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ARTICLE

HEAD KINEMATICS AND FEEDING ADAPTATIONS OF THE PERMIAN AND TRIASSIC DICYNODONTS

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ABSTRACT—The distribution of neck muscles and the shape of the skull shows that Permian and Triassic dicynodonts may be classified into three categories which probably reflect feeding on low, medium and high vegetation. These are distinguished on the basis of the occipital index, the difference between the relative width and height of the occiput, which gives a measure of the relative importance of the lateral and the dorsoventral clusters of neck muscles. The basicranium is relatively shortened in Triassic forms, except in *Vinceria*, *Shansiodon*, *Tetragonias*, and *Jachaleria*, 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 with dietary preferences at the intermediate level correspond to major branching points in dicynodont phylogeny. High-level feeding adaptations among dicynodonts arose by the middle of the Tatarian (latest Permian) and lasted until the Late Triassic. Specialized low feeders existed only in the Middle Triassic.

INTRODUCTION

Dicynodonts were a clade of non-mammalian synapsids that arose in the Late Permian and spread widely all over the world. These therapsids had a superficially turtle-like toothless beak and a jaw joint that allowed a fore-and-aft sliding motion of the lower jaw, adaptations that together allowed them to process vegetation more efficiently than other herbivores. Propaliny was traditionally considered as a major reason for the high diversity and abundance of these herbivores worldwide during the Late Permian and much of the Triassic (Keyser and Cruickshank, 1979; King, 1981, 1988, 1990; Benton, 1983), although, Angielczyk (2004) suggested that propaliny alone might not have been sufficient to account for their success. The general absence of teeth, and the presence of a keratinous beak in dicynodonts makes it hard to assess the efficiency of their feeding system (Reisz, 2006). In such a diverse group, different feeding styles may correspond to different skull morphologies, 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) distinguished two subfamilies of Middle Triassic dicynodonts on the presence or absence of a high parietal crest and the relative width 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 shape of the lips in living rhinoceroses, where the black rhinoceros has pointed lips and a diet based mainly on leaves, and the white rhinoceros has square lips and a diet based mainly on 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, relative length of the interpterygoid space to the length of the internal naris, 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 characterized 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).

Recent cladistic studies of Permian and Triassic dicynodonts (Angielczyk 2001, 2007, Angielczyk and Kurkin 2003; Surkov and Benton, 2004; Surkov et al., 2005) include some discrete-state characters related to the feeding system (e.g., presence of palatal ridges, structure of the intertemporal region, morphology of the dentary). However, such studies generally do not consider skull proportions, although Maisch (2001) and Vega-Dias et al. (2004), in their phylogenetic studies of Triassic forms, included proportional characters such as the relative height of the suspensorium, relative skull width, and height of temporal crest, but they did not relate these features to the evolution of feeding modes. Therefore, the aim of the present research is to analyse dicynodont head kinematics to determine whether head shape and proportions are related to dietary preferences, to phylogeny, or to both.

Institutional Abbreviations—**BMNH**, British Museum (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 Paleoanthropology, 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

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TABLE 1. Estimates of occipital indices (I_{Lat}-I_{Dor}) of the Permian taxa.

	Permian Taxa	Occipital index	Mean	Standard deviation
1	*Aulacephalodon tigriceps* BMNH 36235	0.041	0.03	0.011
2	*Aulacephalodon* SAM PK K6064	0.025		
3	*Cistecephalus* SAM PK K7667	−0.368	−0.291	0.11
4	*Cistecephalus* SAM PK K8584	−0.342		
5	*Cistecephalus* SAM PK 10664	−0.162		
6	*Delectosaurus arefjevi* PIN 4644/1	−0.28		
7	*Dicynodon* sp. CAMZM 1089	−0.060	−0.08	0.010
8	‘*Dicynodon*’ (?) sp. PIN no number	−0.067		
9	*Dicynodon huenei* UT K101	−0.070		
10	*Dicynodon lacerticeps* BMNH 36233	−0.071		
11	*Dicynodon lacerticeps* SAM PK K7011	−0.072		
12	*Dicynodon pardiceps* BMNH 47045	−0.078		
13	*Dicynodon* sp. SAM B88*	−0.080		
14	‘*Dicynodon*’ *amalitzkii* PIN 2005/38a	−0.088		
15	*Dicynodon trigonocephalus* TSK 14	−0.090		
16	*Diictodon testudirostris* BMNH R11184	0.083	0.03	0.056
17	*Diictodon* sp. BMNH R3744	0.042		
18	*Diictodon* sp. BMNH 47052	−0.029		
19	*Elph borealis* PIN 2353/37	−0.05		
20	*Emydops* sp. SAM PK K1517	−0.130	−0.19	0.087
21	*Emydops* sp. SAM PK 3721	−0.144		
22	*Emydops* sp. SAM PK 11060	−0.287		
23	*Eodicynodon* SAM PK 11879	−0.190	−0.19	0.006
24	*Eodicynodon* SAM PK 117569	−0.199		
25	*Geikia locusticeps* UT K114	0.080		
26	‘*Idelisaurus tatarica*’ PIN 156/4	−0.037	−0.04	
27	*Kingoria* sp. CAMZM 749	−0.120	−0.12	
28	*Otsheria netzvetayevi* PIN 1758/5	0.000	0.00	
29	*Oudenodon halli* BMNH R4067	0.159	0.05	0.090
30	*Oudenodon baini* BMNH 36232	0.074		
31	*Oudenodon* SAM PK 10066	0.025		
32	*Oudenodon* SAM PK K5227	−0.056		
33	*Pristerodon* sp. SAM PK 1658	0.001	−0.02	0.029
34	*Pristerodon* sp. SAM PK 10153	−0.040		
35	*Rachiocephalus* UT 100	−0.033	−0.03	
36	*Robertia* SAM PK 11761	−0.002	0.00	
37	*Tropidostoma microtrema* BMNH R1662	0.039	0.03	0.018
38	*Tropidostoma* SAM PK K8633	0.014		
39	*Vivaxosaurus permirus* PIN 1536/1	−0.020	−0.02	
40	*Ulemica efremovi* PIN 2793/1	0.019	0.02	

Explanations in the text.
*Measurements taken from photographs.

TABLE 2. Estimates of occipital indices (I_{Lat}-I_{Dors}) of the Triassic taxa.

	Taxa	Occipital index	Mean	Standard deviation
1	*Angonisaurus* BMNH R 9732	0.123	0.123	
2	*Dinodontosaurus turpior* MCZ 1670*	0.07	0.07	0.08
3	*Dinodontosaurus* MCZ 1678†	−0.01		
4	*Dinodontosaurus* MCZ 1677†	0.15		
5	*Ischigualastia* R54†	−0.11	−0.133	0.03
6	*Ischigualastia* PVL 2693†	−0.17		
7	*Ischigualastia* MCZ 318-19†	−0.12		
8	*Jachaleria candelariensis* UFRGS-PV0151T†	−0.22	−0.22	
9	*Kannemeyeria lophorhinus* CGP R313†	0.14	0.132	0.008
10	*Kannemeyeria latifrons* CAMZM 1037	0.13		
11	*Kannemeyeria simocephalus* UMMP 14530†	0.125		
12	*Lystrosaurus curvatus* BMNH R3597	−0.122	−0.122	
13	*Moghreberia* PMNH ALM 281	−0.29	−0.29	
14	*Myosaurus* SAM PK 3526	−0.07	−0.07	
15	*Parakannemeyeria dolichocephala* IVPP 973‡	−0.155	−0.121	0.077
16	*Parakannemeyeria youngi* IVPP 979‡	−0.17		
17	*Parakannemeyeria youngi* IVPP 978‡	−0.174		
18	*Parakannemeyeria ningwuensis* IVPP 983‡	−0.115		
19	*Parakannemeyeria dolichocephala* IVPP V984‡	0.01		
20	*Placerias**	−0.24	−0.24	
21	*Rechnisaurus**	0.08	0.08	
22	*Rhadiodromus* SGU 161/236	0.124	0.122	0.003
23	*Rhadiodromus* PIN 1579/14	0.12		
24	*Rhinodicynodon gracilis* PIN 1579/50	−0.026	−0.026	
25	*Shansiodon wangi* IVPP 2415‡	−0.083	−0.172	0.125
26	*Shansiodon* IVPP V2416*	−0.26		
27	*Sinokannemeyeria yingchiaoensis* IVPP 974‡	0.078	0.039	0.055
28	*Sinokannemeyeria pearsoni* IVPP 976‡	0		
29	*Stahleckeria* UT n2	0.26	0.26	
30	*Tetragonias njalilus* CAMZM T754	0.06		0.191
31	*Tetragonias njalilus* UT 292	−0.21		
32	*Uralokannemeyeria* SGU D-104/1	0.08	0.08	
33	*Vinceria**	−0.12	−0.12	
34	*Wadiasaurus* ISI R38*	0	0	

Explanations in the text.
*Measurements taken from reconstructions.
†Measurements taken from photographs.
‡Measurements taken by author of original description.

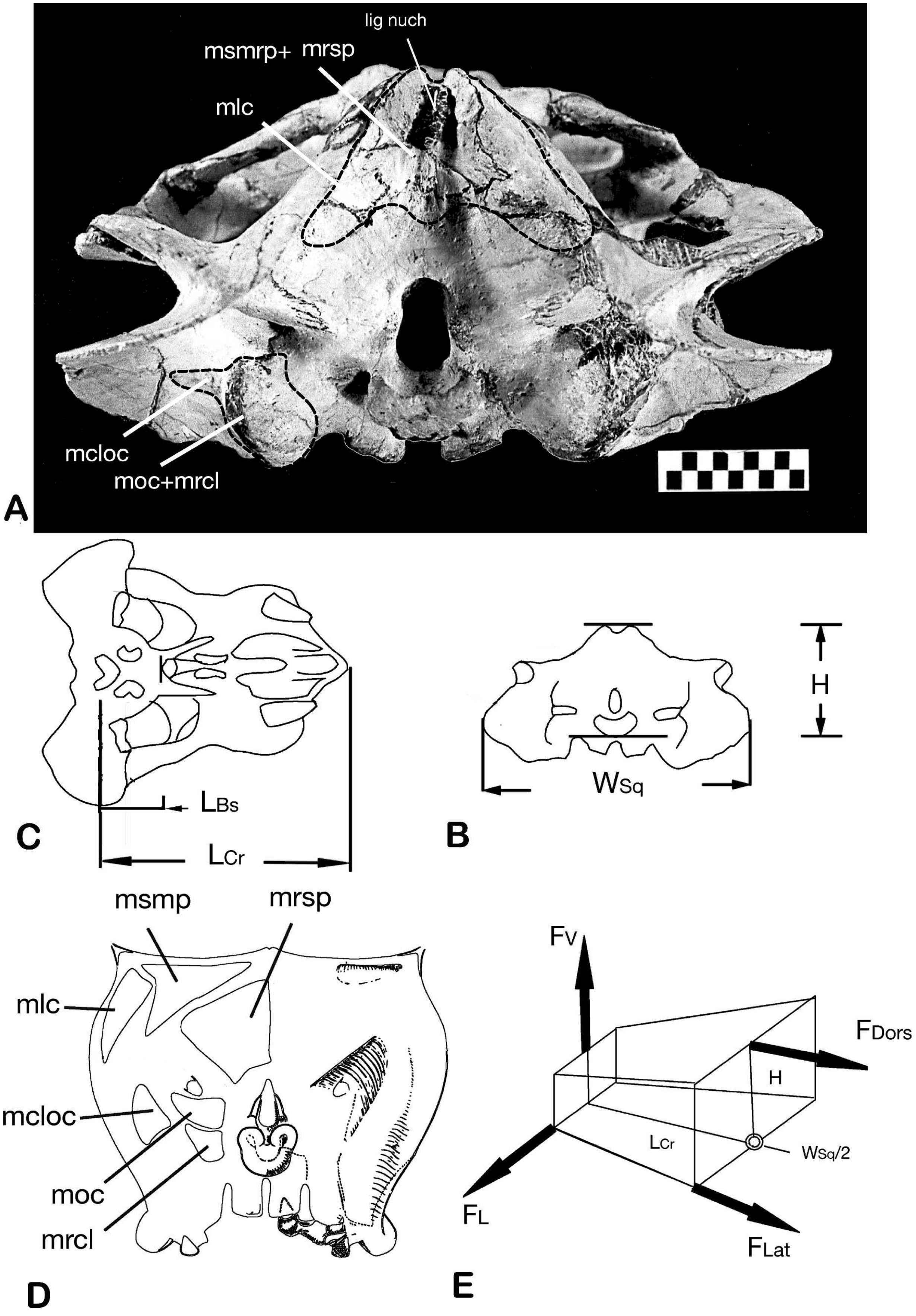
geological collection, Russia; **UT**, Museum und Institut für Geologie und Paläontologie, Universität Tübingen, Germany.

MATERIALS AND METHODS

Taxa, Specimens, and Literature Examined—During this research, we took skull measurements of 73 specimens from the Permian and Triassic. Most measurements were taken from the original material by MVS, but several were from original descriptions (Tables 1, 2) by Case (1934), Yeh (1959), Sun (1963), Cox (1965), Keyser (1973), Cluver and Hotton (1981), King (1981), Bandyopadhyay (1988), Lucas and Harris (1996), and Vega-Dias and Schultz (2004).

Angielczyk and Kurkin (2003), in their phylogenetic analysis of Permian dicynodonts, suggested that the genus *Dicynodon* is paraphyletic, but monophyletic *Dicynodon* could not be rejected unequivocally. Therefore, we consider all *Dicynodon* specimens as one group because all measurements fall in one short interval. However, following Angielczyk and Kurkin's (2003) hypothesis, we place Laurasian specimens of ‘*Dicynodon*’ in apostrophes.

Measurements—In an attempt to understand differences in the head kinematics of dicynodonts we reviewed their main skull proportions, and the key variable characters were length along basicranium, width over squamosals, and height of the skull. Earlier, Cox and Li (1983) considered five main parameters describing the general shape of the skull in Triassic dicynodonts: length along dorsal midline, length over squamosal wings (total skull length), length along midline of palate, height of the occiput, and width over squamosals. We did not use all the characters from Cox and Li (1983), because the three skull length measures (length along dorsal midline, length over squamosal wings, length along midline of palate) were strongly correlated ($r \geq 0.98$). We chose to use only ‘length along midline of palate’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because this measurement also encompasses a key kinematic landmark, the basicranial joint, which acts as a pivot against which the head moves.

There is no evidence for allometry within genera or among close relatives, as indicated by closeness of the regression lines to a slope of one (isometry), when skull height or width are plotted against midline skull length for all taxa included here ($r \geq 0.96$). Admittedly, no juvenile specimens were included. Further, very few of the selected skulls showed evidence of distortion, except in the case of the obviously slightly squashed specimen of *Dicynodon* sp. (SAM PK K7011), for which we restored vertical measurements on the basis of the orbit shape of an uncompressed *Dicynodon* sp. (CAMZM 1089), assuming that there are no pronounced allometric differences between SAM PK K7011 and CAMZM 1089, which is much larger.

We examined the occiputs of dicynodonts to choose landmarks for kinematically reliable measurements of height and width of the skull, and found that there are no significant variations. Generally, only two areas of the occiput may be identified confidently as muscle attachment sites (Fig. 1A), because the bone surface bears rough and ridged patterns for ligament-bone incorporation (Hildebrand, 1982). The first area is the uppermost part of the occiput in the area of the interparietal, the second is marked by the lateral termination of the paraoccipital process (areas outlined by dashed lines, Fig. 1A). The first area is characterized by elongated rough, sometimes ridged surfaces along the midline of the interparietal and rough areas along the dorso-posterior edge of the parietals/squamosal, and posterior edge of the interparietal. This area has been correlated with attachments for m. rectus capitis major and m. semispinalis capitis medialis/ trapezius (Cox, 1959, Ewer, 1961), muscles responsible for upward head movements. The main tension of these muscles matched the uppermost part of the occiput, clearly defined among large-headed dicynodonts (especially Triassic ones) by posterior outgrowth of the interparietal and parietals for attachment of the ligamentum nuchae (Fig. 1A), which was formed primarily from 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 was measured from here to the level of the occipital condyle (Fig. 1B).

The width of the skull over the squamosals was suggested by Cox and Li (1983) as one of the main measurement for description of skull shape. We attempted to understand whether skull width may be correlated with the attachment sites for the lateral neck muscles such as the obliquus capitis (Cox, 1959; Ewer, 1961), which has clear landmarks, namely scars in the area of the lateral termination of the paraoccipital processes (Fig. 1A). We sampled 11 digitized photographs of dicynodont occiputs, and measured in Photoshop the distances between attachments (centers of muscle scars) for the lateral neck muscles and the width of the occiput across the squamosals (Table 3). Both measurements are strongly positively correlated ($r = 0.99$), so general measurements of the occiput, such as its height and width, may be correlated confidently with the relative position of visible attachments for the main neck muscles, such as the m. rectis captis and m. obliquus capitis (Cox, 1959; Ewer, 1961). Therefore, we use three main measurements to describe the shape of the skull: cranial length (L_{Cr}), the 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. 1B, C).

TABLE 3. Measurements between areas for attachments of lateral occipital muscles and width of the occiput.

Taxa	Distance between attachments for lateral occipital muscles	Width over squamosal
1. *Rachiocephalus* UT 100	442	778
2. *Geikia* UT K114	393	751
3. *Dicynodon huenei* UT K101	383	658
4. *Tetragonias njalilus* UT 292	609	1056
5. *Stahleckeria potens* UT no2	476	937
6. *Dicynodon leoniceps* CAMZM 1089	7988	15060
7. *Diictodon testudirostris* BMNH R11184	560	884
8. *Kingoria nowacki* CAMZM 747	6080	9537
9. *Angonisaurus cruickshanki* BMNH R 9732	277	595
10. *Kannemeyeria latifrons* CAMZM 1037	5248	10288
11. *Tetragonias njalilus* CAMZM T754	4422	10370

Values represents pixels.

We also checked King's (1988) statement that the Triassic forms are characterized by a visually shorter basicranium by estimating the ratio of basicranial length (L_{Bs}, Fig. 1B) to cranial length.

Cladistic Analysis—To trace the evolution of kinematic characters of the skull, we estimated a cladogram for a sample of 38 dicynodont taxa for which the skull is reasonably well known. We used all cranial characters from the data matrices of Angielczyk and Kurkin (2003), Vega-Dias et al. (2004), Surkov and Benton (2004), and Fröbisch (2007), eliminating obviously redundant characters, leading to a total of 83 discrete characters (data matrix is available in Supplementary information). We did not recode characters because our key aim is not to dispute the recent, thorough cladistic analyses that have been published, merely to place our taxa of interest in a cladogram. All characters were treated as unordered and weighted according to the rescaled consistency index, and the analyses were run as branch-and-bound searches on PAUP.

ANALYSIS OF HEAD KINEMATICS

Muscles and Forces—The main function of the occipital plate (as well as acting as 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) compared their reconstructions of dicynodont occipital muscles with those of recent reptiles (*Varanus*, *Alligator*, *Sphenodon*) and mammals, and their conclusions are comparable, except for the presence of m. obliquus capitis magnus, which was rejected by Ewer, and a different position of m. de-

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FIGURE 1. Occiput, and major skull measurements and simplified scheme of skull movements in dicynodonts. **A**, occiput of *Oudenodon* (SAM PK 5227) with main areas of muscle attachments (shown by dotted lines). **B**, **C**, scheme of skull measurements in ventral (**B**) and posterior (**C**) views. **D**, scheme of attachments for the main neck muscles (modified from Ewer, 1961). **E**, simplified scheme of forces applied by neck muscles; not to scale. **Abbreviations**: **F_{Dors}**, force applied by the dorsal portion of the neck muscles; **F_L**, lateral component of the force applied to an object; **F_{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_{Bs}**, length of basicranium; **L_{Cr}**, skull length along palatal midline; **lig nuch**, ligamentum nuchae; **mcloc**, attachment for m. cleidooccipitalis; **mlc**, attachment for m. longus capitis; **moc**, attachment for m. obliquus capitis; **mrcl**, attachment for m. rectus capitis lateralis; **mrsp**, attachment for m. rectus capitis posterior; **msmrp**, attachment for m. semispinalis; **W_{Sq}**, width of the skull across squamosal wings.

pressor mandibulae (Ewer, 1961:398). These differences are minor, and in both reconstructions of the occipital muscles, these authors invariably placed the attachments for m. rectus capitis lateralis, m. obliquus capitis and m. cleido-occipitalis (Ewer, 1961:fig. 1D), or these muscles and m.obliquus capitis magnus (Cox, 1959), in the area of the lateral termination of the paroccipital processes, and m. rectus capitis and m. semispinalis in the area of the interparietal and posterior termination of the parietals, as noted above. We agree with the previous studies that muscles on the occipital plate of dicynodonts may be divided into two groups, lateral muscles (m. cleido-occipitalis, m. obliquus capitis, m. rectus capitis lateralis) that moved the head from side to side, and dorsal muscles (m. rectus capitis posterior, m. semispinalis, m. longissimus capitis) that moved it up and down. More complicated movements of the head were effected by the combined action of both sets of neck muscles.

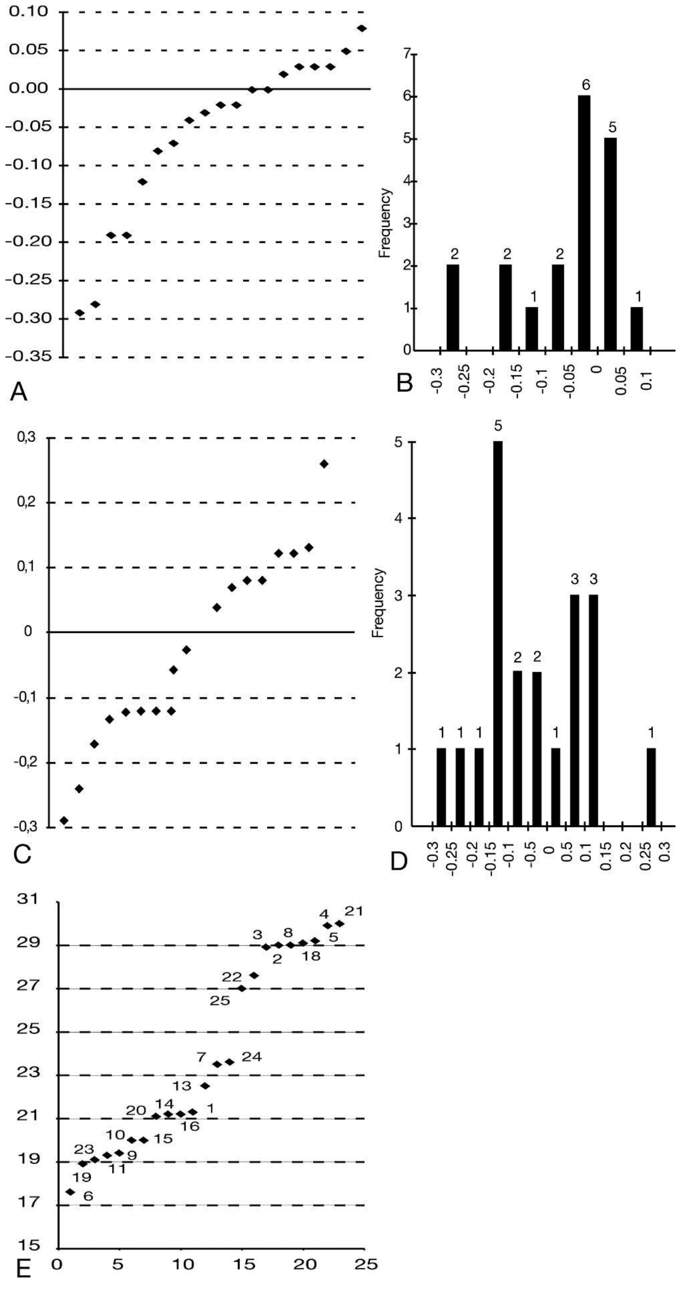

FIGURE 2. Determination of feeding level preferences among Permian and Triassic dicynodonts, assessed by the occipital index (OI; see text): low feeders have values of the OI > 0.5, whereas high feeders have negative OI values (OI < −0.1). The data are shown as distributions by taxon (**A**, **C**) and as frequency histograms (**B**, **D**) for Permian (**A**, **B**) and Triassic (**C**, **D**) dicynodonts. **E**, distribution of values of relative length of the basicranium. Numbers correspond to taxa listed in Table 4.

The forces generated by the sets of occipital muscles may be represented by a simplified scheme of vectors (Fig. 1E). The vertical (F_V) and lateral (F_L) components of the resultant forces correspond to 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 (pivot 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. We treat the occipital condyle as the common fixed point for all taxa, even though some have an occiput that slopes forwards, or a posteriorly projecting parietal; for the purposes of these calculations, we find that these topographic differences make little difference.

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:

$$\frac{F_V}{F_{Dors}} = \frac{H}{L_{Cr}} \text{ or } F_V = F_{Dores} \frac{H}{L_{Cr}}$$

and

$$\frac{F_L}{F_{Lat}} = \frac{W_{Sq}}{2L_{Cr}} \text{ or } F_L = F_{Lats} \frac{W_{Sq}}{2L_{Cr}}$$

TABLE 4. Estimated relative length of the basicranium and measurements of the angle of the intertemporal bar among Late Permian and Triassic dicynodonts.

Taxa	Angle of temporal crest	L_{Bs}/L_{Cr}
1. *Angonisaurus* BMNH R 9732	<10	21.3
2. *Dicynodon* sp. SAM PK K7011	<10	29
3. *Dicynodon* SAM B88*	<10	28.9
4. *Dicynodon* sp. CAMZM 1089	<10	29.9
5. *Dicynodon trigonocephalus*†	<10	29.2
6. *Dinodontosaurus turpior* MZC 1670†	<10	17.6
7. *Ischigualastia* MCZ 318-19†	40	23.5
8. *Jachaleria candelariensis* UFRGS PV0151T*	40	29
9. *Kannemeyeria lophorhinus* CGP R313*	26	19.4
10. *Kannemeyeria simocephalus* UMMP 14530*	40	20
11. *Kannemeyeria latifrons* CAMZM 1037	26	19.3
12. *Moghreberia* PMNH ALM 281	70	?
13. *Parakannemeyeria* IVPP V984‡	~10	22.5
14. *Placerias*†	70	21.2
15. *Rechnisaurus*†	35	20
16. *Rhadiodromus* PIN 1579/14	<10	21.2
17. *Rhinodicynodon* PIN 1579/50	<10	?
18. *Shansiodon* IVPP V2416†	~10	29.1
19. *Sinokannemeyeria* IVPP V 974‡	38	18.9
20. *Stahleckeria* UT n2	~30	21.1
21. *Tetragonias njalilus* CAMZM T754	<10	30.0
22. *Tetragonias njalilus* UT 292	38	27.6
23. *Uralokannemeyeria* SGU D-104/1	38	19.1
24. *Vinceria*†	~35	27
25. *Wadiasaurus* ISI R38†	~30	23.6

Explanations in the text.
*Measurements taken from photographs.
†Measurements taken from reconstructions.
‡Measurements taken by author of original description.

The ratios H/L_{Cr} and $W_{Sq}/2L_{Cr}$, termed the occipital indices, reflect relative efficiency of the lateral and dorsal portions of the neck muscles. Differences between these values may be interpreted in the following way: if the value of the index for the dorsal muscles is more than for the laterals, it is likely that the dorsal muscles are more advantageously and effectively located on the occipital plate than the laterals and vice versa. Therefore, the difference between $W_{Sq}/2L_{Cr}$ (I_{Lat}) and H/L_{Cr} (I_{Dors}) reflects the relative effectiveness of lateral and dorsal portions of the neck muscles and might correspond to the preferred plane of head movement.

Evidence for Two Feeding Classes Among Dicynodonts—Differences between lateral and dorsal occipital indices (OIs) for Late Permian and Triassic dicynodonts (I_{Lat}-I_{Dors}; Tables 1, 2; Fig. 2) indicate a wide range of values, suggesting extreme biomechanical differences from end to end of the distribution. Occipital indices do not vary significantly among specimens within a genus (standard deviation < 0.1 for most taxa), but there is a

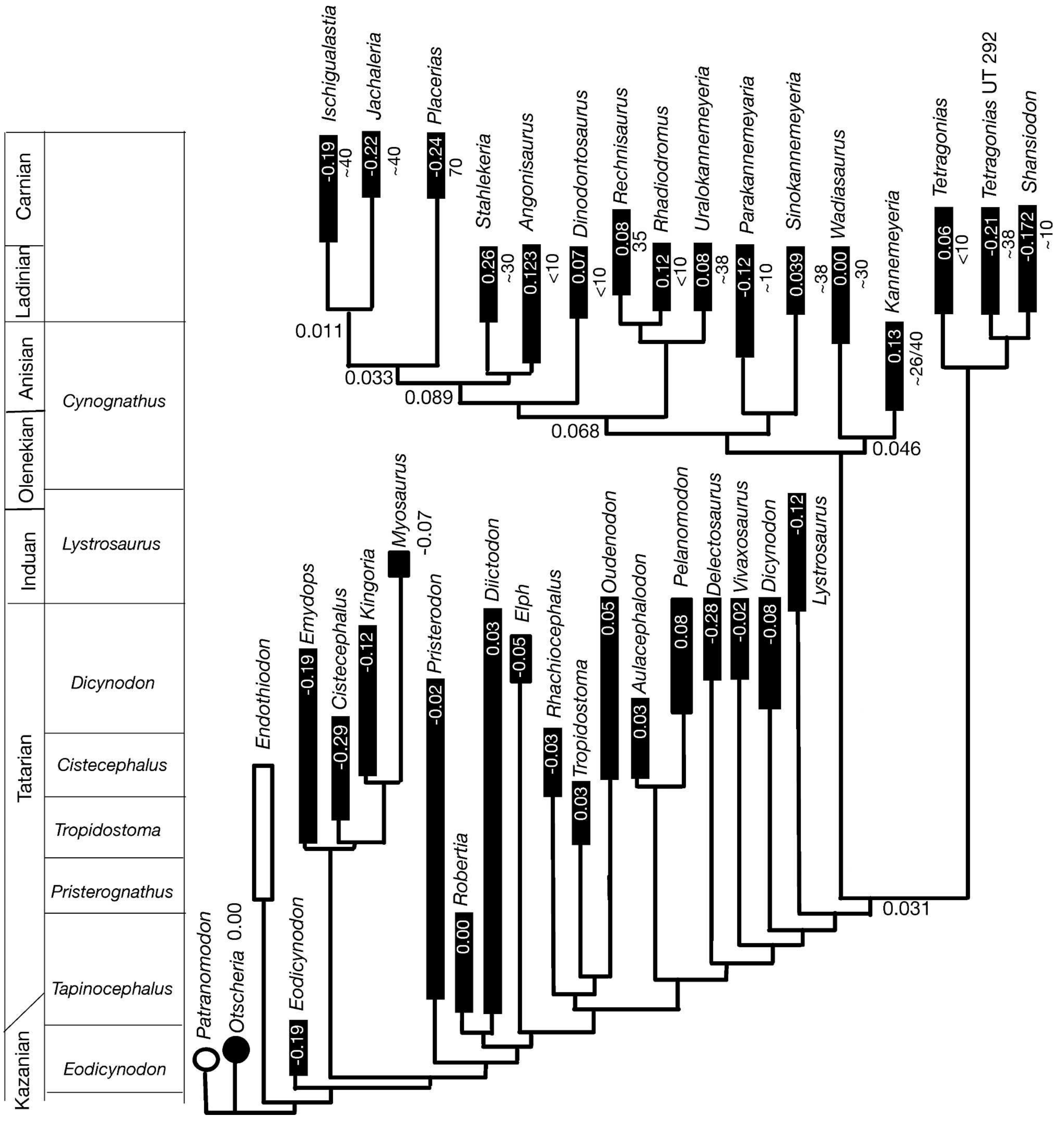

FIGURE 3. Distribution of occipital indices among the main clades of Permian and Triassic dicynodonts. Composite phylogeny based on a cladistic reanalysis of data from Angielczyk and Kurkin (2003), Vega-Dias et al. (2004), and Maisch and Gebauer (2005). Values for the occipital index (OI) of each taxon are indicated beside the taxon name, usually on the black bar. Ancestral values of the OI, as calculated using squared change parsimony, are indicated at the foot of clades. The additional figure for Triassic taxa, is the approximate angle of the temporal crest.

bimodal distribution among genera (Fig. 2B, D), which indicates two subgroups that may relate to different dietary preferences. For Permian taxa, most OI values are in the ranges –0.08 to 0.05 and < –0.08, while for Triassic taxa the ranges are –0.3 to –0.1 and 0.05 to 0.3.

The two subclasses differ in mean values of the OI. The low feeders (n = 17) have mean OI = 0.095, while the high feeders (n = 29) have mean OI = –0.127 (and the intermediates (n = 20) have mean OI = –0.021. Values differ between the Permian and Triassic samples, with values for low feeders in the Permian (n = 5; mean = 0.056) and Triassic (n = 12; mean = 0.111) always considerably higher than those for high feeders from the Permian (n = 16; mean = –0.114) and Triassic (n = 13; mean = -0.144). Intermediates fall between these values when binned for the Permian (n = 13; mean = 0.007) and Triassic (n = 7; mean = –0.109). It is perhaps worth noting that both low and high feeders move to more extreme mean OI values in the Triassic, when compared with the Permian sample (higher for low feeders, and lower for high feeders).

The existence of two classes of dicynodonts based on their OIs (Fig. 2B, D) may be explained by preferred movements of the skull and likely feeding habits. 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 (OI > 0.05; Fig. 2B, D), because they did not have to reach for high vegetation. The cluster of OI values < –0.1 (Fig. 2B, D) 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 had to keep the head up all the time during feeding. OI values in the range –0.1 to 0.05 (Fig. 2B, D) reflect no particular advantage for either the lateral or dorsal neck muscle blocks, so these dicynodonts probably fed equally on low and high vegetation, or at the middle level.

The distributions of OIs differ between the Permian and Triassic dicynodonts (Fig. 2A–D). Dicynodonts with predominantly vertical head movements are rare among Permian taxa whose OIs cluster close to zero (Fig. 2A, B), but this feature is relatively common among Triassic forms (Fig. 2C, D). Generalized dietary preferences characterize the ancestral forms *Otsheria* and *Ulemica*, whose occipital indices are nearly equal to zero (Table 1).

This study confirms King's (1988) observation that most Triassic dicynodonts show shortening of the basicranium (Table 4), although *Vinceria*, *Tetragonias*, *Shansiodon*, and *Jachaleria* retained a basicranium as long as in Permian forms.

Phylogeny—The cladistic analysis of the combined character matrix yielded one tree with consistency index (CI) 0.508 and rescaled consistency index (RI) 0.789 (Fig. 3). This tree agrees broadly with previous analyses, indicating all main groups established before, but sometimes with different order of branching. We found earlier branching for *Endothiodon*, the clade *Emydops-Myosaurus*, and *Vivaxosaurus*. 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 steepness of the parietal crest reveal significant differences between the Cambridge and Tübingen specimens and close affinity of *Tetragonias njalilus* (UT 292; $I_{Lat}\text{-}I_{Dors} = -0.21$) with *Shansiodon* (IVPP V2416; $I_{Lat}\text{-}I_{Dors} = -0.260$). The skulls have not undergone visible compression, and differences in size and skull proportions probably do not reflect sexual dimophism, but rather differences in feeding adaptations. This suggestion is well supported by our cladistic analysis, in which *Tetragonias* from the Tübingen Museum forms a clade with *Shansiodon*. This similarity is clearly seen in Figure 4B. *Shansiodon* is currently known only from China, but there is evidence that it might occur in Africa (Hancox and Rubidge, 2001; MVS, observation of specimen BMNH R12710 from the Manda Formation, Tanzania, tentatively identified as *Shansiodon* sp.).

As noted above, very few Permian dicynodonts show a predominance of vertical head movements, and these include *Eodicynodon* from the Wordian and the *Emydops-Myosaurus* clade and *Tropidostoma* from the mid to late Tatarian of Gondwana. The phylogeny (Fig. 3) shows that this feature appeared twice in the Permian, but the longevity and geographical distribution of taxa with this feature suggests that stable ecological niches for dicynodonts with strengthened dorsal neck muscles had appeared only in the second half of the Wuchiapingian and they were occupied by different clades independently in Gondwana and Laurasia. This observation provides additional support for the suggestion that dicynodont assemblages from Eastern Europe had evolved independently (Angielczyk and Kurkin, 2003; Ivakhnenko, 2003) and raises a question about obstacles that prevented wider dispersal of the Gondwanan fauna.

Triassic dicynodonts divide into three groups (above), ground-level feeders (OI > 0.5), high-level feeders (OI < –0.1), and intermediates (0.1 < OI < 0.5), and when plotted on the cladogram (Fig. 3), certain clades possess similar OIs. Even though the

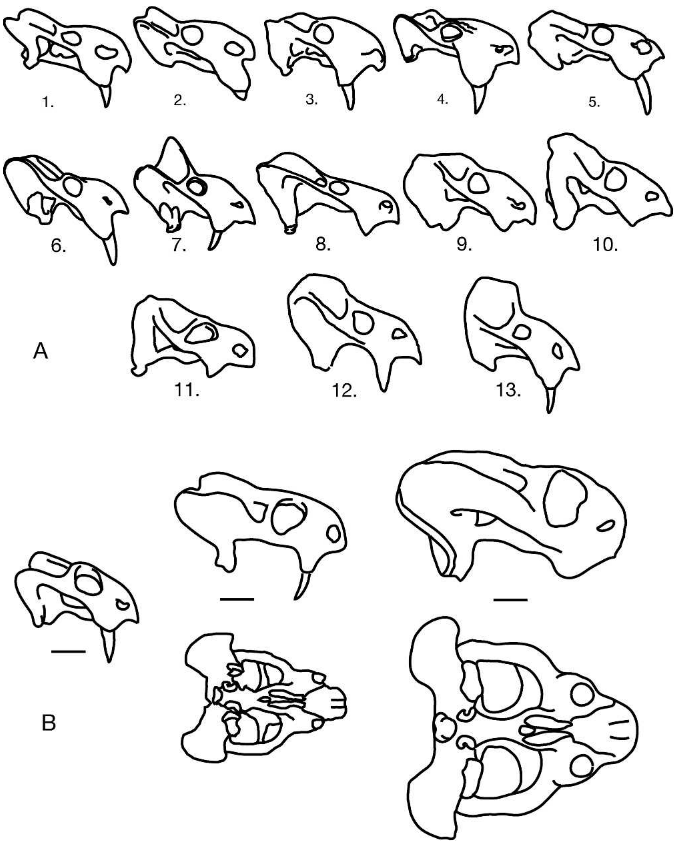

FIGURE. 4. Skull outlines of the Middle-Late Triassic dicynodonts **A**, large taxa with a skull length greater than 350 mm in adult individuals. Not to scale. **B**, skull outlines of *Shansiodon*, *Tetragonias* (UT 292), *Tetragonias* (CAMZM T754), from left to right; Scale bar represents 5 cm. **Abbreviations**: **1**. *Kannemeyeria*; **2**. *Rechnisaurus* (Cox, 1991); **3**. *Parakannemeyeria* (Sun, 1963); **4**. *Sinokannemeyeria* (Sun, 1963); **5**. *Rhadiodromus*; **6**. *Uralokannemeyeria*; **7**. *Rabidosaurus* (Kalandadze, 1970); **8**. *Wadiasaurus* (Bandyopadhyay, 1988); **9**. *Stahleckeria*; **10**. *Ischigualastia* (Cox, 1965); **11**. *Jachaleria* (Araújo and Gonsaga, 1980); **12**. *Placerias* (Cox, 1965); **13**. *Moghreberia*.

cladogram does not include some Triassic taxa, this correspondence is likely the case for most Triassic clades because some taxa are represented by a single node, such as *Placerias*, which may be related to *Moghreberia* (I_{Lat}-I_{Dors} = −0,29) according to Vega-Dias et al. (2004).

The matching of the OI and feeding adaptation shows an interesting pattern of paleogeographic distribution of dicynodonts (Fig. 5). Triassic forms start at the beginning of the Middle Triassic with two different feeding types, low feeders (I_{Lat}-I_{Dors} = >0.06) in Africa and high feeders in South America (I_{Lat}-I_{Dors} = < 0.1), and differentiation in feeding adaptations occurred later and corresponded to greater taxonomic diversity, followed by a reduced diversity of high-level feeders surviving into the Late Triassic.

Analysis of squared-change parsimony among occipital indices has been done with MacClade 3.05. Tracing of continuous change in occipital indices revealed that the initial state for all clades was close to zero, and a low-level or intermediate feeding habit (Fig. 3) was probably basal for the Triassic taxa, while the appearance of high feeders in the Late Triassic was likely a reversal.

The Parietal Crest—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; Renaut and Hancox, 2001), this character was assumed to be a key feature of *Kannemeyeria* and its relatives, and it was widely used in systematic work. 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 individual development of dorsal neck tendons to hold up the heavy head.

The angle of the intertemporal bar relative to the plane of the basicranium in Triassic dicynodonts (Table 4) shows a broad scatter across the cladogram (Fig. 3). This apparently non-phylogenetic distribution, and the occurrence of pronounced angles only in large-sized animals (Fig. 4A), suggests that the raised intertemporal bar is controlled by two factors: the massive head (e.g., *Stahleckeria*) and feeding at a high level (*Placerias*, *Moghreberia*, *Tetragonias* UT 292). In both cases the interparietal bar was substantially raised, so it is hard to assess the height of the interparietal bar unequivocally, except in the case of its extreme autopomorphic development in *Moghreberia*, *Rabidosaurus*, and possibly *Placerias*, so this character may add noise during cladistic estimations.

DISCUSSION

The matching of the occipital index and major clades of Permian and Triassic dicynodonts, as well as the paleogeographic distribution of taxa, suggest that this feature is a good phylogenetic character that matches the preferred head movement in a vertical or horizontal plane, and likely reflects various feeding adaptations. However, in some cases the preferred plane of head movement may match other aspects of lifestyle. For example, strengthening the dorsal neck muscles in the presumed fossorial *Cistecephalus* (Cluver, 1978) may be explained by "headlift" digging to displace and compact the soil, similar to the recent spalacid mole-rats, or using upwards thrusts of the head in combination with the forelimbs to move the soil, like a marsupial mole (Hildebrand, 1985). On the other hand, this feature may indeed reflect the dietary preferences of *Cistecephalus*, because, unlike *Diictodon,* which was obviously a digger and is commonly found in burrows (Smith, 1993), *Cistecephalus* remains are mostly skulls (King and Cluver, 1991), which, judging from the commonly fractured bone surface, were exposed to weathering for a long period before burial (MVS, pers. obs.). Another example may be *Lystrosaurus*, in which the dorsal neck muscles may have been used to keep the head up if it lived underwater at times, as suggested by Ray et al. (2005) and Germain and Laurin (2005). This point of view might be supported by the apparent absence of well-developed terrestrial vegetation after the end-Permian

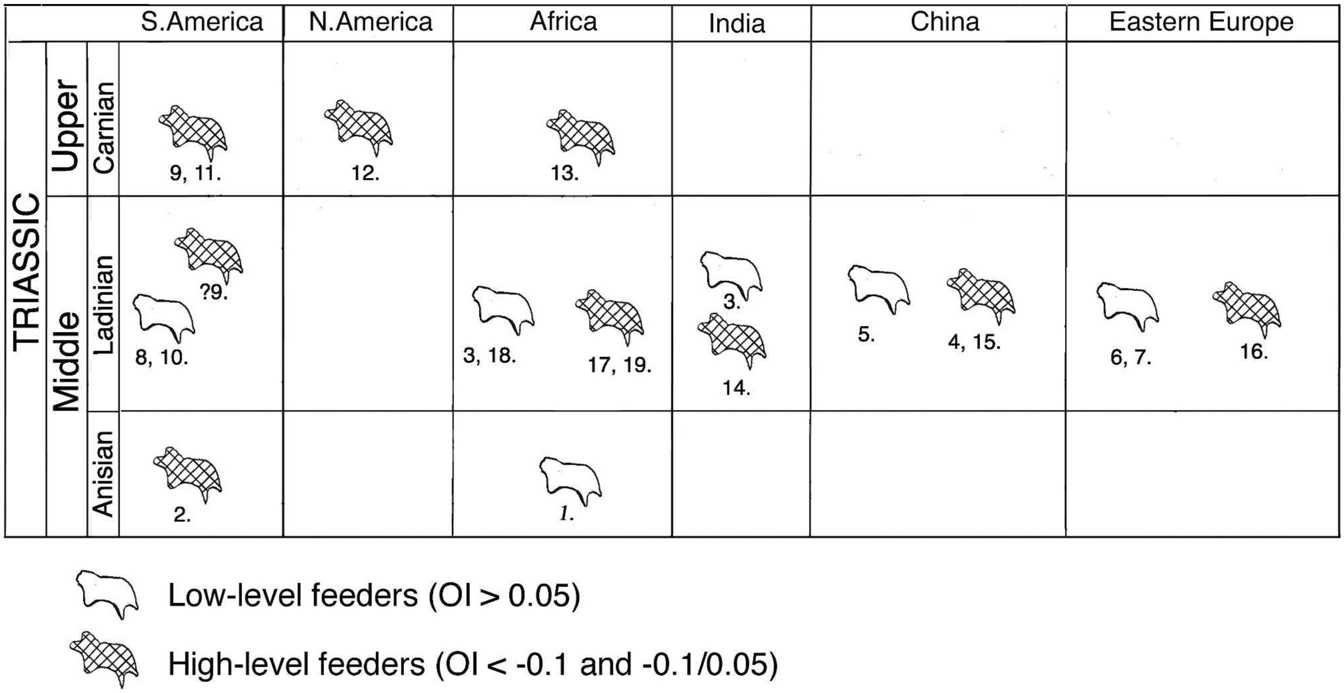

FIGURE 5. Paleogeographic and stratigraphic distribution of Middle and Late Triassic dicynodont high feeders and low feeders. **1**. *Kannemeyeria*; **2**. *Vinceria*; **3**. *Rechnisaurus*; **4**. *Parakannemeyeria*; **5**. *Sinokannemeyeria*; **6**. *Rhadiodromus*; **7**. *Uralokannemeyeria*; **8**.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

crisis. However, we are reluctant to discuss here the possible aquatic or non-aquatic adaptations of *Lystrosaurus* (Broom, 1902; King and Cluver, 1991) until a thorough comparative investigation of its postcranial morphology and skull proportions has been carried out.

CONCLUSIONS

The distribution of occipital indices in the phylogeny of dicynodonts shows that the main branching points are marked by taxa that had no particular preferences in head movement in the Permian, and low-level feeding was probably a basal attribute of Triassic forms. Specialization for vertical head movement appeared first, but existed only from the middle of the Wuchiapingian. Pronounced specialization for lateral head movement appeared only in the Anisian, but existed until the end of the Middle Triassic, when these dicynodonts may have competed with herbivorous gomphodonts, which may have been better adapted than the clumsy dicynodonts to escape from archosaur predators. The Late Triassic is characterized by the sole presence of specialized high feeders (*Moghreberia*, *Ishigualastia, Jachaleria*, *Placerias*) that fed higher then gomphodonts, and so may have inhabited forested areas, where the speed advantage of the archosaurian predators was less obvious.

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