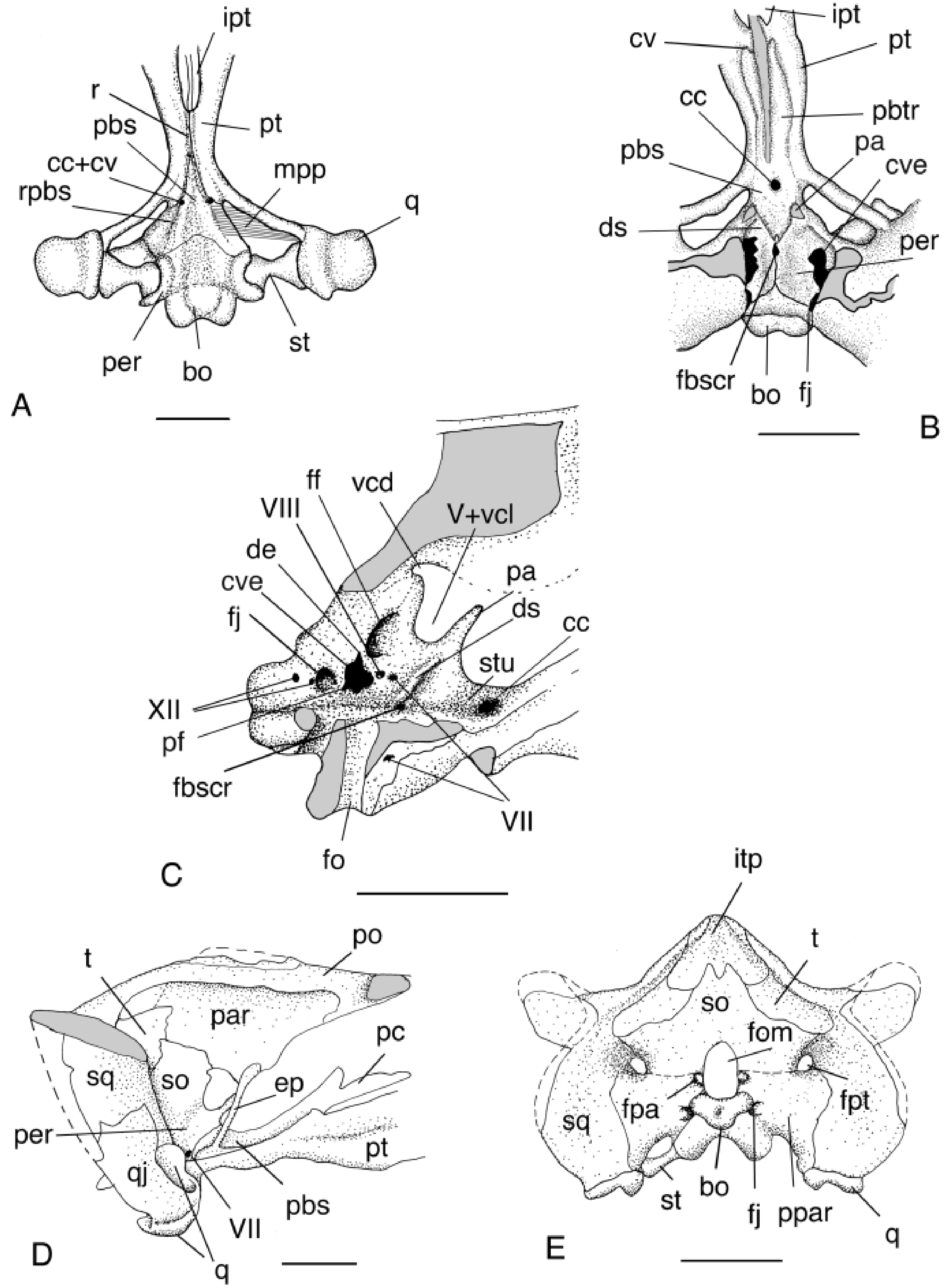
Anterolaterally, the parabasisphenoid wedges between the pterygoids, forming a narrow, elongate contact (pbs, pt, Text-fig. 1B). Along this contact, on the dorsal side, the parabasisphenoid forms a long, narrow parabasisphenoidal process (processus basitrabecularis) which overlaps the dorsal surface of the pterygoids and terminates behind the interpterygoid vacuity (pbtr, Text-fig. 1B).

Dorsally, the posterior end of the parabasisphenoid contacts the periotic (per, Text-fig. 1B). This element, according to Olson (1944), represents the co-ossified prootic and opisthotic, and since they are also fused in *Kingoria* and other dicynodonts with barely visible distinction from the lateral side, we use Olson's terminology in this paper. The posterior contact between parabasisphenoid and periotics is wedge-shaped and extends to the level of the vestibular cavity (cve, Text-fig. 1B) of the inner ear, which is open medially through an unossified portion of the braincase wall. This contact makes step-like ridges on the braincase floor, which meet posteriorly and form a Y-shaped dorsum sellae (ds, Text-fig. 1B).

Remains of a round foramen, or unossified zone, can be seen clearly in the midline of the braincase floor, just posterior to the dorsum sellae at the contact between periotic and parabasisphenoid (fbscr, Text-fig. 1B). The presence of an unossified zone in the middle of the braincase floor among dicynodonts has been mentioned by many authors (Olson 1944; Barry 1967; Cluver 1971) and was reasonably identified as the fenestra basicranialis by Olson (1944) on the basis of its position between the parabasisphenoid and basioccipital.

Periotic. The periotics comprise the lower part of the lateral walls and the posterior part of the braincase floor (per, Text-fig. 1B, D). Anteriorly they contact the parabasisphenoid and form the rod-like process of the pila antotica (pa, Text-fig. 1C) with a notch for the trigeminal nerve and vena capitis lateralis behind (V + vcl, Text-fig. 1C). The vena

TEXT-FIG. 1. Basipterygoid articulation and braincase of *Kingoria nowacki*, CAMZM T748. A–B, basipterygoid articulation in ventral (A), and dorsal (B) views. C–D, braincase in medial (C) and lateral (D) views. E, occiput in posterior view. Scale bars represent 20 mm. Abbreviations in Appendix. (C–E, modified from Cox, 1959.)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capitis dorsalis left the braincase through the notch on the lateral wall (vcd, Text-fig. 1C) at the contact between periotic and supraoccipital. The periotics contact each other medially for some distance along the midline, overlapping the anterior part of the basioccipital (per, bo, Text-fig. 1B). Ventrally, the periotic forms the posterolateral part of the tuber fenestra ovalis.

The facial nerve entered the periotic in the braincase floor just posterior to the pila antotica, and exited by a notch on the lateroventral side of the bone (VII, Text-fig. 1C). This notch was considered by some authors (Cluver, 1971; King, 1981) as a receptacle for the geniculate ganglion. The vestibular cavity opens ventromedially in the middle of the ossified braincase wall (cve, Text-fig. 1C). There is a foramen and a fissure-like ventral notch at the anterior edge of this opening which were identified by Cox (1959) as separate passages for the anterior and posterior rami of the vestibulocochlear nerve (VIII, Text-fig. 1C). The vertical groove above the vestibular cavity (de, Text-fig. 1C) is a remnant of the canal for the ductus endolymphaticus. In more complete specimens of derived dicynodonts, the ductus endolymphaticus terminated in the bone without opening into the braincase (pers. obs. in *Lystrosaurus* sp., CAMZM T758, Kalandadze 1974). The notch in the posteroventral edge of the internal auditory meatus (pf, Text-fig. 1C) might correspond with the opening for the perilymphatic duct. Anterodorsally, on the medial wall of the braincase, a deep subarcuate or floccular fossa (ff, Text-fig. 1C), with an opening in the vestibular cavity, runs posterolaterally.

Posteriorly the periotic contacts the exoccipitals and basioccipital, which form the anterior edge of the foramen jugularis (fj, Text-fig. 1B–C, E). The foramen jugularis was the exit for the jugular vein and cranial nerves IX, X, and XI (Camp and Welles 1956; Cox 1959). The lateral portion of the periotic forms strong, dorsoventrally widened paroccipital processes (ppar, Text-fig. 1E), which contact the squamosal laterally, the supraoccipital dorsally, and accommodate the quadrates anteriorly.

Basioccipital. The basioccipital forms the posteromedial walls of the tuber fenestra ovalis and the lower part of the occipital condyle (bo, Text-fig. 1E). Anteriorly and laterally this bone contacts the periotic and there it is overlapped by the exoccipitals.

Exoccipital. The exoccipitals are paired bones that overlap the basioccipital dorsolaterally, and they are fused with that element and with the paroccipital processes without pronounced suture. They bear prominent processes on the occipital plate for connection to the proatlas (fpa, Text-fig. 1E). The exoccipitals complete the braincase floor posteriorly and surround the lowermost part of the foramen magnum. The hypoglossal nerve exited by independent canals (XII, Text-fig. 1C) through the exoccipital, just behind the foramen jugularis (Camp and Welles 1956; Cox 1959).

Epipterygoid. The epipterygoids are rod-like bones which rise from the dorsal surface of the posterior ramus of the pterygoids to the anteroventral edge of the parietals (ep, Text-fig. 1D), where they are fused. The base of the epipterygoid contacts the processus basitrabecularis posteromedially.

Supraoccipital. The supraoccipital is an unpaired bone, which forms the posterodorsal part of the braincase, and completely surrounds the foramen magnum above the exoccipitals (so, Text-fig. 1E). It contacts the dorsal edge of the periotic and paroccipital process, separating the latter from the parietal on the lateral side of the braincase (so, Text-fig. 1D). In the occiput, the supraoccipital contacts the inner margin of the squamosal, tabulars, and interparietal, and forms the upper edge of the fenestra posttemporalis (fpt, Text-fig. 1E). Anterolaterally the supraoccipital is overlapped by the parietals (par, Text-fig. 1D).

Braincase and basipterygoid articulation of Diictodon

The genus *Diictodon* was described by Broom (1913) and referred by Cluver and King (1983) to the Diictodontoidea. Despite the naming of about 20 species of *Diictodon*, no detailed description of the basicranium has been made. Investigation of specimens of *Diictodon testudirostris* (BMNH R11184) and

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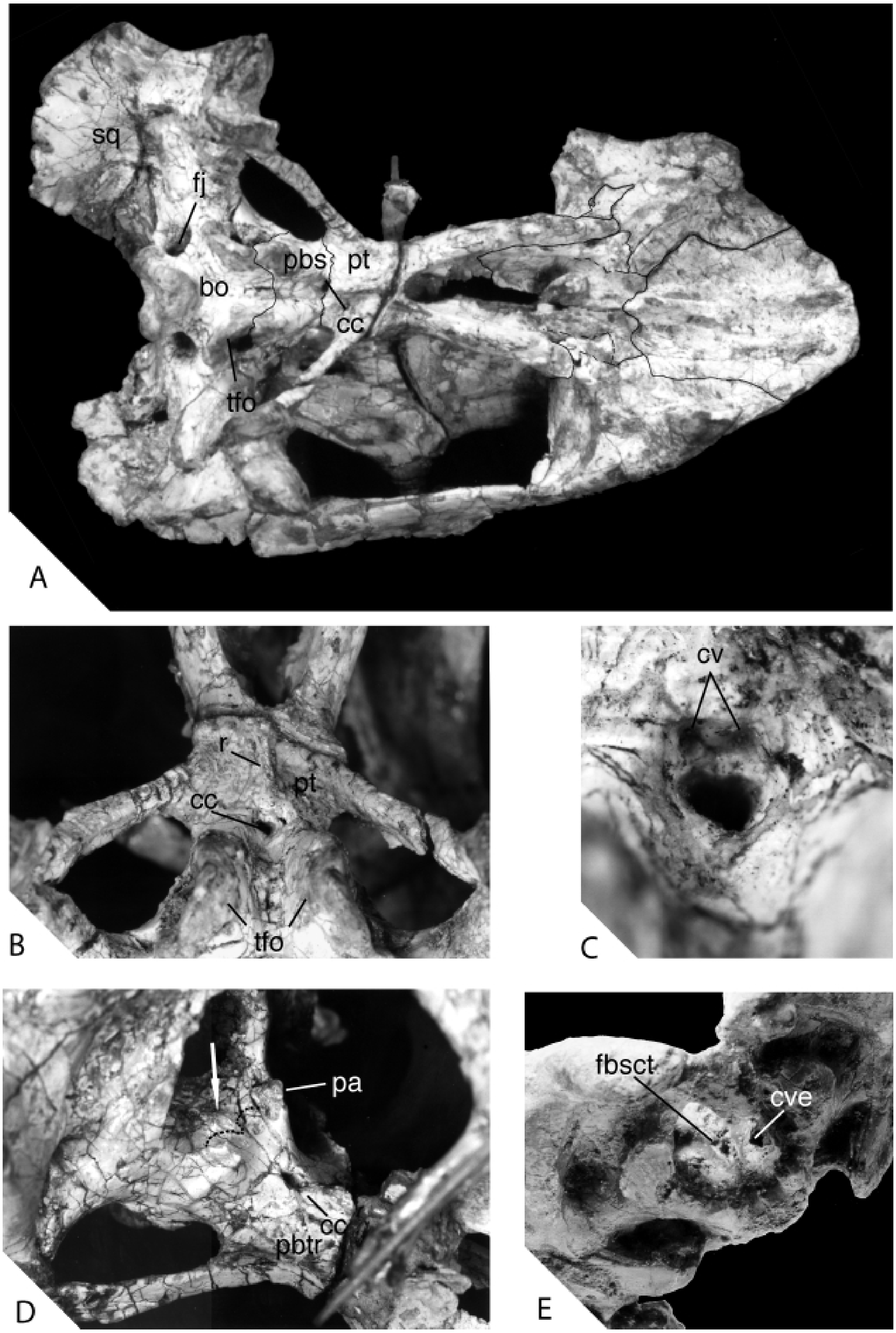
TEXT-FIG. 2. Basipterygoid articulation and braincase of *Diictodon testudirostris*, BNMH 11184 and *Diictodon solassi*, CAMZM T546. A, skull in ventral view (BNMH 11184); ×1·2. B, posteroventral view of the basipterygoid articulation (BNMH 11184); ×3·5. C, entrances of canalis vidii from the same direction (BNMH 11184); ×8. D, laterodorsal view of the braincase and sella turcica (BNMH 11184); ×3. E, anterodorsal view of the braincase (CAMZM T546); ×1. Arrow indicates entrance of canalis vidii (B) and longitudinal ridge (D–E) on the braincase floor. Abbreviations in Appendix.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D. solassi (CAMZM T546) revealed no differences in the construction of the braincase of these two species, but the braincase of *Diictodon* differs from other Late Permian forms.

Parabasisphenoid. This element is short and massive. Even though most of the presphenoid is broken, the presphenoid and parabasisphenoid clearly formed a long, narrow, plate-like process which ascended above the interpterygoid vacuity. The transverse contact with the periotic is clearly seen only from the ventral side where the parabasisphenoid forms the anterior surface of the tuber fenestra ovalis (tfo, Text-fig. 2A). Anteriorly the pterygoids are fused in a wide flat plate along a barely noticeable median ridge (r, Text-fig. 2B).

The carotid arteries enter the parabasisphenoid at the contact with the pterygoids through a single canal and exit in the anterior part of the sella turcica as in *Kingoria* (Text-fig. 2A–B). Even though a single entrance for the carotid canals has not previously been mentioned for dicynodonts, the *Diictodon* material in the South African Museum (SAM-PK-010086; SAM-PK-K08585) reveals that this is normal for this genus. The palatal branches for nerve VII enter the anterior wall of the carotid foramen (cv, Text-fig. 2C) and follow the same route as in *Kingoria*. The processus basitrabecularis widely overlaps the dorsal side of the pterygoid and completely fuses with the medial edge of the epipterygoid base, terminating behind the interpterygoid vacuity.

Strong fusion of braincase elements makes it difficult to trace the posterior edge of the parabasisphenoid exactly from the dorsal side. This contact was outlined tentatively in BMNH R11184 (dashed line, Text-fig. 2D). Unlike *Kingoria*, the parabasisphenoid of *Diictodon* does not expand so far posteriorly and terminates at the level of the periotic notch for the trigeminal nerve. The position of the dorsum sellae is hard to establish, but it is probably located at the posterior boundary of the parabasisphenoid and the anterior termination of the narrow but very pronounced longitudinal ridge (2 mm high in CAMZM T546) situated between the pilae antoticae (arrow, Text-fig. 2D–E). The appearance of such a structure on the braincase floor of the toothless *Diictodon* is rather peculiar, because it has been noticed only in the most basal dicynodonts, *Eodicynodon* (SAM-PK-K10019) and *Kingoria*, where a similar ridge complicates the posterior termination of the dorsum sellae. Homology of this ridge with well-known braincase structures is not possible because of its longitudinal orientation and strictly midline position.

Periotic. As in *Kingoria*, the periotic forms the lateral walls and most of the floor of the ossified braincase. The only feature that should be mentioned is the unusually posterior position of the fenestra basicranialis (fbscr, Text-fig. 2E), which is situated far behind the pila antotica and dorsum sellae, exactly between the openings in the vestibular cavities.

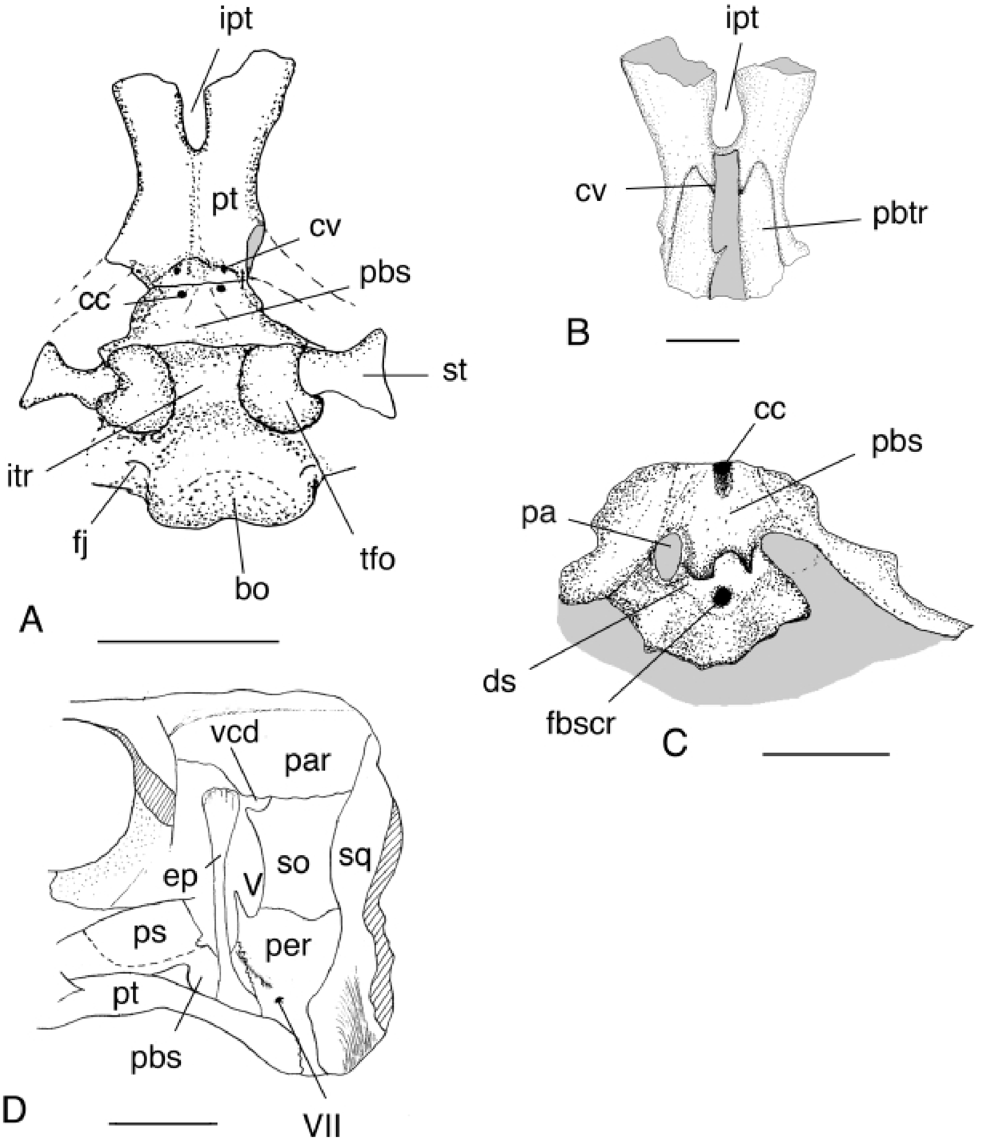
Basioccipital, exoccipital, supraoccipital. These elements are as in *Kingoria*. Anterolaterally, the supraoccipital is overlapped by the parietals, but it separates the periotic from the parietals on the lateral side of the braincase.

Epipterygoid. Only basal parts of the epipterygoid remain. The base widely overlaps the medial part of the pterygoid and is fused with the lateral edge of the processus basitrabecularis (pbtr, Text-fig. 2D). Despite the absence of most of the epipterygoids, their remains suggest they were rod-like as in *Kingoria* and ran to the anteroventral edge of the parietals.

Braincase and basipterygoid articulation of Dicynodon

Even though the genus *Dicynodon* has been known for over 150 years (Owen 1845), only a general description of its braincase has been given (King 1981) and only a few features of this region were mentioned in relation to its taxonomic position (Cluver and King 1983; King 1988). Investigation of the available *Dicynodon* material in the collections of the BMNH, CAMZM, PIN, and UT revealed a similar construction in this region, but one that is different from that of *Diictodon* and *Kingoria*. Since these features are equally well represented in all specimens, remains of *Dicynodon* sp. (PIN 4415/1) and *Dicynodon leoniceps* (CAMZM T979, T1089) were used as a basis for the description.

Parabasisphenoid. The shape and contacts of the parabasisphenoid are as in *Kingoria* and *Diictodon*, but the ventral surface (Text-fig. 3A) shows no distinctive ridges. The carotid arteries (cc, Text-fig. 3A, C) and the palatal branches of the facial nerve (cv, Text-fig. 3A–B) pursue the same routes as in other dicynodonts. The processus basitrabecularis (pbtr, Text-fig. 3B) is wide, nearly completely overlapping the pterygoid and contacting the base of the epipterygoid posterolaterally. The sella turcica is wide and contacts the periotic at the level of the pila antotica. The dorsum sellae, unlike that of *Kingoria*, does not extend further posteriorly than the level of the notch for the trigeminal nerve, forming a Y-like shape by a raised contact of the parabasisphenoid and periotic (ds, Text-fig. 3C). It is a low, transverse ridge on



TEXT-FIG. 3. Elements of braincase and basipterygoid articulation of *Dicynodon leoniceps*, CAMZM T979 and *Dicynodon* sp., PIN 4415/1. A, basicranium in ventral view (CAMZM T979). B, anterior portion of the basipterygoid articulation in dorsal view (CAMZM T979). C, dorsal view of the sella turcica (CAMZM T979). D, braincase in lateral view (PIN 4415/1). Scale bars represent 40 mm (A, D) and 20 mm (B–C). Abbreviations in Appendix.

the braincase floor, which in large forms (e.g. *D. leoniceps*, CAMZM 1089) can be rather pronounced. A remnant of the fenestra basicranialis (fbscr, Text-fig. 3C) is represented as a small round foramen at the contact of parabasisphenoid and periotic just behind the dorsum sellae.

Periotic. The exit of the trigeminal nerve and vena capitis lateralis is clear in a lateral view of the periotic (per, V, Text-fig. 3D), but the suture with the basioccipital is concealed by fusion. The passage of the facial nerve (VII, Text-fig. 3D) is as in other dicynodonts. Vestibular cavities open in the middle of the periotic in the ventromedial part of the braincase wall. No distinctive features have been noticed in the construction of the inner ear of *Dicynodon*. None of the *Dicynodon* specimens reveals the existence of the subarcuate fossa in the medial wall of the braincase. As in *Kingoria* and other dicynodonts, the posterior boundary of the periotic contacts the exoccipital and forms the anterior edge of the foramen jugularis (fj, Text-fig. 3A), and the lateral portions form strong, dorsoventrally widened paroccipital processes.

Basioccipital, exoccipital, supraoccipital. These bones are as in *Kingoria* and *Diictodon*. Between the tubera fenestrae ovales the basioccipital forms a prominent transverse ridge (itr, Text-fig. 3A). Cluver (1971) thought this ridge was the attachment of the m. rectus capitis ventralis, while Cluver and King (1983) and King (1988) treated it as a feature of derived Late Permian pristerodontids. The exoccipitals are fused without sutures with the surrounding bones.

Epipterygoid. As in *Kingoria*, the epipterygoid is a thin rod-like bone, which rises from the posterior ramus of the pterygoids to the parietals. In some forms of *Dicynodon* [*D. trautscholdi* (= *D. amalitskii*) Sushkin 1926; *Dicynodon* sp., PIN 4415/1], the connection between the epipterygoid and parietal (ep, par, Text-fig. 3D) can remain cartilaginous.

Braincase and basipterygoid articulation of Lystrosaurus

Lystrosaurus is known from numerous specimens from the Lower Triassic of South Africa, Antarctica, India, China, Mongolia, and Russia. Its cranial morphology was investigated in detail by Cluver (1971), who also described the *Lystrosaurus* braincase and compared it with the available data on *Dicynodon*. Additional investigation of *Lystrosaurus* cranial remains (CAMZM T758, CAMZM T788) revealed some additional information. Since most features of the *Lystrosaurus* braincase were described by Cluver (1971), the description here is brief, with a focus on distinguishing characteristics.

Parabasisphenoid. The parabasisphenoid is very short and massive, and in ventral view is similar to that of *Dicynodon*. The carotid canals and the canalis vidii (cc, cv, Text-fig. 4A–D) follow the same routes as in *Dicynodon*, but the canalis vidii enters the basicranium slightly more laterally from the carotid canal. The processus basitrabecularis (pbtr, Text-fig. 4A, C) is short and wide, and almost completely overlaps the dorsal surface of the pterygoid. There is a deep, wide, rectangular depression at the parabasisphenoid/ periotic contact in CAMZM T758 (d, Text-fig. 4A). A similar depression in *L. declivis* (SAM K1284) was reasonably identified by Cluver (1971) as remains of the fenestra basicranialis, and its shape is a characteristic feature of *Lystrosaurus*. The whole appearance of this depression suggests that it was undoubtedly filled with a soft body, and this inspired Cluver (1971) to suggest the hypophysis. The true nature of this supposed filling became clear after investigation of the longitudinally sectioned specimen of *L. curvatus* (CAMZM T788) whose fenestra basicranialis contains an independently ossified element (arrow in Text-fig. 4D). This ossification forms a high dorsum sellae, up to the tip of the pila antotica. In smaller forms of *Lystrosaurus* (e.g. *L. declivis* and *Lystrosaurus* sp., CAMZM T758) this structure remained cartilaginous, so explaining the depression in the bone. The fact that the dorsum sellae is an independent element in the *Lystrosaurus* braincase probably reflects its separate development during ontogeny. Formation of the dorsum sellae as a separately chondrified element has been mentioned by de Beer (1937, p. 383) for some Recent mammals (*Lepus*, *Felis*, *Macaca, Semnopithecus*, *Homo*) where it relates to specialized development of the hypophysial cartilage. In other dicynodonts, features reflecting development of the dorsum sellae are obscured by strong ossification of the braincase elements. For the moment, an independently ossified dorsum sellae may be considered an autapomorphy of *Lystrosaurus*.

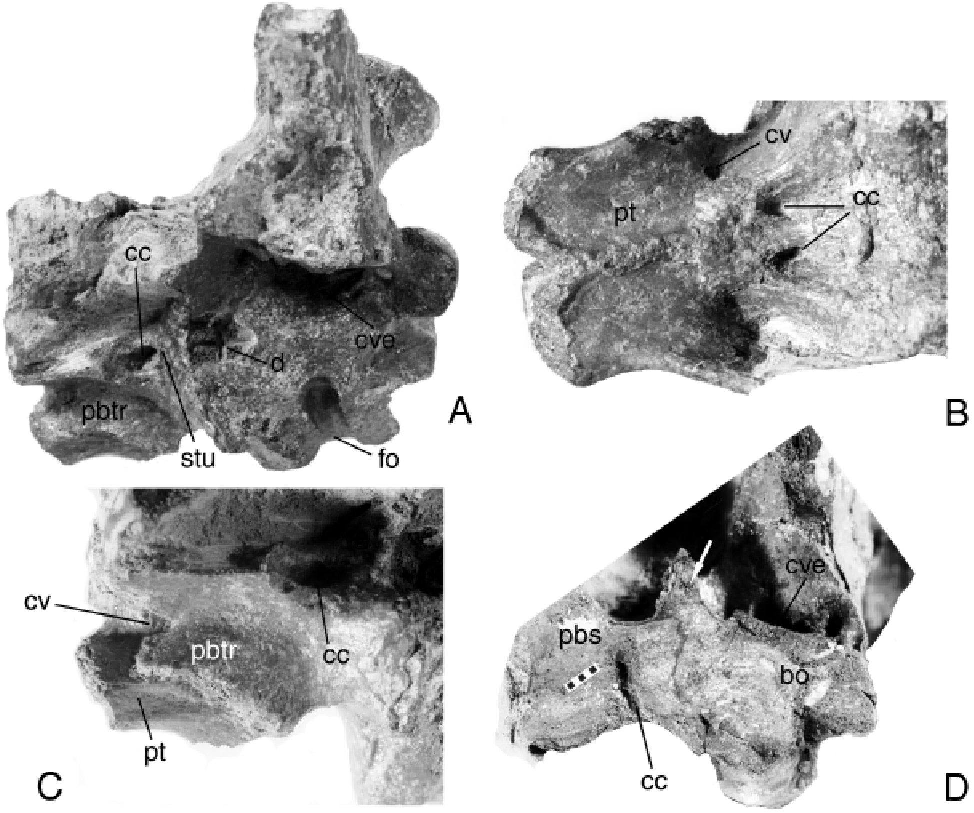
Periotic. The periotic of *Lystrosaurus* (Text-figs 4, 5A) is very like that of *Dicynodon*. The only difference is the greatly widened paroccipital process which forms the medial boundary of the posttemporal fenestra, completely excluding participation of the supraoccipital.

Basioccipital, exoccipital, supraoccipital. These elements (bo, ex, so, Text-figs 4D, 5A) are as in other dicynodonts. The basioccipital has a smooth, slightly convex surface in the midline of the braincase floor, and it forms the posteromedial walls of the tubera fenestrae ovales with a very pronounced intertuberal ridge.

Epipterygoid. The epipterygoid is similar to that of other dicynodonts except that its base in *Lystrosaurus* is placed more anteriorly, on the medial part of the pterygoids.

Braincase and basipterygoid articulation of Rechnisaurus *and other Middle and Late Triassic forms*

Data on the braincase of Middle and Late Triassic dicynodonts have only rarely appeared in the literature (Camp and Welles 1956; Cox 1991) and there has been no detailed comparison of the braincase structure

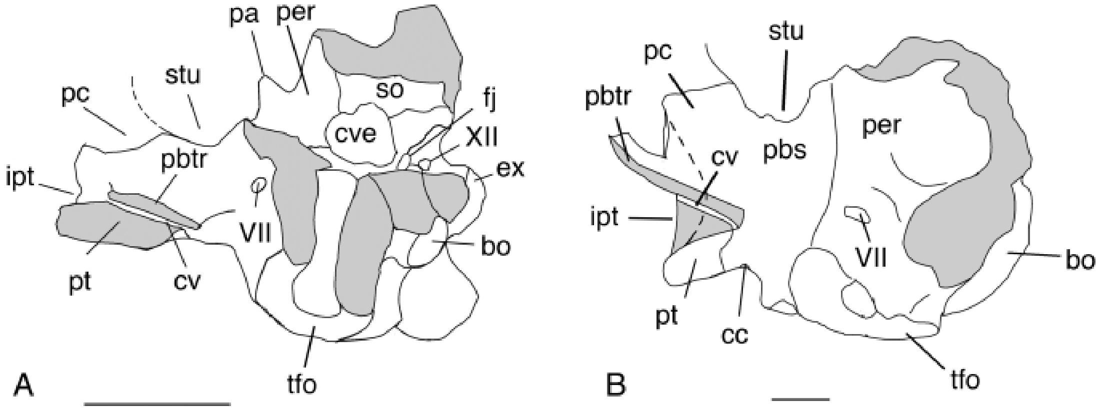


TEXT-FIG. 4. Braincase and basipterygoid articulation of *Lystrosaurus curvatus*, CAMZM T788 and *Lystrosaurus* sp., CAMZM T758. A, basicranium in dorsal view (CAMZM T758); ×1·3. B–C, parabasisphenoid and basipterygoid articulation in ventral (B) and dorsal (C) views (CAMZM T758); ×1·7. D, longitudinal section of the dorsum sellae (CAMZM T788). Arrow indicates entrances and exits of the canalis vidii (B–C) and independently ossified element of the dorsum sellae (D); scale bar represents 5 mm. Abbreviations in Appendix.

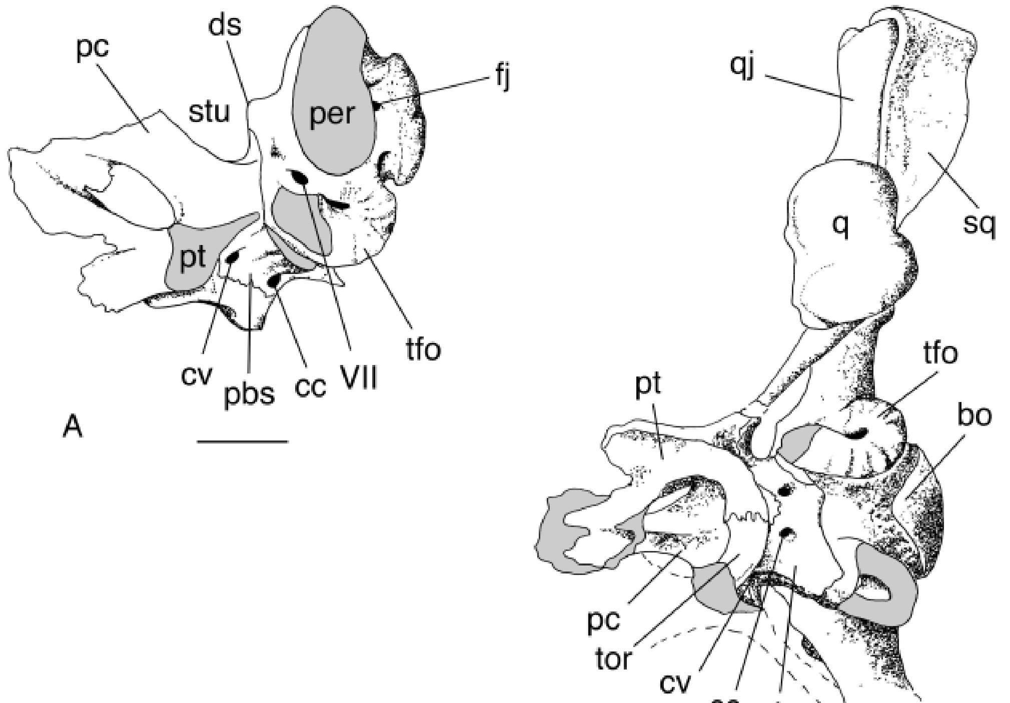
and basipterygoid articulation of different forms. The only feature that has been mentioned as distinctive was progressive ossification of the lateral wall (Keyser, 1974). Our investigation of this region in Middle Triassic dicynodonts covered all available material of well-known taxa such as *Tetragonias* (CAMZM T 750-T756, T1140; UT 292), *Angonisaurus* (BMNH R9732), *Rechnisaurus* (BMNH R11955), *Kannemeyeria* (BNMH R3059–3739), *Rhadiodromus* (PIN 1579/14), *Stahleckeria* (UT n1, n2, n3), and *Shansiodon* (BMNH R12710), and numerous braincase fragments from the BMNH, CAMZM, and SGU. This investigation revealed some distinctive features of the basicranium of Triassic forms which can be illustrated well in the *Rechnisaurus* specimen.

Parabasisphenoid. The parabasisphenoid (pbs, Text-fig. 6A–B) is short and massive. The contact with the periotic is straight, and both elements form a high dorsum sellae (ds, Text-fig. 6B). Nothing can be said about the fenestra basicranialis in the *Rechnisaurus* braincase, because part of the dorsum sellae and brain cavity behind it are filled with matrix. Investigation of other specimens revealed its position at the contact between the parabasisphenoid and periotic in all Middle Triassic forms. Because of the high dorsum sellae and the very steep processus cultriformis, the sella turcica (stu, Text-figs 5B, 6A) looks unusually deep. The processus cultriformis (pc, Text-fig. 6B) is wide ventrally and narrows anteriorly, completely covering the posterior third of the interpterygoid vacuity.

The processus basitrabecularis, the carotid canals, and the canalis vidii (cc, cv, Text-figs 5B, 6A–B) show the normal relationships. In ventral view, the interpterygoid vacuity is surrounded by a high and massive torus along the posterolateral edge (tor, Text-fig. 6B).



TEXT-FIG. 5. Longitudinal section along canalis vidii in Early and Middle Triassic dicynodonts. A, *Lystrosaurus* sp. (CAMZM T758). B, *Rechnisaurus cristarhynchus* (BMNH R11955). Scale bars represent 40 mm. Abbreviations in Appendix.



TEXT-FIG. 6. Braincase and basipterygoid articulation of *Rechnisaurus cristarhynchus*, BMNH R11955 (after Cox 1991). A, lateral view. B, ventral view. Scale bar represents 40 mm. Abbreviations in Appendix.

Periotic. As in most derived dicynodonts no sutures can be traced in the periotic of *Rechnisaurus*. No traces of the pronounced pila antotica have been noticed on the anterior edge of the periotic, and the trigeminal nerve leaves the braincase through the shallow notch just above the dorsum sellae (ds, Text-fig. 6A). The exit for the facial nerve is in the same position as in Permian forms, on the lateroventral side of the periotic (VII, Text-figs 5B, 6A).

Exoccipital and basioccipital. These bones are fused with the periotic without sutures, forming an undivided occipital condyle. The ventral part of the basioccipital, together with the periotic, forms pronounced and massive tubera fenestrae ovales (tfo, Text-figs 5B, 6B), but no intertuberal ridge was noticed between them. The exit for the foramen jugularis (fj, Text-fig. 6A) is, as in the Permian forms, lateral to the occipital condyle at its base.

Other features of the braincase of Triassic forms

The basicranium of *Rechnisaurus* (BMNH R11955) is incomplete, and some additional notes based on other taxa must be added.

The parietals of most Middle Triassic forms broadly overlap the supraoccipital anteriorly and form a contact with the periotic, displacing the lateral exposure of the supraoccipital posteriorly. This feature was mentioned by Keyser (1974) as progressive ossification of the braincase among Middle–Late Triassic forms. Investigation of the dicynodont material revealed this condition among all such taxa except *Stahleckeria*.

The vestibular cavity in all large Middle Triassic dicynodonts opens dorsally in the ventrolateral recess of the braincase floor. Although we found no distinctive features in the construction of the inner ear, it is worth noting that, because of the deep position of the vestibular cavity, the perilymphatic canal is represented, not as a notch on the posterior edge of the latter, but as a thin channel which is confluent with the foramen jugularis through the periotic (see also Camp and Welles 1956; Kalandadze 1974). Note that Camp and Welles (1956) erronously considered the perilymphatic canal as the canal for nerve VIII (Kalandadze 1974).

PHYLOGENETIC IMPLICATIONS

Taxa and characters

The descriptions have given an indication of several braincase characters that might be used in the study of dicynodont phylogeny. We investigated the phylogenetic use of braincase morphology by constructing a data matrix of phylogenetic characters for the main basal toothed (*Eodicynodon*, *Pristerodon*, *Robertia*) and derived dicynodont taxa from the Permian (*Aulacocephalodon, Dicynodon*, *Diictodon*, *Kingoria nowacki*) as well as most Triassic genera (*Angonisaurus*, *Kannemeyeria simocephalus, Lystrosaurus*, *Placerias*, *Rechnisaurus*, *Rhadiodromus*, *Sangusaurus*, *Shansiodon*, *Stahleckeria*, *Tetragonias*, *Uralokannemeyeria*) for which braincase material is adequately known. *Eodicynodon* was treated as a representative of the most basal dicynodonts, following King (1988) and Angielczyk (2001), and considered in the analysis as the outgroup. We distinguished 19 characters which are believed to be taxonomically significant. Two of these were excluded as phylogenetically uninformative in the context of this analysis.

Basicranial characters included in the analysis

1. Confluent ridges running anteriorly from the tuber fenestra ovalis along the ventral side of the parabasisphenoid (present = 0, absent = 1). These ridges have been observed in all basal toothed dicynodonts, *Eodicynodon*, *Pristerodon*, *Robertia*, as well as in *Kingoria.* The plesiomorphic condition was probably inherited from basal dicynodonts, since similar ridges were described in *Suminia* (Rybczynski 2000).
2. Posterior expansion and overlapping of the interpterygoid vacuity by the parabasisphenoid rostrum (absent = 0, present = 1). All Permian forms have a narrow parabasisphenoid rostrum, which divides the interpterygoid vacuity along its midline. Tatarinov (1966) described a widened parabasisphenoid rostrum in the kannemeyerioid PIN 952/6, which overlaps the posterior third of the interpterygoid vacuity. Personal observation revealed posterior expansion of the parabasisphenoid rostrum in *Kannemeyeria* (BNMH R3059, 3739), *Sangusaurus* (CAMZM T1340, T1226) and *Rechnisaurus* (BMNH R11955; see also Cox 1991). This feature has also been illustrated in *Placerias* (Camp and Welles 1956).
3. Width of the processus cultriformis (narrow = 0, wide = 1). The processus cultriformis is usually narrow or rapidly narrowed anteriorly in dicynodonts, dividing the interpterygoid vacuity longitudinally in ventral view. *Tetragonias* (UT 292, CAMZM T754) and *Angonisaurus* (BMNH R9732) have a wide processus cultriformis that nearly overlaps the interpterygoid vacuity along its length, leaving only a narrow lanceolate foramen on each side.

4. Relative position of the canalis vidii to the carotid canals (enters anterior wall of carotid canals = 0, enters separately from carotid canals = 1). In all observed basal toothed dicynodonts *Eodicynodon, Pristerodon, Robertia*, as well as in *Kingoria* (CAMZM T748) and *Diictodon* (BMNH 11184; SAM-PK-010086; SAM-PK-K08585) the palatal branch of cranial nerve VII splits off at the beginning of the carotid canals, and the canalis vidii enter on the anterior wall of the carotid canals. Separate exits for palatal branches of the VII nerve at the pterygoido-parabasisphenoidal connection are seen in the Late Permian dicynodonts *Aulacocephalodon* (SAM-PK-K06064), *Dicynodon* (CAMZM T979, T982, 1089; PIN 4415/1; SAM-PK-K07482) and Middle–Late Triassic dicynodonts. The only exception is a specimen of *Dicynodon* sp. (SAM-PK-K07011) with the vidian canals entering in the walls of the carotids. Even though this might be considered as an aberrant occurrence, we used a multistate coding of this character for *Dicynodon* which was treated as uncertain during the cladistic analysis.

5. Relative position of the carotid canals on the ventral side of the parabasisphenoid (canals situated far separately = 0, placed close beside each other and entering parabasisphenoid as a single double channelled tube = 1). Separate entrances for the carotid canals have been observed in *Eodicynodon*, *Robertia*, *Kingoria*, *Aulacocephalodon*, *Dicynodon* and all Triassic forms. Closely placed entrances for the carotid canals were seen in *Diictodon* and the toothed dicynodonts *Pristerodon* and *Emydops*, but the latter was not included in the analysis because of insufficient basicranial data. The stable appearance of this feature among investigated specimens as well as its clear polarity suggest that the presence of closely placed carotid canals is a synapomorphy for some Permian forms.

6. Exit of carotid canals in the sella turcica (as a single foramen = 0, as paired foramina = 1). In all Late Permian dicynodonts investigated, the carotid canals exit through a single foramen in the sella turcica. Paired exits for the carotid canals are known only in Middle–Late Triassic forms such as *Angonisaurus* (BMNH R9732), *Placerias* (Camp and Welles 1956), *Rhadiodromus* (PIN 1579/14), *Shansiodon* (BMNH R12710), *Stahleckeria* (UT n1–3), and *Uralokannemeyeria* (SGU D-104/1).

7. Anterior termination of the processus basitrabecularis and exit of the canalis vidii (behind the interpterygoid vacuity = 0, processus basitrabecularis takes part in the posterior edge of the interpterygoid vacuity and vidian canal enters it = 1). The termination of the processus basitrabecularis at the posterior edge of the interpterygoid vacuity and the exit there of the vidian canal was first mentioned for an indeterminate kannemeyeriid (PIN 952/6) by Tatarinov (1966) and illustrated for *Placerias* (Camp and Welles (1956). Our investigation revealed that this feature is common among Middle and Late Triassic forms, and hence is a synapomorphy.

8. Height of the dorsum sellae (low and not expressed in the relief of the braincase floor = 0, moderate dorsum sellae, which is clearly distinct, but does not reach the height of the pila antotica = 1, and high dorsum sellae, which is equal in height to the pila antotica or is about one-third of the height of the cavum epiptericum = 2). In most Late Permian dicynodonts the dorsum sellae is represented as a low ridge on the braincase floor. A high dorsum sellae has been observed in *Placerias* (Camp and Welles 1956), *Sangusaurus* (CAMZM T1340, T1226), *Stahleckeria* (UT n1–3) and *Rechnisaurus* (BMNH R11955). Development of the raised dorsum sellae undoubtedly corresponds with an increase in size of the hypophysis.

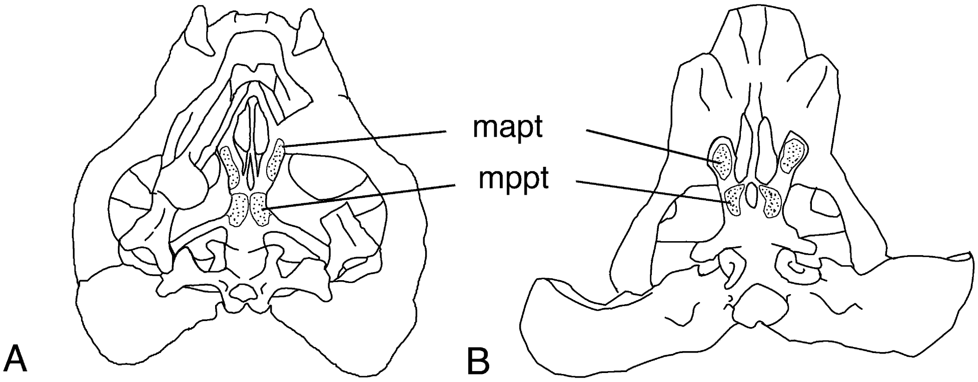
9. Shape of the dorsum sellae (Y-shaped dorsum sellae with posterior termination behind pila antotica = 0, dorsum sellae as a transverse ridge at the level of the pila antotica = 1). A Y-shaped dorsum sellae represented as confluent posteromedial ridges is seen in *Eodicynodon* and *Kingoria*. In all Triassic forms and the investigated Late Permian ones, the dorsum sellae is a transverse ridge at the level of the trigeminal notch behind the pila antotica. A Y-shaped dorsum sellae in *Eodicynodon* suggests that the similar appearance of this feature in *Kingoria* is plesiomorphic.

10. Longitudinal ridge on the braincase floor (absent = 0, present = 1). A midline longitudinal ridge or ridge-like structure was noticed in *Eodicynodon*, *Kingoria*, and *Diictodon*. Even though the functional significance of this ridge is problematic, this does not prevent us from using it for phylogenetic analysis.

11. Position of the fenestra basicranialis (behind the level of the pila antotica and trigeminal notch = 0, at the level of the pila antotica = 1). A posterior position of the fenestra basicranialis was observed in *Diictodon, Eodicynodon*, *Kingoria* and *Robertia*, while in all derived Permian (*Aulacocephalodon*, *Dicynodon*) and all Triassic dicynodonts the fenestra basicranialis is situated at the level of the pila antotica. Therefore we consider the anterior position of the fenestra basicranialis as a synapomorphy for dicynodonts.

12. Development of the pila antotica as a rod-like process on the anterior edge of the periotic and a corresponding notch for the trigeminal nerve behind it (pila antotica with deep trigeminal notch behind it = 0, pronounced pila antotica absent, trigeminal notch is a horizontal hollow in the anterior edge of the periotic = 1). Reduction of the pila antotica relates to progressive ossification of the lateral wall of the braincase and development of the dorsum sellae. A well-developed pila antotica is known in all Late Permian forms and was observed also in *Lystrosaurus*, *Tetragonias*, *Angonisaurus* and *Rhinodicynodon*.

13. Floccular fossa (present = 0, absent = 1). A floccular fossa has been observed in all basal toothed dicynodonts and the toothless *Kingoria* and *Diictodon.* In the derived Late Permian *Aulacocephalodon* and *Dicynodon*, and in all Triassic forms, the floccular fossa is absent. Olson (1944) believed that the pronounced development of the floccular



TEXT-FIG. 7. Reconstruction of attachments for m. pterygoidei in the Late Permian and Middle Triassic dicynodonts. A, *Dicynodon trigonocephalus* (after King 1981). B, *Stahleckeria potens* UT n2. Not to scale. Abbreviations in Appendix.

fossa was a derived feature in therapsids, which related to enlargement of the flocculi of the cerebellum. Successive reduction of this structure in the dicynodont braincase might relate to increasing volume of the ossified braincase or relative repositioning of the flocculi themselves. Even though reasons for the reduction of the floccular fossa in dicynodonts should be more closely investigated, this feature is well polarised and obviously can be used for phylogenetic analysis.

14. Ridge between the tubera fenestrae ovales (absent = 0, present = 1). Cluver and King (1983) and King (1988) argued that this ridge is a feature of derived Late Permian pristerodontids, which includes the derived Late Permian forms (e.g. *Aulacocephalodon*, *Dicynodon*) and the clade of Triassic forms. However, this ridge is absent in *Kannemeyeria simocephalus* (BNMH R3059, 3739) and *Rechnisaurus* (BMNH R11955).

15. Connection between periotic and parietal (absent = 0, present = 1). A connection between the periotic and parietal is absent in all Permian forms, but present in all Middle–Late Triassic forms except *Stahleckeria*, where the supraoccipital still forms a substantial part of the lateral wall of the ossified braincase and participates in its anterior edge. This feature relates to downgrowth of the parietal which overlaps the supraoccipital and forms a substantial contact with the periotic. Since this is characteristic of most Middle–Late Triassic forms, we consider downgrowth of the parietal as a synapomorphy.

16. Ventral longitudinal midline ridge along the junction of the pterygoids (present = 0, absent = 1). A median ridge along the ventral exposure of the pterygoids was considered by Cluver and King (1983), and King (1988) as a taxonomically significant feature for such basal Permian dicynodonts as *Robertia* and *Pristerodon*. Study of the Permian material revealed this ridge in all investigated Late Permian forms except *Dicynodon.* In all Triassic forms, the pterygoids are flat or even sometimes concave along the midline. Hence this ridge is absent in all derived dicynodonts, and its appearance is plesiomorphic.

17. Swollen edges of the interpterygoid vacuity or presence of the torus around it (edges of the interpterygoid vacuity unpronounced = 0, posterior edge of the interpterygoid vacuity swollen or formed into a prominent torus = 1, anterior and lateral edges of the interpterygoid vacuity swollen or edged by torus = 2). Late Permian and Early Triassic forms show no pronounced edges around the interpterygoid vacuity. Thickened edges of the interpterygoid vacuity appear only in the Middle–Late Triassic *Angonisaurus* (Cox and Li 1983), *Placerias* (Camp and Welles 1956), *Rechnisaurus* (Cox 1991), *Rhadiodromus*, *Sangusaurus*, and *Stahleckeria*. This feature most probably relates to shortening of the basicranial axis or posterior displacement of the interpterygoid vacuity. In both cases, the interpterygoid vacuity became surrounded by the m. pterygoidei posterior which was the cause of the thickening of its edges. This situation is seen very clearly in *Stahleckeria* (UT n2), where attachments of the m. pterygoidei are distinguishable as swollen and rugose areas on the ventral side of the pterygoids and the position of the attachments for these muscles may readily be reconstructed (mapt, mppt, Text-fig. 7).

Uninformative characters. The following two characters are phylogenetically uninformative, since they are present in only one taxon in the present analysis.

18. The position of the epipterygoid base between the pterygoid rami or on the posterior ramus of the pterygoid. A medial position of the epipterygoid base was seen only in *Lystrosaurus* and is probably an autapomorphy.

19. Independent ossification of the dorsum sellae. As mentioned above, this feature is present only in the genus *Lystrosaurus* and is currently considered autapomorphic.

Phylogenetic analysis

Analysis. A data matrix for the 19 taxa and 17 characters discussed above is shown in Table 1. *Eodicynodon* is treated as the outgroup. The permutation probability (PTP) test (Faith and Cranston 1991) was applied using PAUP (version 4.08, Swofford 1998) on a Macintosh iMac computer. Characters were equally weighted and 1000 random data sets were generated. The result was PTP = 0·01, whether or not *Eodicynodon* was included, indicating that the data set contains hierarchical structure.

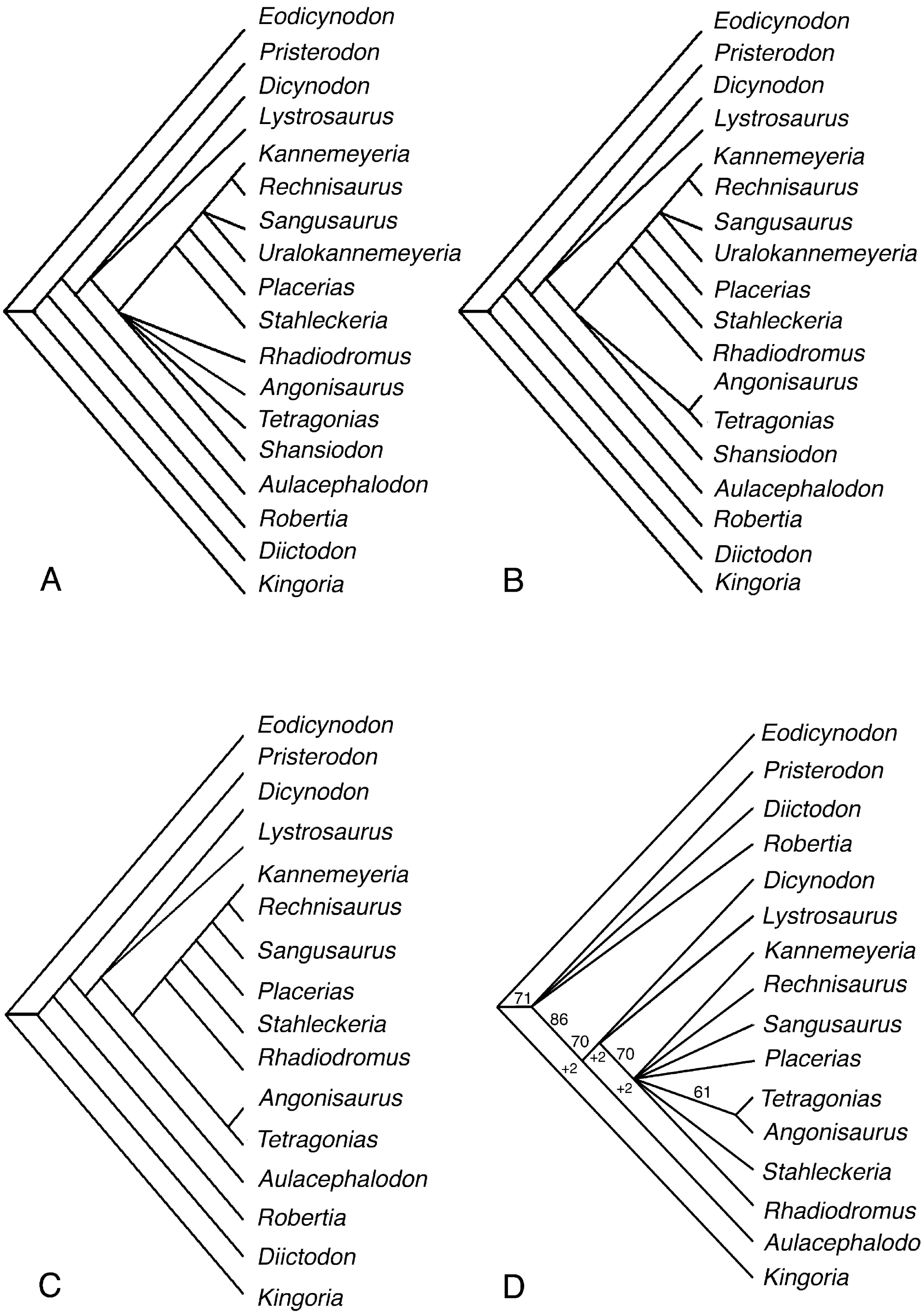
Parsimony analysis of the data set was also carried out using PAUP (branch and bound search, characters equally weighted and unordered, trees rooted with the outgroup *Eodicynodon*). The search yielded 12 equally most parsimonious trees (MPTs), with length (L) = 30; consistency index (CI) = 0·633; retention index (RI) = 0·831. Strict and Adams consensus trees were computed (Text-fig. 8A–B). *Eodicynodon* aside, seven clades were revealed: *Pristerodon*, *Robertia*, *Aulacocephalodon*, *Kingoria*, *Diictodon*, *Dicynodon* + *Lystrosaurus*, and a clade of Triassic taxa. The latter contains two groups which were not resolved in the consensus trees: *Sangusaurus* + *Uralokannemeyeria* and *Rhadiodromus* + *Shansiodon* + *Tetragonias* + *Angonisaurus*.

This lack of resolution is predictable from examination of the data matrix (Table 1) because the genus *Uralokannemeyeria* shares the same features as *Sangusaurus* with the exception of missing values. A similar situation can be observed for *Shansiodon*. According to Wilkinson's (1995) strategy of safe taxonomic reduction, *Uralokannemeyeria* and *Shansiodon* may be removed from the analysis without affecting the result. Branch and bound analysis of the reduced data matrix yielded a single MPT (L = 30; CI = 0·633; RI = 0·814; Text-fig. 8C). The PTP test of the data set (Table 1) without *Uralokannemeyeria* and *Shansiodon* yielded a value 0·01, for all and for in-group taxa (based on 1000 random permutations). Therefore, *Eodicynodon* aside, there are seven clades in the tree: *Aulacocephalodon*, *Diictodon*, *Kingoria*, *Pristerodon*, *Dicynodon* + *Lystrosaurus*, *Robertia* and the clade of Middle–Late Triassic forms. The latter is subdivided into two clades, *Angonisaurus* + *Tetragonias* and the group of kannemeyerioid dicynodonts. Heuristic bootstrapping (1000 replicates) and estimation of decay indices showed moderate to strong support for the clades *Pristerodon* + *Robertia* + *Diictodon*, *Kingoria*, *Dicynodon* + *Lystrosaurus*, and all Middle–Late Triassic forms including a separate clade of *Angonisaurus* + *Tetragonias* (Text-fig. 8D).

We investigated the role of *Eodicynodon* in the analysis. On removal of *Eodicynodon* from the matrix, character 9 became uninformative and was removed. Branch and bound analysis yielded a single MPT (L = 29, CI = 0·621, RI = 0·784). Lundberg rooting of this network with the character states of *Eodicynodon* treated as the ancestral condition produced the same in-group relationships as observed in Text-figure 8C. Therefore, inclusion of *Eodicynodon* does not perturb ingroup relationships.

Comparison and phylogenetic value of basicranial characters. Our hypothesis of relationships among dicynodonts based on the basicranial data generally agrees with previous hypotheses of relationships among the Permian (King 1988; Angielczyk 2001) and Triassic (Cox 1965; Keyser and Cruickshank 1979; Cox and Li 1983) forms, but contradicts some previous findings: the inclusion of *Lystrosaurus* in the clade of kannemeyerioid dicynodonts by King (1988) and Angielczyk (2001), the placement of *Kingoria* one step above *Pristerodon* by Angielczyk (2001), and monophyly of *Diictodon* and *Robertia* (King 1988; Angielczyk 2001).

Various topological constraints were employed to investigate the robustness of the relationships represented in Text-figure 8C in comparison with previous phylogenetic hypotheses. The tree with monophyletic *Placerias* + *Kannemeyeria* + *Rhadiodromus* + *Rechnisaurus*, *Stahleckeria*, *Angonisaurus* + *Tetragonias* and with *Sangusaurus* excluded as *incertae sedis* (according to the views of Cox 1965, 1991; Cox and Li 1983) yielded a shorter MPT (L = 29) and CI (0·655), and nearly the same RI (0·811). Discarding monophyly of *Angonisaurus* and *Tetragonias* in the sense of Keyser and Cruickshank (1979), and with all the Middle–Late Triassic dicynodonts considered as a single family Kannemeyeriidae,



TEXT-FIG. 8. Most parsimonious hypotheses of the relationships of selected Late Permian and Triassic dicynodonts (Table 1) based only on data on braincase morphology. A–B, strict (A) and Adams (B) consensus of the 12 most parsimonious trees. C, the most parsimonous tree after safe reduction (deletion of *Shansiodon* and *Uralokannemeyeria*). D, heuristic bootstrap tree (1000 replicates). Bootstrap (only values >50%) and Bremer support (only indices >1) values are shown.

TABLE 1. Braincase character states for selected Late Permian and Triassic dicynodonts. The characters are discussed in the text.

	Characters																
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Eodicynodon	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Emydops	0	0	0	0	1	?	0	?	?	?	?	0	?	0	0	0	0
Robertia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pristerodon	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0
Diictodon	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0
Kingoria	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Dicynodon	1	0	0	1/0	0	0	0	0/1	1	0	1	0	1	1	0	1	0
Aulacocephalodon	1	0	0	1	0	0	0	1	1	0	1	0	1	0	0	0	0
Lystrosaurus	1	0	0	1	0	0	0	2	1	0	1	0	1	1	0	1	0
Kannemeyeria	1	1	0	1	0	0	1	1	1	0	1	1	1	0	1	1	0
Rechnisaurus	1	1	0	1	0	0	1	2	1	0	1	1	?	0	?	1	1
Stahleckeria	1	0	0	1	0	1	1	2	1	0	1	1	1	1	0	1	2
Rhadiodromus	1	0	0	1	0	1	1	0	1	0	1	1	1	1	1	1	1
Angonisaurus	1	0	1	?	0	1	1	0	1	0	1	0	1	1	1	1	2
Shansiodon	1	?	?	?	0	1	?	0	1	0	1	?	1	1	1	1	?
Tetragonias	1	0	1	1	0	?	1	0	1	0	1	0	1	1	1	1	0
Placerias	1	1	?	1	0	1	1	2	1	0	1	1	1	?	?	1	1
Sangusaurus	1	1	0	1	0	0	1	2	1	0	1	1	1	1	?	1	2
Uralokannemeyeria	1	?	?	1	0	0	1	2	1	0	1	1	1	1	1	1	?

yielded a MPT with the same parameters as in Text-figure 8C. Inclusion of *Lystrosaurus* as a monophyletic taxon in the Middle and Late Triassic clade, and excluding *Sangusaurus* and *Rechnisaurus* (*sensu* King 1988; Angielczyk 2001), yielded a slightly shorter MPT ($L = 29$, $CI = 0{\cdot}655$), but with lower RI (0·792). Application of constraints, with branching of *Kingoria* later than *Pristerodon* and a monophyletic *Robertia* + *Diictodon* (*sensu* Angielczyk 2001) yielded a longer MPT ($L = 34$, $CI = 0{\cdot}559$, $RI = 746$), than the monophyly only for *Robertia* + *Diictodon* (King 1988; $L = 31$, $CI = 0{\cdot}613$, $RI = 0{\cdot}797$).

These results are important as an assessment of the value of dicynodont basicranial characters in phylogenetic analysis, especially since they have not been used before. The consideration of topological constraints indicates that the relationships between dicynodonts achieved on braincase characters are not very different from the hypotheses of Keyser and Cruickshank (1979), Cox and Li (1983), King (1988), and Angielczyk (2001), which were based on more superficial skeletal features. Our investigation supports King's (1988) point of view about the lower position of *Kingoria* in the phylogeny of the Permian forms, but inclusion of *Lystrosaurus* in the Triassic clade, as proposed by King (1988) and Angielczyk (2001), is rejected here on the basis of basicranial characters. The latter was also not accepted by either Keyser and Cruickshank (1979) or Cox and Li (1983), and it has been confirmed by research on postcranial features (Surkov 1999) and other data (Maisch 2002).

Consideration of the homoplasy level and fraction of synapomorphic changes in the basicranium revealed that the most informative characters concern the construction of the basipterygoid articulation and inner braincase structures (characters 2–4, 7, 9–13; CI, $RI = 1{\cdot}00$), whereas features which reflect the superficial appearance of the braincase and basipterygoid (characters 5–6, 8, 14–17; CI, $RI \leq 0{\cdot}75$) tend to be less informative. Such a distribution of phylogenetic structure suggests that the main changes in the dicynodont basicranium concerned strengthening of the basipterygoid articulation and inner structures of braincase rather than their superficial appearance. However our data are far from exhaustive and we are reluctant to claim full confidence in this suggestion.

CONCLUSIONS

This first attempt to consider the taxonomic significance of the dicynodont basicranium revealed several phylogenetically significant features which document aspects of dicynodont evolution. Cladistic analysis of these features showed relationships among Permian and Triassic dicynodonts that were generally similar to those achieved before (Keyser and Cruickshank 1979; Cox and Li 1983; King 1988, Angielczyk 2001; Maisch 2002) based mostly on superficial features of the skull. Strong support (decay indices and bootstrap) has been revealed for clades of derived Late Permian dicynodonts (*Aulacocephalodon*, *Dicynodon* + *Lystrosaurus*) and Middle–Late Triassic forms, and this supports the idea (Surkov 1999; Maisch 2002) that *Lystrosaurus* is an offshoot of the Late Permian *Dicynodon*-like dicynodonts rather than a member of the clade of Middle–Late Triassic forms (King 1988, Angielczyk 2001). Application of constraints also confirms King's (1988) idea about the low phylogenetic position of *Kingoria* among Permian forms.

The low homoplasy level of features of the basipterygoid articulation and inner braincase structures compared with superficial characters suggests that the former regions document the pattern of dicynodont evolution better than the latter. However, the large proportion of characters with CI, RI $\leq 0{\cdot}75$ (nine out of 17 characters) suggests that dicynodont basicranial features alone cannot be the panacea for resolving dicynodont systematics without the application of other cranial and postcranial characters. On the other hand, the close similarities in the computed pattern of relationships with previous hypotheses suggests that basicranial characters may significantly support relationships among groups of high taxonomic rank and might be important in revealing the main evolutionary transformations in this group.

Acknowledgements. MVS acknowledges a Royal Society/NATO Postdoctoral Fellowship allowing him to work in Bristol during the year 2001, as well as a Sylvester-Bradley award from the Palaeontological Association and an INTAS fellowship for the year 2002, which supported a visit to the South African Museum. We are grateful to Jenny Clack and Ray Symons, University Museum of Zoology in Cambridge, for the loan of some dicynodont specimens and guidance in the collection, as well as Remmert Schouten and Simon Powell (Bristol University) for preparation and photography. MVS is especially grateful to Sandra Chapman (The Natural History Museum, London) as well as Derek Ohland and Sheena Kaal (South African Museum) for their support and guidance in the museum collections. We also thank the referees and Susan Evans for considerable help in improving the paper.

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Typescript received 4 December 2001
Revised typescript received 17 January 2003

APPENDIX

Specimens of dicynodont skulls studied for the present paper

BMNH R9732: *Angonisaurus cruickshanki*, skull and postcranial remains from the basin of the Rutukira river, Tanzania; Manda Formation, Middle Triassic.

BMNH R11184: *Diictodon testudirostris*, skull from South Africa; *Cistecephalus* Assemblage Zone, Upper Permian.

BMNH R3059, R3739: *Kannemeyeria simocephalus*, skull from South Africa; *Cynognathus* Assemblage Zone, Middle Triassic.

BMNH R12710: *Shansiodon* sp., skull fragments and postcranial remains from Ruhuhu Valley, Songea District; Tanzania; Manda Formation, Middle Triassic.

BMNH R11955: *Rechnisaurus cristarhynchus*, skull fragments from locality 17, Songea District; Tanzania; Manda Formation, Middle Triassic.

CAMZM T546: *Diictodon solassi*, skull fragments and postcranial remains from South Africa, Upper Permian.

CAMZM T758: *Lystrosaurus* sp., skull from Harrismith locality, South Africa; *Lystrosaurus* Assemblage Zone, Lower Triassic.

CAMZM T788: *Lystrosaurus curvatus*, longitudinally sectioned skull from South Africa; *Lystrosaurus* Assemblage Zone, Lower Triassic.

CAMZM 1089: *Dicynodon leoniceps*, skull from Site B19, Ruhuhu Valley, Tanzania; Kawinga Formation, Upper Permian.

CAMZM, T979, T982: *Dicynodon leoniceps*, incomplete skulls from Site B4, Ruhuhu Valley, Tanzania; Kawinga Formation, Upper Permian.

CAMZM T747: *Kingoria nowacki*, skull and postcranial remains from Site B19, Ruhuhu Valley, Tanzania; Kawinga Formation, Upper Permian

CAMZM T748, T792: *Kingoria nowacki*, skull and cranial remains from Site B19, Ruhuhu Valley, Tanzania; Kawinga Formation, Upper Permian.

CAMZM T749: *Kingoria nowacki*, cranial remains from Site B19 (Matamondo), Ruhuhu Valley, Tanzania; Kawinga Formation, Upper Permian.

CAMZM T1340, T1226: *Sangusaurus parringtoni*, cranial remains from Njalila, Tanzania; Manda Formation, Middle Triassic.

CAMZM T750–T756, T1140: *Tetragonias njalilus*, skull and postcranial remains from Njalila, Tanzania; Manda Formation, Middle Triassic.

PIN 4415/1: *Dicynodon* sp., incomplete skull from Kluchovka locality, Orenburg Region, Russia; *Scutosaurus karpinskii* Assemblage Zone, Vyatka Gorizont, Upper Permian.

PIN 1579/14: *Rhadiodromus* sp., skull from Berdyanka-1 locality, Orenburg region, Russia; Donguz Gorizont, Middle Triassic.

SAM-PK-10019: *Eodicynodon oosthuizeni*, skull from Western Cape, South Africa; *Eodicynodon* Assemblage Zone, Upper Permian.

SAM-PK-11879: *Eodicynodon oosthuizeni*, skull from Western Cape, South Africa; *Eodicynodon* Assemblage Zone, Upper Permian.

SAM-PK-17569 (Oosthuizen collection): *Eodicynodon oosthuizeni*, skull from Western Cape, South Africa; *Eodicynodon* Assemblage Zone, Upper Permian.

SAM-PK-17574 (Oosthuizen collection): *Eodicynodon oosthuizeni*, basipterygoid articulation and braincase from Western Cape, South Africa; *Eodicynodon* Assemblage Zone, Upper Permian.

SAM-PK-006560: *Pristerodon* sp., skull from Kuilspoort, Western Cape, South Africa; *Tropidostoma* Assemblage Zone, Upper Permian.

SAM-PK-010153: *Pristerodon* sp., skull from Quagga Fontain 82, Western Cape, South Africa; *Cistecephalus-Tropidostoma* Assemblage Zone, Upper Permian.

SAM-PK-K01658: *Pristerodon* sp., skull from Luee Kloof 43, Western Cape, South Africa; Upper Permian.

SAM-PK-010086: *Diictodon galeops*, skull from Quagga Fontain, Western Cape, South Africa; *Cistecephalus-Tropidostoma* Assemblage Zone, Upper Permian.

SAM-PK-K08585: *Diictodon* sp., skull from unknown locality, Western Cape, South Africa; Upper Permian.

SAM-PK-011461: *Robertia broomiana*, skull from Buffels Valley, Western Cape, South Africa; Upper Permian.

SAM-PK-011761: *Robertia broomiana*, skull from Klein Koedois Kop, Western Cape, South Africa; Upper Permian.

SAM-PK-K07807: *Robertia broomiana*, skull from unknown locality, South Africa; Upper Permian.

SAM-PK-K06064: *Aulacocephalodon* sp., skull from Grootvlei 193, Western Cape, South Africa; Upper Permian.

SAM-PK-K07482: *Dicynodon* sp., skull from Dreinfontain, Western Cape, South Africa; Upper Permian.

SAM-PK-K07011: *Dicynodon* sp., skull from the Seekoeigat locality at Matjesvalley, Western Cape, South Africa; Upper Permian.

SGU D-104/1: *Uralokannemeyeria vjuschkovi*, skull and postcranial remains from Karagachka locality, Orenburg region, Russia; Donguz Gorizont, Middle Triassic.

UT 292: *Tetragonias njalilus*, skull and postcranial remains from the basin of Rutukira River, Ruhuhu Valley, Tanzania; Manda Formation, Middle Triassic.

UT n1, n2, n3: *Stahleckeria potens* skulls and postcranial skeleton from Chiniqua, Rio Grande do Sul, Brazil; lower member of Santa Maria Formation, Middle Triassic.

Anatomical abbreviations

bo, basioccipital; cc, canalis caroticus; cv, canalis vidii; cve, cavum vestibulum; d, depression; de, ductus endolymphaticus; ds, dorsum sellae; ep, epipterygoid; ex, exoccipital; fbscr, fenestra basicranialis; ff, floccular fossa; fj, foramen jugularis; fo, fenestra ovalis; fom, foramen magnum; fpa, facet for the pro-atlas articulation; fpt, fenestra posttemporalis; ipt, interpterygoid vacuity; itp, interparietal; itr, intertuberal ridge; mapt, attachment for m. anterior pterygoideus; mpp, m. protractor pterygoidei; mppt, attachment for the m. posterior pterygoideus; op, opisthotic; pa, pila antotica; par, parietal; pbs, parabasisphenoid; pbtr, processus basitrabecularis; pc, processus cultriformis; per, periotic; pf, perilymphatic foramen; po, postorbital; ppar, paroccipital process; pr, prootic; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; r, ridge; rpbs, ventrolateral ridge on the parabasisphenoid; so, supraoccipital; sq, squamosal; st, stapes; stu, sella turcica; t, tabular; tfo, tuber fenestra ovalis; tor, torus; vcd, notch for the vena capitis dorsalis; V + vcl, notch for the trigeminal nerve; VII, foramen for the facial nerve; VIII, foramen for the vestibulocochlear (auditory) nerve; XII, foramen for the hypoglossal nerve.