ENDOTHIODONT DICYNODONTS FROM THE LATE PERMIAN KUNDARAM FORMATION, INDIA

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ABSTRACT. The Kundaram Formation, a Lower Gondwana unit of the Pranhita-Godavari valley, contains the only known Permian dicynodonts in India. This dicynodont assemblage is dominated by *Endothiodon*. Two species (*Endothiodon mahalanobisi* sp. nov and *Endothiodon uniseries* Owen 1879) are described here. This is the first detailed study of *Endothiodon* from outside Africa. The study shows that *Endothiodon* jaw articulation permitted propalinal action when the opposing serrations in the upper and the lower jaw teeth occluded with the horn covered areas and helped in shearing and mastication. The presence of oblique wear facets on the upper and lower jaw teeth and a masseter-like muscle suggest a slightly lateral movement of the lower jaw which enhanced slicing of plant matter. A robust stapes with posterolateral notch constitutes the middle ear region though *Endothiodon* depended mainly on ground vibrations for hearing. Other features included a reduced olfactory sense and large eyes for vigilance and ease of detecting predators. Based on its vertebrate fauna, this fossiliferous Gondwana horizon of the Pranhita-Godavari valley is broadly correlated with the *Tropidostoma* and/or *Cistecephalus* Assemblage Zones of the Beaufort Group, Karoo Supergroup, South Africa. It indicates a probable Tatarian age for the Kundaram Formation.

THE dicynodonts are an extinct group of herbivorous therapsids of the Permian and Triassic periods. They diversified into numerous genera and species during the Late Permian but suffered a marked reduction in generic diversity at the onset of the Triassic. The success of these dicynodonts lay in acquiring certain unique features, particularly in their skull morphology, that helped them in adapting to herbivory. The Permian dicynodonts are mostly documented from the continents that formed Gondwana except for reports from Scotland, Russia and China.

In India, the Kundaram Formation, a Lower Gondwana unit of the Pranhita-Godavari valley (Text-fig. 1A) yields the only Permian reptilian fauna (Kutty 1972; Ray 1997), though Permian fishes and amphibians are known from other Indian Gondwana basins. The vertebrate fauna of the Kundaram Formation consists of a dicynodont assemblage, dominated by *Endothiodon*. Other forms include *Cistecephalus*, *Pristerodon*, ?*Oudenodon* and *Emydops*-like forms. The non-dicynodont member is a captorhinid (Kutty 1972). *Endothiodon* is so far known from African countries like South Africa, Tanzania, Zambia and Mozambique. Some fragmentary remains of *Endothiodon* are also reported from Brazil. The paper presents the first detailed study of *Endothiodon* from outside Africa.

GEOLOGICAL SETTING

The fossil material was recovered from the Kundaram Formation in the north-western part of Pranhita-Godavari valley (Kutty 1972; Ray 1997) near Golet in Adilabad district, Andhra Pradesh (Text-fig. 1B). The Kundaram Formation, underlain and overlain by the Barakar and Kamthi Formations respectively (Table 1) is characterized by red mudstone, sandstone, sandstone-mudstone alternations and ferruginous shale.

The laterally persistent, trough cross-stratified sand bodies of the Kundaram Formation exhibit unimodal palaeocurrent direction and are formed by the lateral migration and avulsion of channels. Over these were deposited fine-grained sediments as overbank deposits. The overbank deposits, formed chiefly by an extensive mudstone unit, contain abundant land-dwelling vertebrate fossils including *Endothiodon*. Most of the materials are encrusted with hard iron matrix and form spherical and oblate nodules.
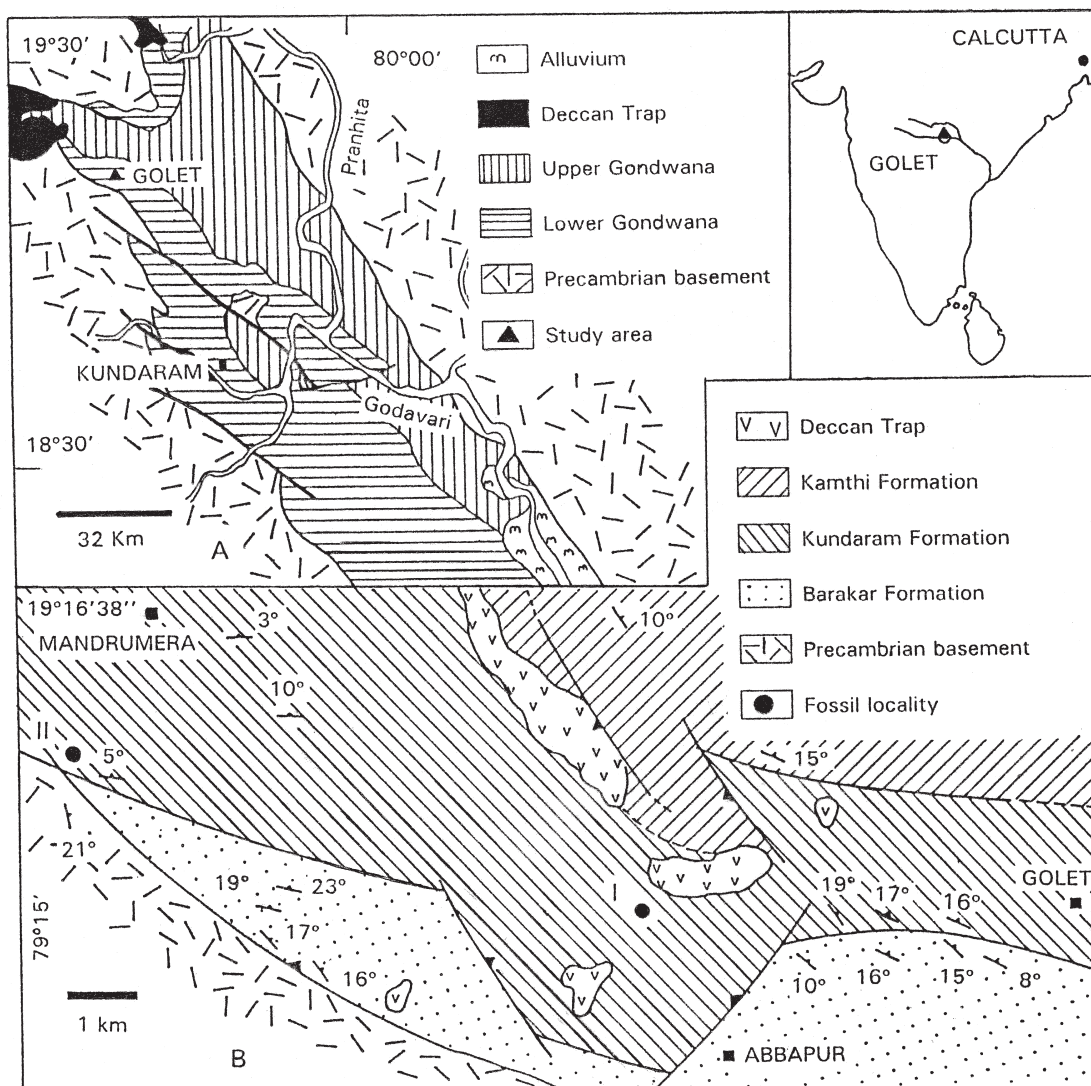
TEXT-FIG. 1. Geological maps. A, Pranhita-Godavari valley, India (after King 1881); inset, study area in India. B, study area showing the fossil localities I and II (after Ray 1997).

Institutional abbreviations. BMNH, Palaeontological Collection, The Natural History Museum, London; ISI, Geology Museum, Indian Statistical Institute, Calcutta.

SYSTEMATIC PALAEONTOLOGY

Infraorder DICYNODONTIA Owen, 1859
Family ENDOTHIODONTIDAE Lydekker, 1890

Genus ENDOTHIODON Owen, 1876

Type species. Endothiodon bathystoma Owen, 1876 from the Beaufort Group, South Africa.

TABLE 1. Lower Gondwana stratigraphy of the Pranhita-Godavari valley, India (after Kutty *et al.* 1987; Bose and Sengupta 1993; Ray 1997).

Formation	Main lithologies	Important fossils	Age
Kamthi			
Middle	Sandstone and	*Glossopteris* flora,	Triassic
Lower	siltstone	?dicynodont	
Kundaram	Mudstone, sandstone and ferruginous shale	Dicynodonts captorhinid	Late Permian
Barakar	Sandstone, carbonaceous shale and coal	*Glossopteris* flora	Late−Early Permian
Talchir	Tillite, greenish shale and sandstone	*Glossopteris* flora	Early Permian

Endothiodon mahalanobisi sp. nov.

Plate 1, figures 1−7; Plate 2, figures 1−3; Text-figures 2−10

Derivation of name. The name is given in honour of Professor Prasanta Chandra Mahalanobis, the founder of the Indian Statistical Institute who initiated systematic vertebrate palaeontological research in the Geological Studies Unit of ISI.

Holotype. ISI R201, a nearly complete skull with an associated lower jaw.

Paratypes. A nearly complete skull except the squamosals (ISI R214), several snouts and anterior parts of the skulls (ISI R202, ISI R211−215, ISI R218, ISI R220, ISI R340, ISI R342−343, ISI R345−347, ISI R359), anterior parts of skulls with associated lower jaws (ISI R341, ISI R344), posterior parts of the skulls (ISI R219, ISI R356−357) and several fragments of lower jaw (ISI R206−207, ISI R216, ISI R348−350, ISI R352, ISI R354−355, ISI R358, ISI R360).

Locality and horizon. The fossil localities (marked as I and II in Text-fig. 1B) are near Golet, Adilabad District, Andhra Pradesh, India; Lower Gondwana Kundaram Formation, Pranhita-Godavari valley, Late Permian.

Diagnosis. Small *Endothiodon*; skull length 160−172 mm; skull triangular in outline; greatest width across occiput; a prominent, broad and longitudinal ridge on the snout; elliptical pineal foramen situated on a very low boss, midway on the intertemporal bar; a deep depression near the dorsomedial margin of the occiput; stout stapes with deeply excavated notch; slender dentary symphysis; bulbous swellings on the anterolateral sides of dentary; deep angular cleft.

DESCRIPTION

Skull

General features (Pl. 1, figs 1−4; Text-figs 2−5). The skull is small in comparison to that of other known *Endothiodon* species. It is widest across the occiput resulting in a triangular outline. The snout tapers anteriorly and bears a prominent, broad and longitudinal ridge. The anterior margin of the snout bears a deep median notch. Along its border, the surface is characterized by numerous minute foramina. The nasal cavities open near the extremity of the snout by
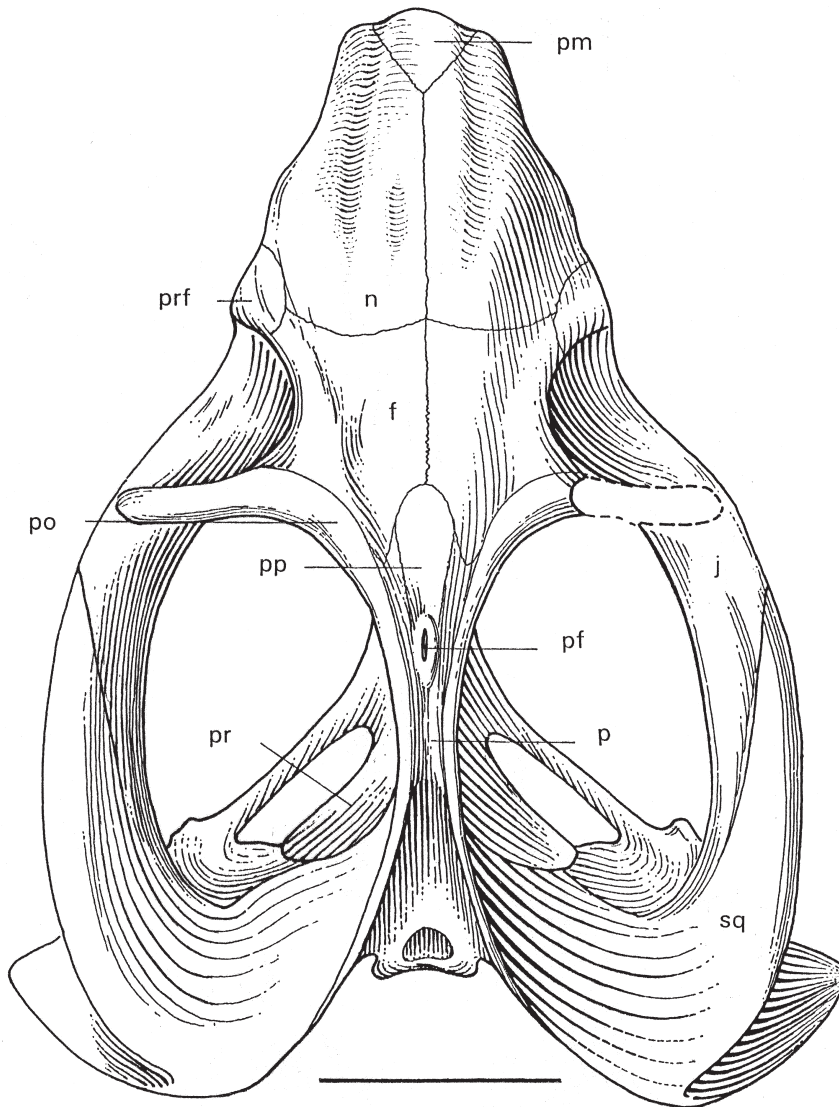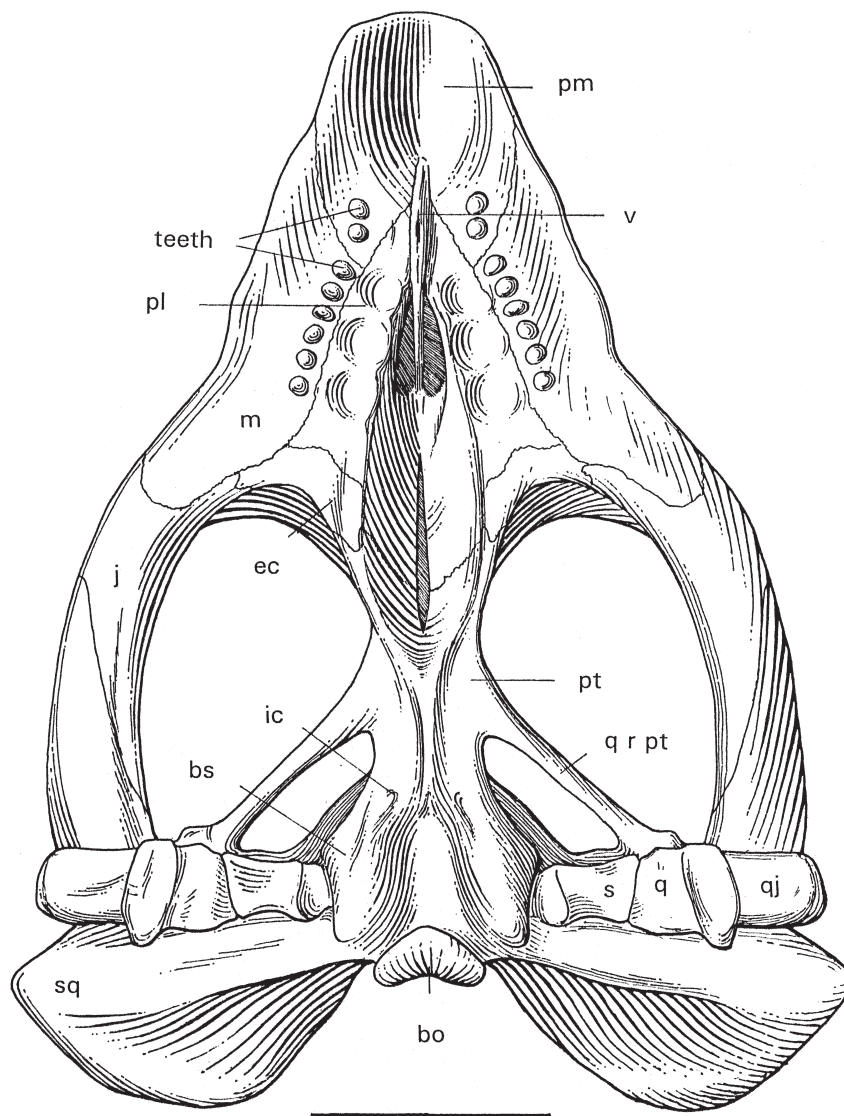
TEXT-FIG. 2. *Endothiodon mahalanobisi* sp. nov. ISI R201, restored skull in dorsal view. Scale bar represents 50 mm.

EXPLANATION OF PLATE 1

Figs 1–7. *Endothiodon mahalanobisi* sp. nov. 1–4, ISI R201, holotype; skull and lower jaw in 1, dorsal, 2, ventral, 3, lateral, and 4, occipital views; × 0·45. 5, ISI R219, partial occiput; × 0·8. 6–7, ISI R351, anterior part of the lower jaw in 6, dorsal, and 7, lateral views; × 0·4.

PLATE 1

RAY, *Endothiodon*

TEXT-FIG. 3. *Endothiodon mahalanobisi* sp. nov. ISI R201, restored skull in palatal view; additional features from ISI R211, ISI R214, and ISI R219. Scale bar represents 50 mm.

external nares and internally by a pair of elliptical internal nares. The external naris is oval-shaped (the long axis is 20 mm) and placed anterolaterally. The internal nares (*c*. 20 mm) are situated close to the midline of the palate. The measurements of the holotype skull ISI R201 are given in Table 2 and the measurements of other skulls and skull elements of *E. mahalanobisi* without any distortion corrections, are given in Table 3.

The orbital cavity relative to the skull size is quite large (along long axis 37 mm), nearly oval and anterolaterally positioned. The boundary surrounding this cavity is well defined and raised to form a prominent rim. The interorbital region is broad and measures about 50 mm in the holotype. In other specimens the interorbital region varies between 31·2 and 54·25 mm (Table 3). The width of the intertemporal bar is 12 mm in the holotype. In other specimens it varies between 12 and 26 mm, thus indicating its relative narrowness in comparison to the interorbital region. An elliptical

pineal foramen, situated on a very low boss, is located at the middle of the intertemporal bar. The temporal fenestra is large and extended posteriorly, a little beyond the level of the occipital condyle.

The anterior toothless region of the skull in palatal view is highly vaulted. The interpterygoid vacuity is about 80 mm in length. Laterally, a prominent posteroventrally directed boss is located at the junction of the suborbital, postorbital and zygomatic arches. The parietal crest is raised above the frontal plate. The occiput is about twice as broad as high and is characterized by the presence of a deep depression near its dorsomedial margin. The rest of the occiput is at a high angle or nearly vertical to the skull roof.

TABLE 2. Measurements in mm of the holotype skull (ISI R201) of *Endothiodon mahalanobisi* sp. nov.

1. Skull length	
(a) Measured along dorsal midline	160
(b) Over the squamosal wings	220
(c) At palatal midline	200
2. Preorbital snout length	59
3. Postorbital snout length	100
4. Length from anterior edge of premaxilla to the anterior edge of the pineal foramen	130
5. Length of pineal foramen	6
6. Skull width across the squamosals	155
7. Interorbital width	50
8. Intertemporal width	12
9. Snout width	78
10. Length of temporal fossa	121
11. Width of temporal fossa	72
12. Greatest width of occiput	175
13. Least squamosal width of occiput	86
14. Width of occipital condyle	19
15. Occipital height	68.4
16. Secondary palate length	56
17. Length of interpterygoid vacuity	80
18. Interquadrate distance	85

TABLE 3. *Endothiodon mahalanobisi* sp. nov. Measurements in mm of other specimens.

ISI Mus. Regn. No.	Snout length		Snout Width	Interorbital Width	Intertemporal Width	Occiput Height	Skull length	
	Preorbital	Postorbital					at dorsal midline	at palatal midline
ISI R202	45	76	35	35·45	13·05	—	—	—
ISI R211	42	82	67·25	42·4	—	—	—	—
ISI R212	50	—	38·75	31·2	—	—	—	—
ISI R213	64	—	67·25	—	—	—	—	—
ISI R214	50	86	76·8	54·25	21	78·9	172	175
ISI R215	67	—	59·2	45	—	72	—	—
ISI R219	—	—	—	—	—	70	—	—
ISI R220	46	—	68·15	—	—	—	—	—
ISI R340	53	—	55	—	—	—	—	—
ISI R341	44	—	55·85	43	—	—	—	—
ISI R342	51	—	50	44·55	—	—	—	—
ISI R344	27	—	46	35·35	16·1	—	—	—
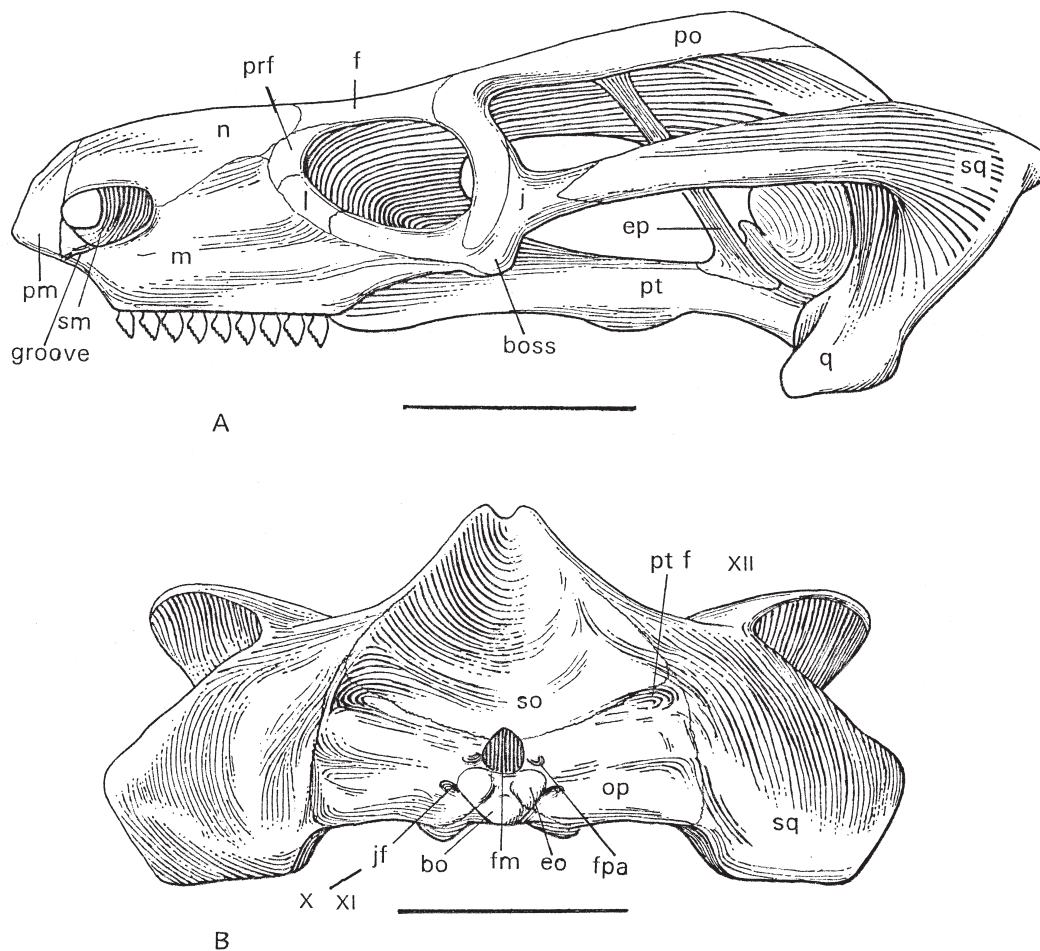
TEXT-FIG. 4. *Endothiodon mahalanobisi* sp. nov. ISI R201, restored skull in A, lateral, and B, occipital views; additional features from ISI R211, ISI R214, and ISI R219. C, facing page, index to Tables 2–3. Scale bars represent 50 mm.

Snout and skull roof (Text-figs 2, 4–5A). The anterior margin of the premaxilla is interrupted by a deep, median, V-shaped notch. Its dorsal surface bears a prominent, broad and longitudinal ridge, which continues posteriorly as the naso-frontal ridge. Anterolaterally the snout bears a prominent groove, just in front of the external nares. In dorsal view, a pair of large nasals occupies most of the skull roof along with the posteriorly placed paired frontals. The premaxillary ridge continues posteriorly over the nasals and is bordered on either side by a narrow depression. The small subrounded septomaxilla is completely recessed within the nasal cavity and forms its posteroventral margin. A small prefrontal posterolateral to the nasal is seen only in dorsal view. Posterior to the nasals is a pair of broad frontals with a highly interdigitated sutural contact between them. This region of the skull roof is slightly concave medially. The frontals form the raised dorsal rim of the orbit. Posterolaterally the frontal is also raised and continues posteriorly, and gradually converges and forms the anterior end of the parietal crest. A small, subrounded lacrimal, visible only in lateral view (Text-fig. 4A), and the posteroventrally placed jugal form the ventral margin of the orbit. The jugal is a triradiate element with its anterior end extended to form the posteroventral margin of the orbit. The jugal and the maxilla form a prominent boss, directed posteroventrally.

The postorbital ventrally meets the jugal with a U-shaped suture. Dorsally it continues posteriorly as a ridge forming the lateral boundaries of the narrow intertemporal bar. A semi-elliptical preparietal is placed medially on the skull roof and forms the anterior margin of the elliptical pineal foramen. Posterolateral to the preparietal, the paired and elongated parietals occur and continue backwards to the end of the parietal crest. The pineal foramen situated on a low
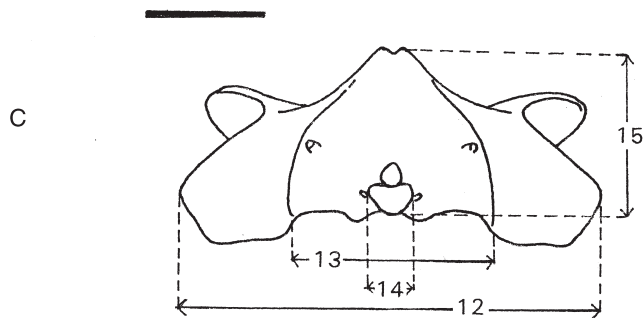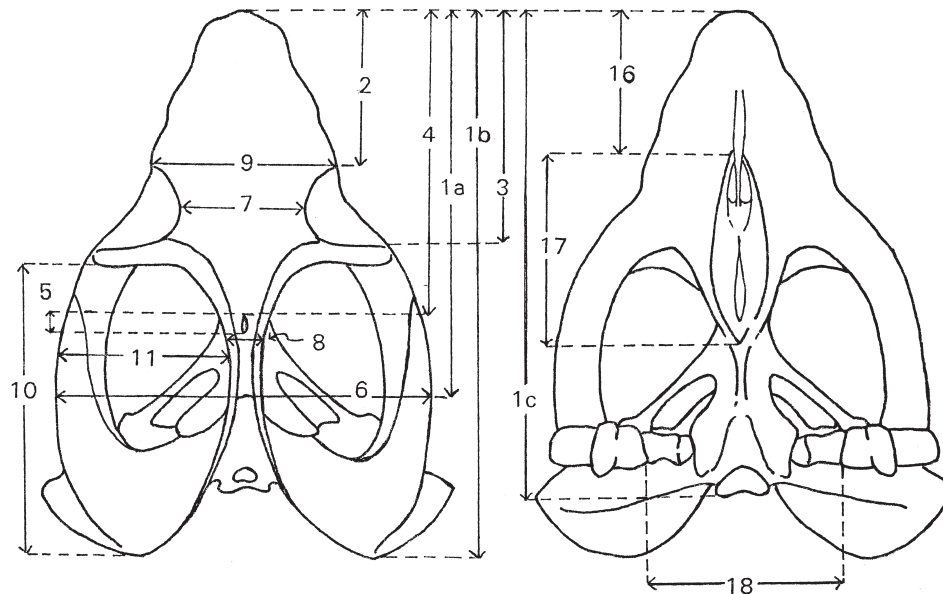
boss is bounded completely by the parietals except for its anterior margin, which is formed by the preparietal. The parietals meet at a long midline suture and have raised lateral edges on either side in such a way that a median groove runs longitudinally posterior to the pineal foramen. The parietal extends ventrally as a median lamina, posterior to the pineal foramen and is in contact with the supraoccipital at its ventral margin.

The posteriormost element in dorsal view is the squamosal, bearing the typical characteristic features of dicynodonts. Attached to the anterior face of the squamosal is the small fan-shaped quadratojugal. It is an extended plate-like element fused tightly with the quadrate placed medially.

Palate (Text-figs 3, 5). The anteriormost bone in palatal view is the premaxilla. It is composed of an anterior, deeply vaulted, toothless region and a posterior region bearing two teeth on either side of the palate. Medially the posterior margin of the premaxilla is interrupted by the presence of a vomer. Posterolateral to the premaxilla is the maxilla forming the sharp lateral rim of the palatal complex. The maxilla also bears a uniserial tooth row placed medially. A detail discussion on the dentition is given later. The slender sheet-like vomer located medially is trapezoid in shape in lateral view (Text-fig. 5B). This thin, median, ossified septum separates the pair of internal choanae and is in contact with the parasphenoid rostrum dorsally. It bears a longitudinal groove on its ventral surface and forms the anterior margin of the interpterygoid vacuity. The vomer possibly continued dorsally as a cartilaginous internasal septum.
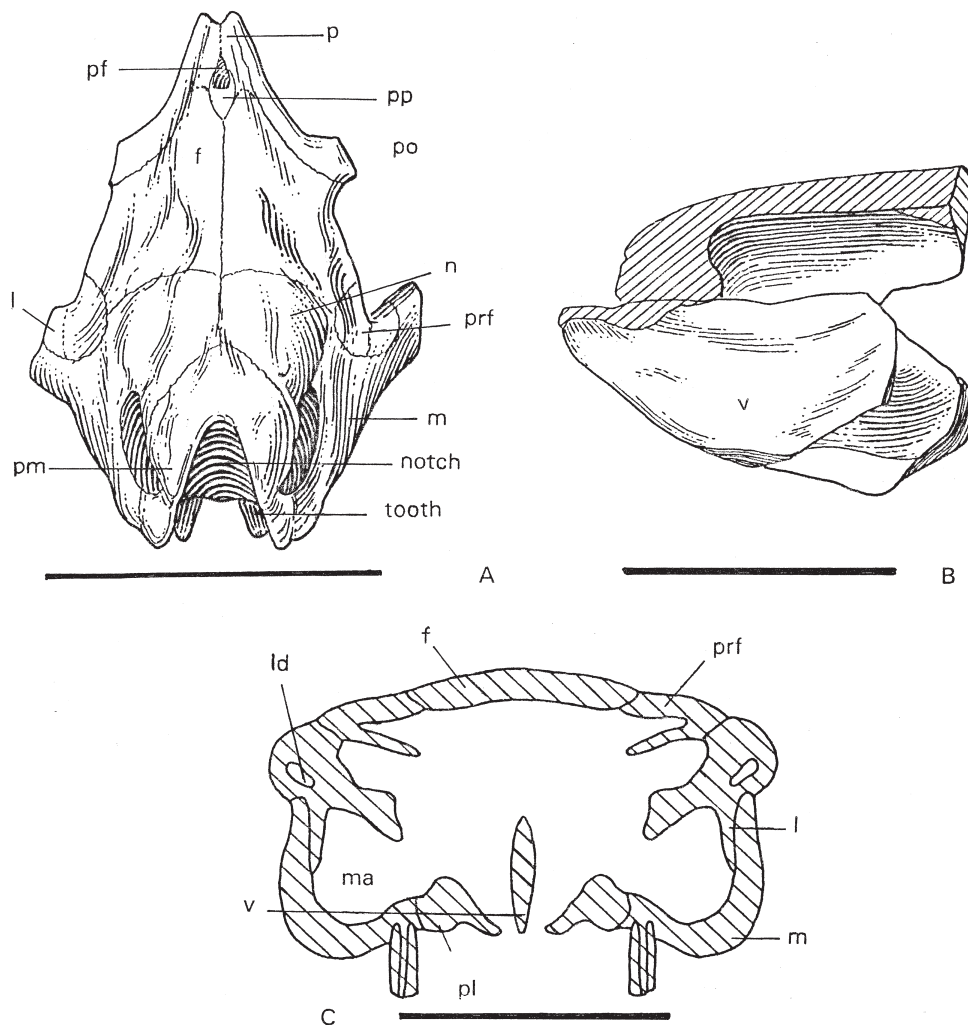
TEXT-FIG. 5. *Endothiodon mahalanobisi* sp. nov. A, ISI R202, anterior view of a partial skull showing the median notch. B, ISI R342, longitudinal section of the nasal cavity. C, ISI R220, transverse section through the posterior part of the snout. Scale bars represent 50 mm.

Large palatines border the upper jaw tooth row lingually. The ventral surface of the palatine is undulatory, bearing concavities, and has numerous small foramina. Anterodorsally it separates the maxillary antrum (Text-fig. 5c) from the nasal cavity. Beyond the palatine is the relatively small ectopterygoid. The major element located posteriorly on the ventral surface of the skull is the tetraradiating pterygoid. The two palatal rami of the pterygoid converge posteriorly behind the interpterygoid vacuity to form a thick and stout plate with a prominent median ridge. The two quadrate rami of the pterygoid are moderately thick, rod-like with expanded posterior ends and diverging from the pterygoid plate to meet the quadrate.

The parasphenoid-basisphenoid complex (Text-fig. 3) is fused with the posterior end of the pterygoidal plate. The basisphenoid consists of two anteriorly converging tubera separated by a deep median cleft. The faces of the tubera are laterally oriented, concave with a prominent median fenestra ovalis. Anteriorly there are deep notches marking the internal carotid canal at the convergence of the basisphenoid tubera. The parasphenoid is broad posteriorly while anteriorly it forms a slender rostrum extending between the interpterygoid vacuity and is attached to the vomer (ISI R202).
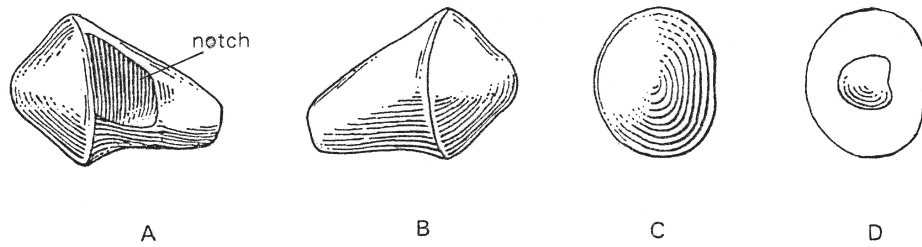
TEXT-FIG. 6. *Endothiodon mahalanobisi* sp. nov. ISI R219; right stapes in A, anteroventral, B, posterodorsal, C, medial, and D, distal views. Scale bar represents 20 mm.

The epipterygoid or the *columella cranii* is a slender rod-like bone (Text-fig. 4A) and rests on an expanded footplate. The footplate is situated on the anterior end of the quadrate ramus of the pterygoid. The epipterygoid ascends upward and slightly forward making an acute angle with the pterygoid. Medially it is attached to the ventrally directed parietal lamina. The quadrate-quadratojugal complex is divisible into two parts: a medial condyle with a shallow median depression and a wide plate extending laterally to form the much bigger lateral condyle. The medial condyle extends well below the ventral border of the lateral condyle resulting in an asymmetric Z-shaped profile. The medial face of the quadrate has a shallow concave facet on which rests the distal end of the stapes.

The stapes (Pl. 1, fig. 5; Text-fig. 6) is composed of a shaft with distal and proximal ends and lies loosely between the fenestra ovalis and the medial face of the quadrate. The medial region or the shaft of the stapes is short, robust and rod-like with slightly expanded ends. It is excavated posterodorsally to form a deep notch. The proximal end of the stapes is convex, slightly conical in shape and is fitted into the fenestra ovalis. The distal end is blunt and abuts against the concave medial face of the quadrate.

Occipital and otic regions (Text-figs 4B, 7). In posterior view the occiput is triangular in outline and bears a broad depression near its dorsomedial margin. The triangular occipital condyle with ventrally directed apex is situated in a median position near the ventral margin of the occiput. The central part of the condyle is concave while the sides (exoccipitals) and the lower part (basioccipital) are convex. Above the condyle and resting on its slightly concave dorsal surface is a large subtriangular foramen magnum. On either side is preserved a facet for articulation with the proatlas. Lateral to the condyle and piercing the exoccipitals is a pair of jugular foramina. The lateral margin of the occiput is formed by the thick, wing-like posterior part of the squamosal.

The upper part of the occiput is composed of a large, medially placed supraoccipital. It forms the dorsal margin of the foramen magnum. Ventrally it meets the rod-like opisthotics in a straight suture interrupted only by the prominent post-temporal fenestra. This fenestra forms a channel running anteromedially from the occipital plane to the anterior face of the occiput. The opisthotic also forms the posterior wall of the otic capsule. On the anterior face of the occiput, on either side, is a pair of large, flat, oval-shaped proötics, which form the anterior margin of the otic capsule.

Braincase (Text-fig. 7B–C). The basioccipital, forming the floor of the foramen magnum, extends anteriorly to form the floor of the braincase. The braincase is bordered posteriorly by the exoccipital and its roof is formed by the supraoccipital. The thick lateral sides of the braincase formed by the opisthotic posteriorly and proötic anteriorly, also enclose the otic capsule. The otic capsule continues as a canal and opens out ventrolaterally as the fenestra ovalis through the lateral face of the basisphenoid. This canal is bounded laterally by the basioccipital, anteriorly and posteriorly by the proötic and opisthotic respectively. Anteromedially from the ventral margin of the proötic a pila antotica rises on either side, extending upward towards the skull roof and enclosing the proötic incisure, a broad notch in the anterior margin of the proötic. The proötic meets the basispheniod anteriorly and the suture runs down from the base of pila antotica to the lateral rim of the fenestra ovalis. A prominent opening interrupts this suture. From the posterior face of the occiput, the jugular foramen extends anteromedially as a deep groove on the floor of the braincase between the basioccipital and the proötic.
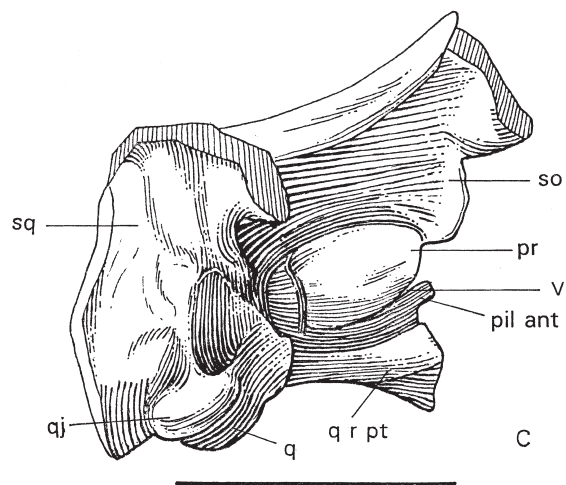
Anterior to the otic region, the basisphenoid forms the floor of the braincase and is fused ventrally to the parasphenoid. The sella turcica or the pituitary fossa forms a deep depression anteriorly beneath the brain
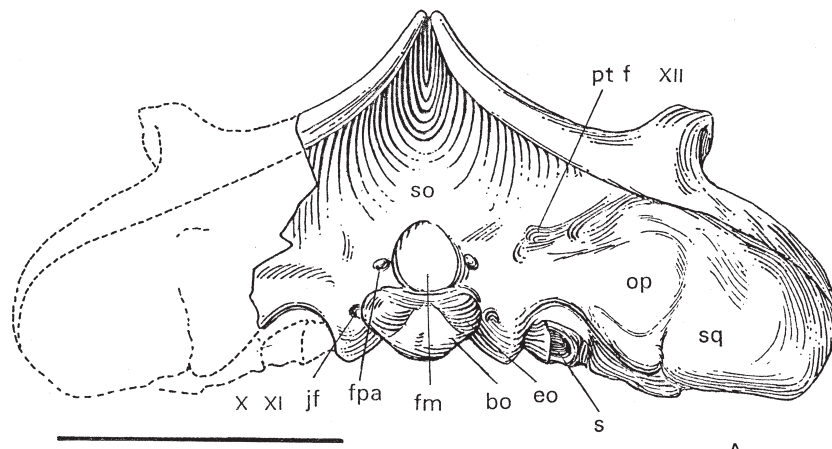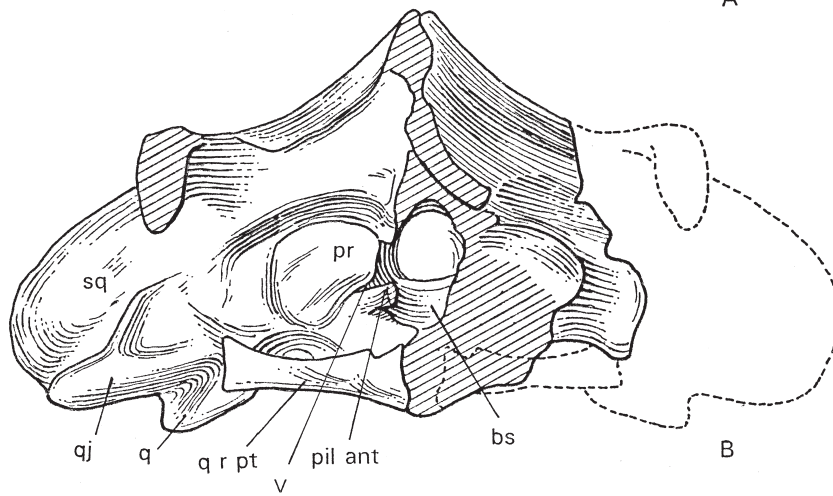
cavity (ISI R219). A vertical wall of the dorsum sellae lies posterior to this depression and forms a part of the braincase floor.

The braincase continues anteriorly as a narrow structure, the sphenethmoid complex, which is bordered ventrally by the parasphenoid. It is partly preserved in ISI R202. The spenethmoid ossification consists of a vertical plate, the presphenoid, bounded laterally and ventrally by the parasphenoid rostrum. Anterodorsally above the presphenoid, the mesethmoid complex is not clearly discernible in the specimens.

Blood vessels and cranial nerves. The number of foramina, cavities and notches present in the skull and braincase give some evidence regarding the passage of the blood vessels and cranial nerves. Most of the blood vessels and cranial nerves postulated by various workers for other dicynodonts (Camp and Welles 1956; Cox 1959; Kemp 1969; Cluver 1971; King 1981, 1988, 1990) can be seen in *E. mahalanobisi*. The passage of the internal carotid artery is marked by a deep notch at the base of the basisphenoid tubera (Text-fig. 4B), near the junction of the pterygoid and basisphenoid.

On the occipital surface, lateral to the foramen magnum, the jugular vein and cranial nerves X (Vagus) and XI (Accessory) presumably passed through the jugular foramen. This foramen extends anteromedially as a deep groove on the floor of the braincase. It also possibly allowed the emergence of an extension of the perilymphatic system of the inner ear (Romer 1956). Nerve IX (Glossopharyngeal) probably emerged separately through a nearby foramen posterior to the jugular foramen on the dorsal surface of the braincase floor. The posttemporal fenestra at the margin between the supraoccipital and opisthotics formed the opening for the passage of the nerve XII (Hypoglossal). It also served as a passage for the *vena capitis dorsalis*, which in modern reptiles drains the occipital musculature.

The trigeminal nerve (V) passed through the proötic incisure (Text-fig. 7C). A large opening interrupting the suture between the proötic and basisphenoid in the lateral sides of the braincase possibly indicates the passage of nerve VII (Facial). The *vena capitis lateralis* passed between the pila antotica medially and the epipterygoid laterally and through the pterygoparoccipital foramen to leave the skull by lateral head vein channel (Cluver 1971). Anteriorly, a small opening on either side of the dorsum sellae marks the passage of nerve VI (Abducens) from the braincase to the pituitary body. The cranial nerves I to IV (i.e. Oculomotor, Olfactory, Optic and Trochlear) were present in the sphenethmoid complex and their points of exit are not clearly seen in *E. mahalanobisi*.

Lower jaw

The anterior end of the lower jaw (Pl. 1, figs 6–7; Pl. 2, figs 1–3; Text-figs 8–9) formed by the fused dentary is quite massive in comparison to the post-dentary region. It is pointed, toothless and upturned so that it fits into the vaulted premaxillary region of the secondary palate. This anterior part of the dentary is characterized by numerous foramina indicating the presence of keratinized epithelium during its life. The anterolateral sides of the lower jaw are characterized by the presence of bulbous swellings positioned just anterodorsally with respect to the large elongated Meckelian fenestra. The extent of the Meckelian fenestra cannot be determined, as all the specimens are broken.

The dorsal surface of the dentary bears teeth and buccally on either side there is a deep groove, perforated by numerous foramina. A detailed discussion on lower jaw dentition is given later. The groove bordered by steep and high ridges (Text-figs 8A, 10), continues posteriorly and is expanded into a relatively large area where the groove becomes relatively shallow and is bordered by rounded ridges. Anteroventrally in the inner side of the mandible is the small, wedge-shaped splenial forming the ventral margin of the lower jaw.

In external view an elongated angular occupies the posteroventral part of the jaw ramus just below the surangular. It is characterized by the presence of a reflected lamina, which extends well below the ventral border of the lower jaw (Text-fig. 9A). The reflected lamina forms the ventral and posterior margin of the mandibular fenestra. The external surface of the jaw ramus posteriorly bears a prominent recessed area, the angular cleft, between the reflected lamina of the angular and the lateral margin of the articular. The prearticular (Pl. 2, fig. 3; Text-fig. 9B) is attached to the medial surface of the articular and runs along the inner surface of the jaw ramus as a broad and thick rod. The dorsal surface of the articular is widened transversely and bears typical dicynodont characteristics. Its lateral condyle is divisible into an anteriorly placed deeply concave facet and a posteriorly placed slightly convex area. The latter continues posteroventrally in the form of a prominent retroarticular process.

Dentition

The dental pattern of *E. mahalanobisi* is described here from single jaw quadrants such as ISI R206, ISI R207, ISI R216, ISI R349, ISI R354 and ISI R360. Associated right and left halves of the lower jaw (ISI R344) are also used for the description.

TEXT-FIG. 7. *Endothiodon mahalanobisi* sp. nov. ISI R219; partial occiput in A, posterior, B, anterior, and C, lateral views; hatched lines indicate broken surfaces. Scale bars represent 50 mm.

Upper jaw dentition (Text-figs 3, 9c). The upper jaw is characterized by a single row of thecodont teeth placed medially on either side of the palate. The tooth row is bordered laterally by a shallow, flat maxillary area. The two rows of teeth tend to converge anteriorly towards the median longitudinal axis of the palate. The number of teeth in each row is nine (ISI R346) with the first two on the premaxilla. The number varies between five and seven in other specimens (ISI R202, ISI R220, ISI R344). Each individual tooth is long (*c*. 10 mm in length), bearing a distinct crown and a long, tapering and cylindrical root. The crown is slightly posteriorly inclined, highly polished, often with oblique, subtriangular facets on the lingual sides. Though mostly broken, the anterior edges of the teeth on the mesial side bear prominent serrations. The mesial edges of the crown are slightly compressed giving it a pear-shaped cross-sectional area, the diameter of which varies between 4 and 6 mm.

Lower jaw dentition (Pl. 2, figs 1−2; Text-figs 8a, 9c−10). The tooth-bearing region of the lower jaw is mainly confined to the mid-dorsal surface of the dentary, which is bordered laterally by a deep longitudinal groove. The lower jaw tooth rows reflect diagonal tooth replacement where the anteriormost tooth is replaced sequentially by the one that is posteromedial to it on the lingual side. The multiple rows of teeth in specimens ISI R206 and ISI R207 can be arranged in oblique 'zahnreihen' or replacement waves. The diameter of the outermost oldest tooth is about 5 mm in ISI R206 whereas the inner one is the youngest and much smaller.

Lower jaw teeth are smaller and more closely spaced than the upper jaw teeth. In cross section the mesial edge is rounded whereas the lateral margins are slightly compressed posteriorly giving rise to a pear-shaped cross-sectional area. In ISI R207 the cross-sectional diameter of a functional tooth, measured parallel to the median longitudinal axis of the lower jaw is about 4 mm whereas the diameter transverse to it is about 2 mm. Lower jaw teeth are quite long, vary between 5 and 10 mm in different specimens, and bear distinct crowns. The distal edges of the lower teeth bear serrations and are mostly visible in the younger members of the replacement waves. In two of the specimens (ISI R349 and ISI R360) the lower jaw is comparatively smaller and bears only a single row of functional teeth. Each row contains about five or six teeth out of which only two are preserved intact in ISI R360. These two teeth are long (7 mm), pointed, conical, procumbent or inclined anteriorly with minute serrations on the distal margin, and circular in cross section (3 mm in diameter). The buccal side of the crown bears oblique wear facets. These two teeth show much simpler morphology.

Genus ENDOTHIODON Owen, 1876

Endothiodon uniseries Owen, 1879

Plate 2, figures 4−6; Text-figure 11

Holotype. Anterior half of a skull (BMNH 49414) from Beaufort West, South Africa and is housed at The Natural History Museum, UK. Horizon uncertain, Late Permian.

Referred specimens. Partial braincases (ISI R203, ISI R221, ISI R362), the latter with impressions of semicircular canals and lower jaw fragments (ISI R204, ISI R361/1−2, ISI R363−364).

Locality and horizon. The fossil localities (marked as I and II in Text-fig. 1b) are near Golet, Adilabad District, Andhra Pradesh, India; Lower Gondwana Kundaram Formation, Pranhita-Godavari valley, Late Permian.

Diagnosis. Medium-sized *Endothiodon*; skull length 275−350 mm; three prominent longitudinal ridges on the snout; circular pineal foramen situated on a high boss at the anterior end of the intertemporal bar; slender dentary symphysis.

EXPLANATION OF PLATE 2

Figs 1−3. *Endothiodon mahalanobisi* sp. nov. 1−2, partial lower jaw rami. 1, ISI R206; × 1·0. 2, ISI R207; × 1·0. 3, ISI R352, posterior part of the left mandible in internal view; × 1·0.
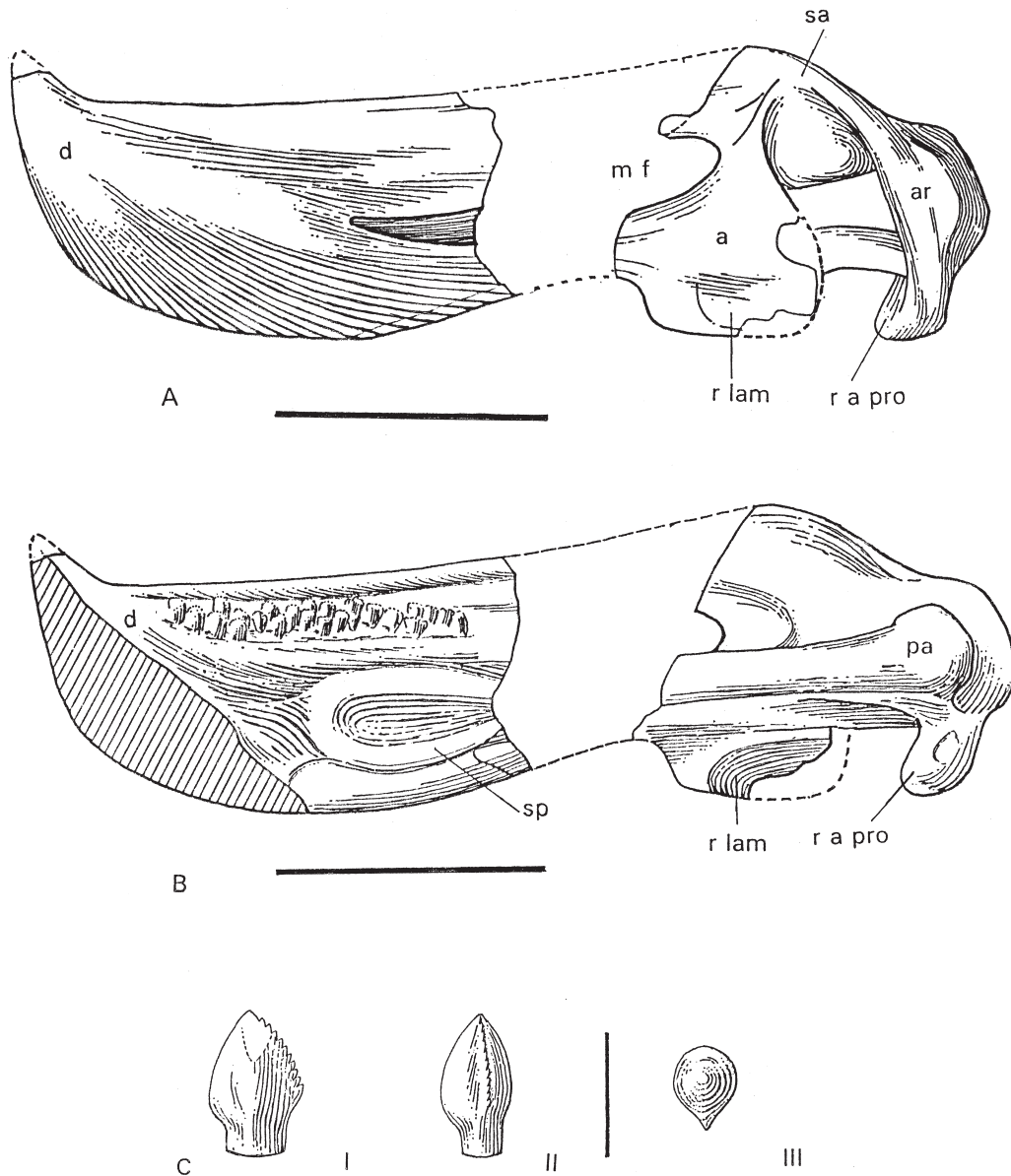Figs 4−6. *Endothiodon uniseries* Owen, 1879; 4, ISI R203, partial braincase in dorsal view; × 0·8. 5−6, ISI R363, anterior part of the lower jaw in 5, dorsal, and 6, lateral views; × 0·4.

PLATE 2
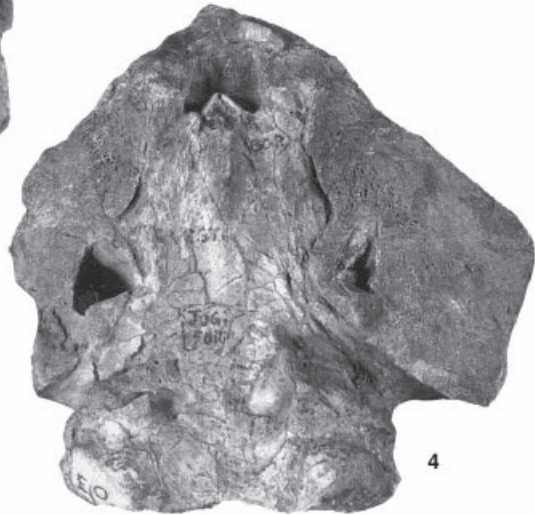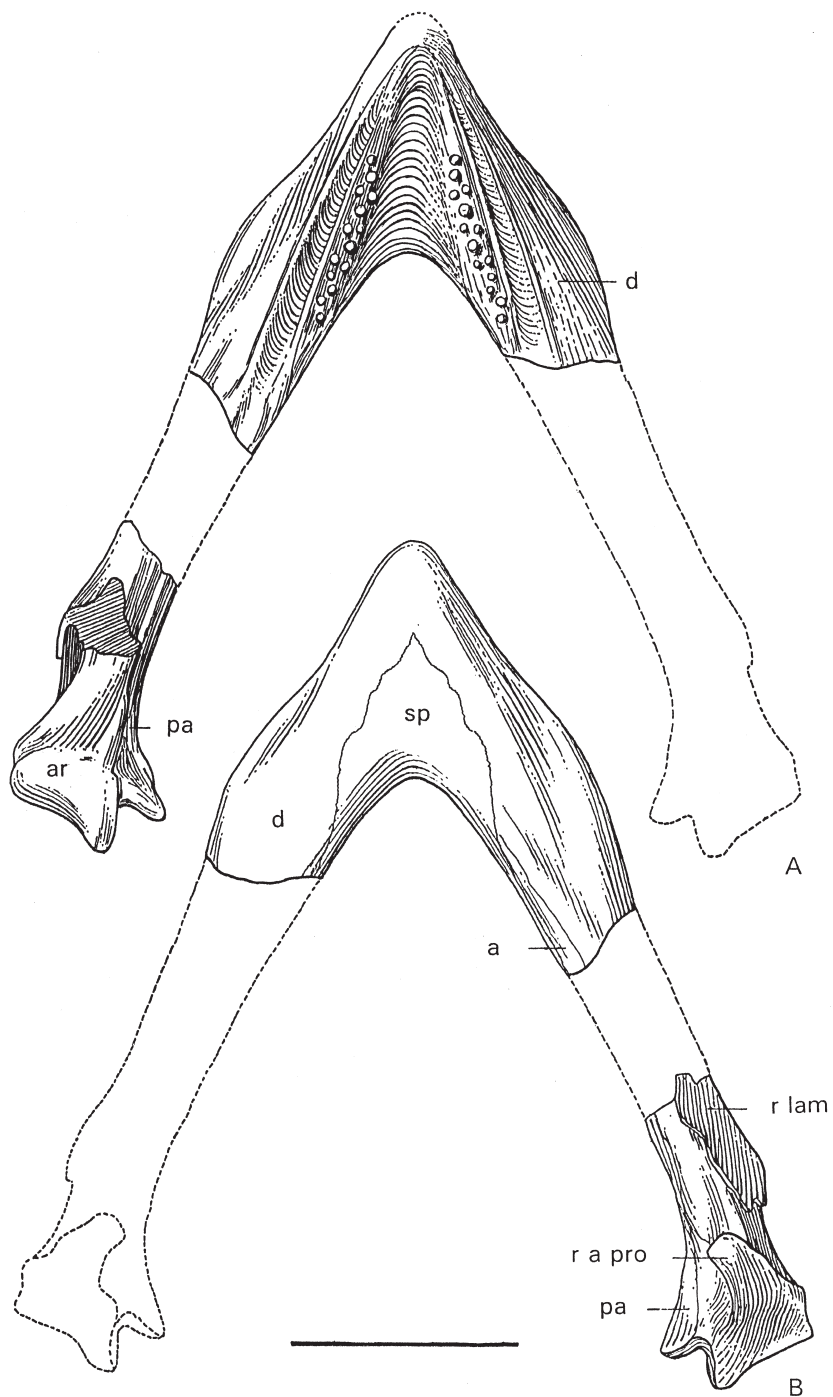
RAY, *Endothiodon*

TEXT-FIG. 8. *Endothiodon mahalanobisi* sp. nov. Restored lower jaw in A, dorsal, and B, ventral views; based on ISI R206, ISI R351–352 and ISI R354. Scale bar represents 50 mm.

TEXT-FIG. 9. *Endothiodon mahalanobisi* sp. nov. Restored lower jaw in A, external, and B, internal views; based on ISI R206, ISI R351−352 and ISI R354. Scale bars represent 50 mm. C, lower jaw tooth in I, lingual, II, distal, and III, occlusal views. Scale bar represents 10 mm.

DESCRIPTION

The *Endothiodon* specimens including several partial braincases and lower jaw fragments are relatively larger than *E. mahalanobisi*. The skull lengths are inferred to be about 350 mm and the dentary symphyseal regions are quite slender. The specimens are thus assigned to *Endothiodon uniseries* based on the larger skull and slender lower jaws.
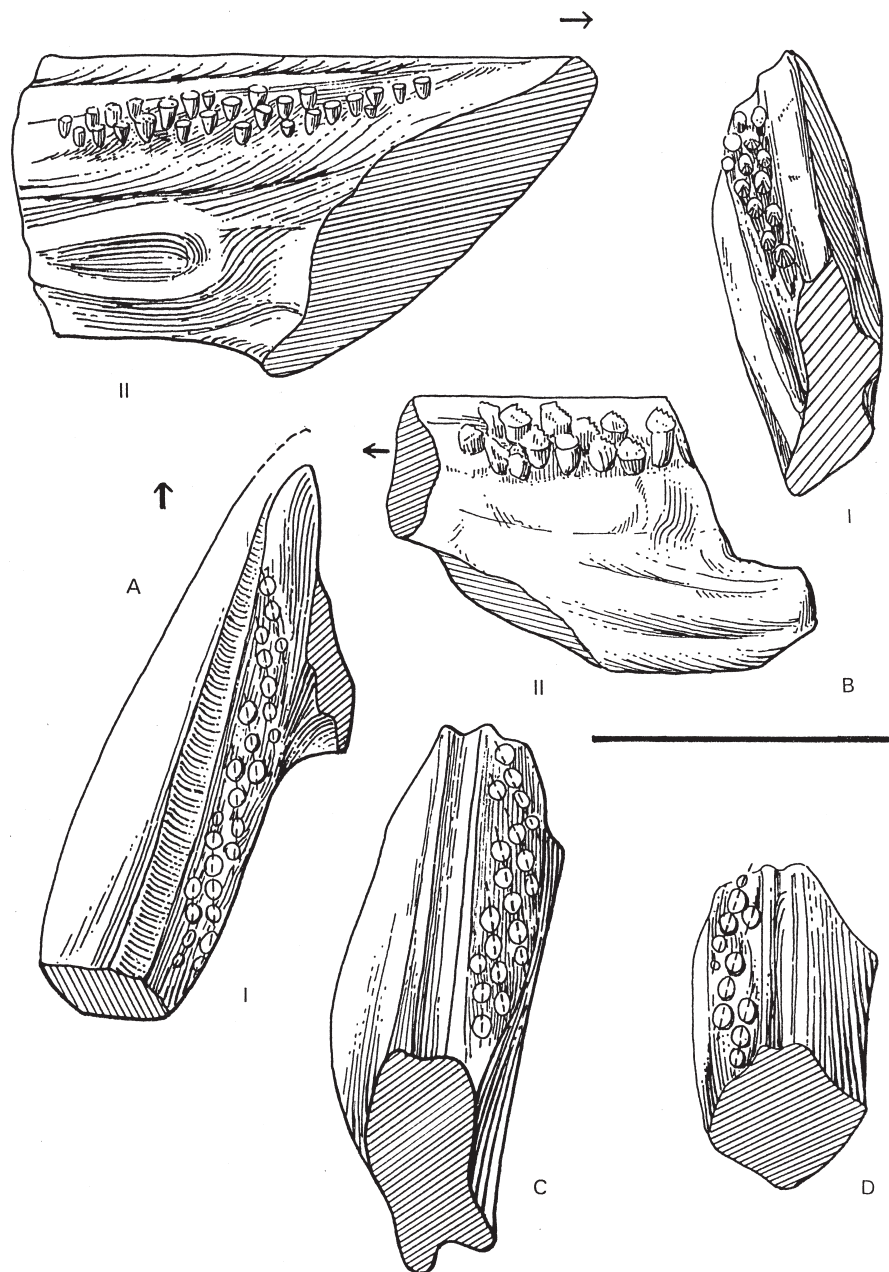
TEXT-FIG. 10. Partial lower jaw rami of *Endothiodon mahalanobisi* sp. nov. A, ISI R206, in I, dorsal, and II, internal views. B, ISI R207 in I, dorsal, and II, internal views. C, ISI R216 in dorsal view. D, ISI R348 in dorsal view; anterior end is marked by an arrow and the dashed lines indicate the replacement waves. Scale bar represents 50 mm.

Skull

Occipital region. The occipital region and the braincase are described from the specimens ISI R203, ISI R221 and ISI R362. A large kidney-shaped occipital condyle (long axis *c.* 54 mm) with a ventrally directed apex is situated in a median position near the ventral margin of the occiput (ISI R203). The sides of the condyle, formed by the exoccipitals
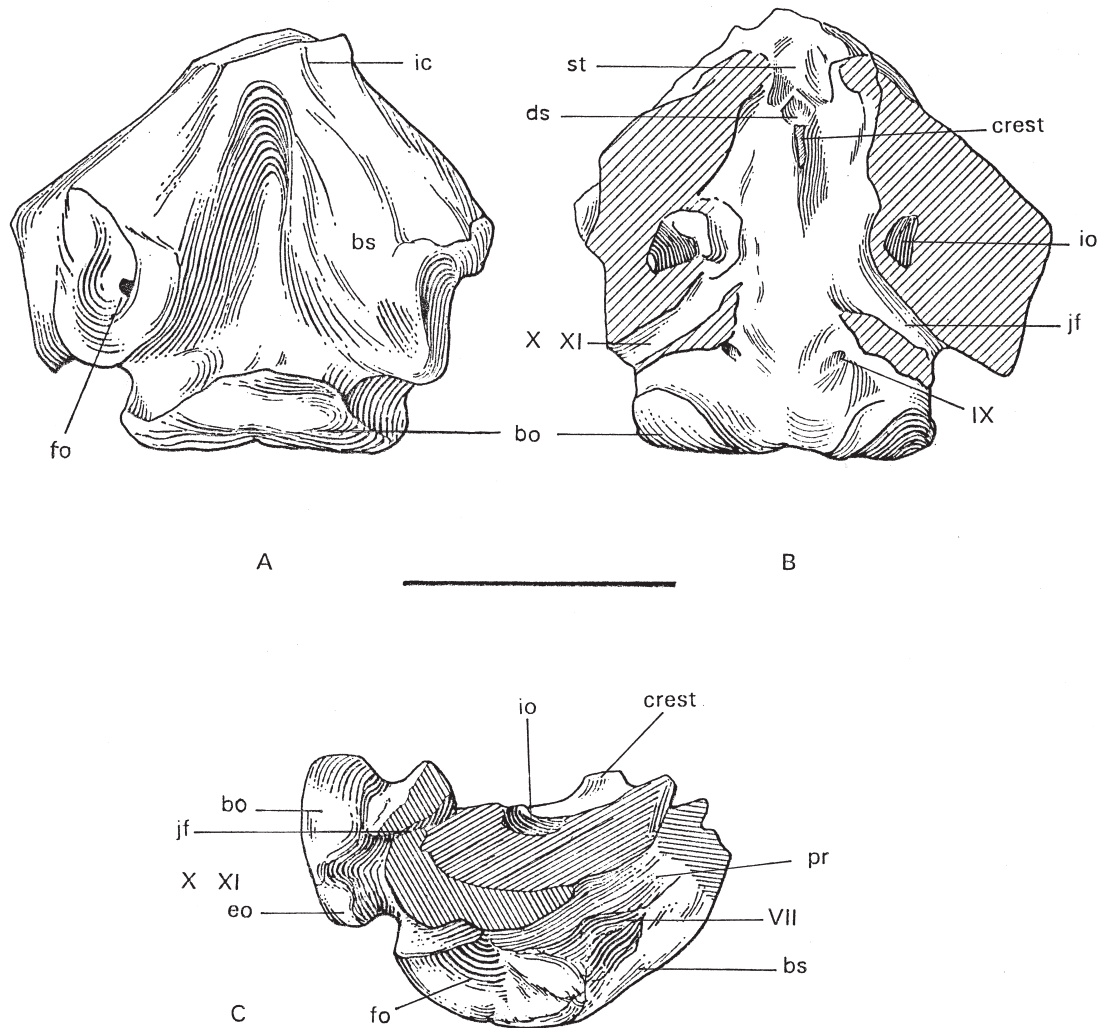
TEXT-FIG. 11. *Endothiodon uniseries* Owen 1876. ISI R203; partial braincase in A, ventral, B, dorsal, and C, lateral views; hatched lines indicate broken surfaces. Scale bar represents 50 mm.

are convex. The lower convex part of the condyle is formed by the basioccipital. The occipital condyle is quite depressed centrally. Lateral to the condyle and piercing the opisthotics is a prominent opening, the jugular foramen, for the passage of the jugular vein and cranial nerves X (Vagus) and XI (Accessory).

In ventral view, ISI R203 consists of two prominent tubera which converge anteriorly and are separated by a deep median cleft (Text-fig. 11A). The faces of the tubera are oriented laterally and contain prominent fenestra ovalis. Anteriorly there are two deep notches where the tubera meet and mark the passage of the internal carotid artery.

Braincase (Pl. 2, fig. 4; Text-figs 11B–C). Part of the braincase is available for study. The floor of the braincase and the inner opening of the internal otic meatus is seen in the dorsal view of the specimen ISI R203. A part of the otic capsule with impressions of the semicircular canals is preserved in ISI R221. The floor of the braincase is formed by the forward extension of the basioccipital and the basisphenoid. The floor is slightly concave, cup-like and gradually rises anteriorly to form a median crest. Anteromedially from the ventral margin of the proötic rises the pila antotica. Anteriorly, just below the floor of the braincase, is a deep depression, the sella turcica. The posterior wall of this fossa

is formed by the floor of the braincase. The inner openings of the internal otic meatus are present on either side of the braincase floor. A large opening on the lateral sides of the braincase, at the junction of proötic and basisphenoid indicates the passage of cranial nerve VII (Facial).

Lower jaw

The description of the lower jaw is based on ISI R204, ISI R361/1–2, ISI R363–364, which comprise mainly the symphyseal region of the dentary. The posterior part of the lower jaw is not preserved (Pl. 2, figs 5–6). The anterior part of the lower jaw, formed by the dentary, is slender, upturned and toothless. The dentary symphysis is strongly fused. The presence of numerous foramina on the anterior part of the dentary indicates probable covering of this area with tough integument. Teeth arranged in diagonal replacement waves characterize the tooth-bearing region of the dentary. The dentary extends near the posterior margin of the Meckelian fenestra. Internally there is a small wedge-shaped splenial, which also forms the anteroventral margin of the lower jaw.

SOME COMMENTS ON *ENDOTHIODON*

The family Endothiodontidae, originally proposed by Lydekker (1890), contained numerous divergent forms grouped together based on the retention of the postcanine teeth. The four main endothiodont genera, *Endothiodon*, *Esoterodon*, *Endogomphodon* and *Emydochampsa*, were separated under a new subfamily Endothiodontinae (Haughton and Brink 1954) based on certain characters such as the presence of a single or multiple rows of teeth, the degree of flattening of the skull, and the pointed or blunt snout. Cox (1964) first started to sort out all the endothiodont taxa and showed that the differentiating characters mentioned earlier were not valid. He considered (p. 10) the degree of flattening of skull and the pointedness of the snout as a 'postmortem artefact of fossilization' and synonymized the four genera into *Endothiodon*. Cox (1964) defined *Endothiodon* as medium to large dicynodonts (skull length 275–570 mm) with a wide interorbital region, narrow intertemporal bar, high parietal crest and a single row of teeth placed far posteriorly and internally.

Three species of *Endothiondon* were distinguished on the basis of the skull size and robustness of the lower jaws (Cox 1964; Cluver and King 1983; King 1988). These are *Endothiodon uniseries* [skull length (SL) 275–350 mm and slender dentary symphysis], *Endothiodon bathystoma* (SL *c*. 380 mm, robust dentary symphysis), and *Endothiodon whaitsi* (SL *c*. 570 mm, robust dentary symphysis). The present study has resulted in the description of a new species of *Endothiodon*, namely *E. mahalanobisi*. It has certain unique features such as small size, with the skull length varying between 160 and 172 mm, a single, broad, longitudinal ridge on the snout, elongated pineal foramen situated on a low boss, located midway on the intertemporal bar, and slender dentary symphysis. The features distinguishing all the different *Endothiodon* species are given in Table 4. This shows that the generic diagnosis of *Endothiodon* as proposed by Cox (1964) and Cluver and King (1983) requires some modification.

Some of the features used earlier for generic diagnosis actually indicate specific distinctions while the addition of certain new features results in further precision of the diagnosis. Cox (1964) and Cluver and King (1983) considered the skull length of *Endothiodon* as an important diagnostic feature at both the generic and specific level. The skull size of *Endothiodon mahalanobisi* is found to range between 160 and 172 mm. However, the highly interdigitated sutural contact between bones and quite well-developed teeth indicate that the skulls and lower jaws belonged to adult individuals: small size is not, therefore, because the animals were juveniles.

Another diagnostic feature of *Endothiodon* was the presence of three longitudinal ridges on the snout (Cox 1964). However, *E. mahalanobisi* is characterized by single broad ridge running longitudinally and posteriorly over the nasals. Thus, this feature forms a diagnostic character at specific level. The shape and position of the pineal foramen on the intertemporal bar are also indicative of specific distinction. In *E. mahalanobisi* the pineal foramen is elliptical and situated midway on a very low boss on the intertemporal bar while in all the other species of *Endothiodon*, it is circular in shape and situated on a high boss at the anterior end of the intertemporal bar. As suggested by Cox (1964) the depth and robustness of the symphyseal region of the dentary is also found to vary at specific level. In *E. uniseries* and *E. mahalanobisi*, the anterior part of the dentary is quite slender in comparison to the highly robust and deep dentary of

TABLE 4. Distinguishing features of the *Endothiodon* species (all measurements in mm).

Feature	E. mahalanobisi sp. nov.	E. uniseries	E. bathystoma	E. whaitsi
Skull size	160–172	275–350	c. 380	c. 570
Snout	a broad and longitudinal ridge	←——— three longitudinal ridges ——————→		
Interorbital region	wide	←——— wide with swollen prefrontal ——————→		
Intertemporal bar	←——— very narrow with the postorbitals overlapping the parietals ——————→			
Parietal crest	←——— highly raised above the frontal plate ———→			
Pineal foramen (pf)	elliptical pf, situated on a low boss midway on the intertemporal bar	circular pf, situated on a high boss at the anterior end of the intertemporal bar		
Tooth row	←——————— uniserial tooth row shifted medially ——————————→			
Dentary symphysis	←——————— slender ——————→		←——— robust ———→	

E. bathystoma and *E. whaitsi*. Another feature found in all species of *Endothiodon* is a prominent bulbous swelling on the anterolateral sides of the dentary; this may be considered a characteristic feature of the genus. The presence of a shallow groove lateral to the upper jaw tooth row was suggested by Cox (1964) and Cluver and King (1983) to be a diagnostic feature.

Thus the present study reveals that the genus *Endothiodon* includes dicynodonts of variable sizes, the skull length ranging between 160 and 570 mm. Other characteristic features, apart from those cited by Cox (1964), include longitudinal ridge(s) on the snout, pineal foramen situated on a boss, large palatines bearing concavities, slender or robust dentary symphysis, prominent bulbous swelling on the anterolateral sides of the dentary, teeth on the mid-dorsal surface of the dentary, a deep, longitudinal groove occuring lateral to the tooth row, lower jaw teeth arranged in replacement waves and an angular bearing a cleft.

FUNCTIONAL MORPHOLOGY

Feeding

The dicynodonts are considered to be the most successful land herbivores of the Permian and Triassic periods. The interaction between the dicynodonts and the existing vegetation (lycopods and horsetails) of these periods resulted in certain innovative features in dicynodont skull morphology such as the preorbital shortening of the skull, enlarged temporal fenestra to increase the site of origin of the adductor jaw muscles and a jaw hinge structure permitting propaliny. Features such as acquisition of beak and horn-covered areas in the mouth at the expense of the teeth were also effective in mastication.

The jaw articulation of *E. mahalanobisi* lies exclusively between the quadrate-quadratojugal complex and articular (Text-fig. 12). Though these bones do not vary much from those of the other typical dicynodonts, the quadrate-quadratojugal complex, which corresponds with the articular surface, has an asymmetric Z-shaped profile (Text-fig. 12A). Laterally the articular is further divisible into an anterior, deeply concave facet for jaw retraction and a posterior, slightly convex surface for jaw protraction during the fore and aft movement of the lower jaw (Text-fig. 12B). This type of jaw articulation permitting antero-posterior movement of the lower jaw was essential for masticating plant matter. The articulating surfaces were probably carpeted by smooth, slippery, pressure-bearing tissues capable of sustaining considerable loading force. The asymmetric Z-shaped profile of the jaw joint and the presence of a plate-like lateral condyle of the quadrate-quadratojugal complex possibly gave greater mobility to the lower jaw with the mouth remaining closed and in a protracted position as discussed later.

Jaw musculature (Text-fig. 13). The fore and aft movement of the lower jaw was made possible by the peculiar pattern of dicynodont jaw musculature that is reflected in *E. mahalanobisi*. The jaw musculature
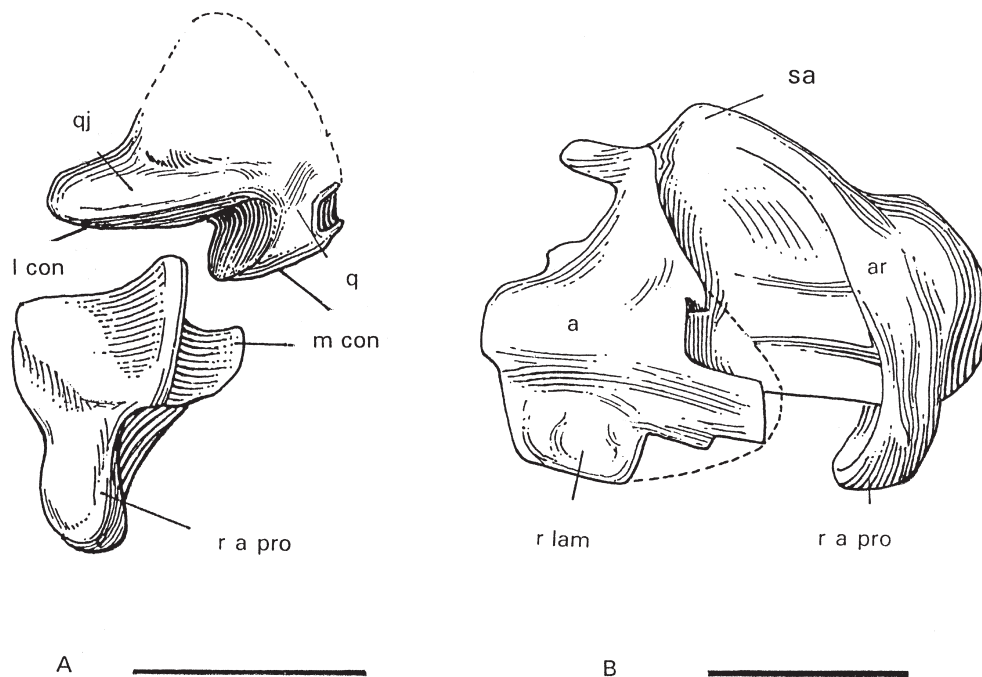
TEXT-FIG. 12. *Endothiodon mahalanobisi* sp. nov. A, quadrate-quadratojugal complex and articular in posterior view; based on ISI R219 and ISI R352. B, ISI R352, posterior part of the left mandible in external view. Scale bars represent 30 mm.

in *E. mahalanobisi* is reconstructed here based on the works of Watson (1948), Ewer (1961), Crompton and Hotton (1967), Cluver (1971, 1975), Barghusen (1973), King (1981) and King *et al.* (1989).

1. *Areas of origin of jaw adductor muscles.* The highly enlarged temporal region of the skull of *E. mahalanobisi* (ISI R201) provides an area for the origin of two major external adductor muscles. The lateral external adductor (a e l) originated from the posterolateral region of the zygomatic arch and the anterolateral face of the wing-like squamosal while the medial external adductor (a e m), orginated from the lateral, posteror and the medial margins of the antero-posteriorly elongated temporal fossa. A prominent recesssed area below the lateral margin of the intertemporal bar bounded medially by parietal lamina and anteriorly by the ascending epipterygoid was considered by Cluver (1975) to be the site of origin of the pseudotemporalis muscle. King (1981) suggested that a deeper slip of the a e m originated from this recess. The pseudotemporalis originates from the epipterygoid in the modern chelonians. A part of the muscle also originates from the anterior part of the supratemporal fenestra in *Sphenodon* and lizards. This recessed area in *E. mahalanobisi* skull is not very deep or large but the pseudotemporalis may have originated from the lateral surface of the epipterygoid as in *Oudenodon* (King 1981).

Cox (1959, 1964) considered the posteroventrally directed boss formed by the maxilla and jugal as the site of origin of strong masseter muscles in *Endothiodon*. There is a prominent boss in *E. mahalanobisi* (Text-fig. 3A) similar to that found in the Triassic cynodont *Diademodon* (King 1996). It probably served as the area of origin of a small, undivided muscle similar to the mammalian masseter (ms). The antero-medial face of the quadrate-quadratojugal complex of *E. mahalanobisi* is a large, plate-like complex and was probably the site of origin of the posterior adductor muscle as in extant reptiles. The lateral face of the anterior process of the quadrate in *Dimetrodon* and *Chelydontops* are also considered to be the site of origin of the posterior adductor muscle (Barghusen 1973; Cluver 1975).
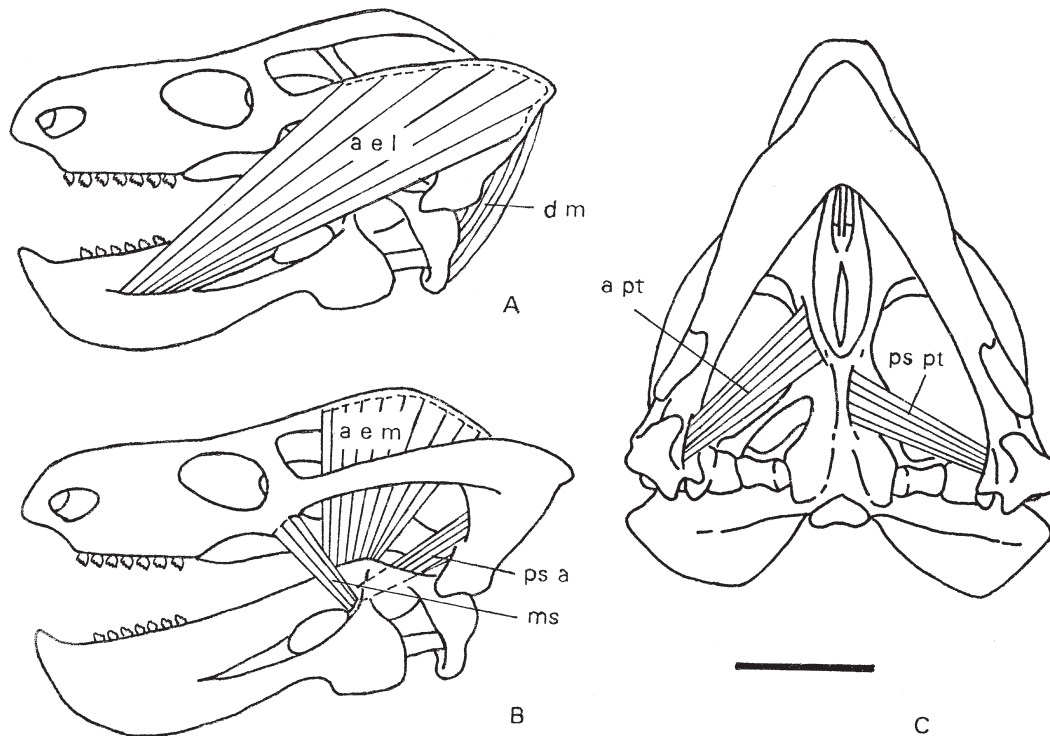
TEXT-FIG. 13. Reconstruction of the main jaw musculature in *E. mahalanobisi* sp. nov. Scale bar represents 50 mm.

In the dicynodonts, the transverse process of the pterygoid is much reduced resulting in the reduction of the sites of origin of the pterygoideus muscles, which were also much reduced in bulk and strength (King 1990). Two parts of the pterygoideus muscles are recognized, the anterior and posterior (Barghusen 1973; King *et al.* 1989; King 1990). In *E. mahalanobisi* the median pterygoid plate in the palatal surface consists of a prominent crest. The lateral edge of the anterior ramus of the pterygoid and the lateral edge of the median pterygoid crest are the sites of origin of the anterior and posterior pterygoideus muscles respectively.

2. *Areas of insertion of jaw adductor muscles.* The lateral dentary shelf present in most dicynodont lower jaws was considered by various workers, such as Crompton and Hotton (1967), Cluver (1971) and King (1981, 1988, 1990), as the probable site of insertion of the a e l. The lateral sides of the lower jaw of *Endothiodon mahalanobisi* have bulbous swellings just anterior to the Meckelian fenestra (Text-fig. 8). These dorsal surfaces of the swellings are marked by short, deep and irregular striations and are the probable insertional areas for the lateral external adductor muscle.

There are several views regarding the areas of insertion of the a e m on dicynodont lower jaws. Crompton and Hotton (1967) suggested that the longitudinal grooves on the dorsal surface of the dentary and the anterior part of the surangular were the sites of insertion of an a e m. The 'coronoid eminence' of *Chelydontops* was considered by Cluver (1975) as the insertional sites of an a e m. According to King (1981) the medial face of the lower jaw of *Dicynodon trigonocephalus* is the probable insertional area. The deep, longitudinal grooves bordered by steep ridges on the dorsal surface of the dentary lateral to the tooth row in *E. mahalanobisi* are pitted with foramina, indicating that the lower jaw of *E. mahalanobosi* in this area was also horn-covered, thereby decreasing the possibility of an a e m insertion in this region. On the other hand, the dorsal surface of the dentary in *E. mahalanobisi* expands posteriorly and bears prominent but rounded ridges. These ridges are considered to be the insertional areas for an a e m.

The masseter-like muscle in *Endothiodon* was inserted on the external surface of the lower jaw ramus. Different views exist regarding the insertional area of this muscle in the cynodonts (Barghusen 1968; Kemp 1979). Crompton (1995) inferred that the masseter muscle in the early cynodonts was inserted on the 'tip of the coronoid process'. Such a feature is not present in the *Endothiodon* lower jaw. It may be suggested that the masseter-like muscle was probably inserted on the posterolateral surface of the dentary, just above the Meckelian fenestra.

The internal adductor muscles in dicynodonts are much reduced compared with the external adductors. The pseudotemporalis muscle had a fleshy attachment on the inside of the lower jaw just above the Meckelian fossa in *Chelydontops* (Cluver 1975). The insertion area of this muscle in *E. mahalanobisi* is same as in *Chelydontops altidentalis*. The sites of insertion of posterior adductors were considered by Cluver (1975) in and around the Meckelian fossa on the inner side of the lower jaw. The posterior end of the fossa in the inner side of the lower jaw of specimen ISI R352 bears fine striations and is the probable site for muscle insertion of the posterior adductor in *E. mahalanobisi*. The rod-like prearticular in the inner side of the mandible borders a recessed area dorsally. This is the possible insertional area of the pterygoideus muscle.

3. *Jaw opening muscle*. The main jaw opening muscle or the depressor mandibulae (dm) originates on the lateral edge of the wing-like squamosal in *E. mahalanobisi*. The posteroventral end of the articular is extended into a prominent retroarticular process in *E. mahalanobisi* and is the probable area of insertion of the depressor mandibulae.

Dentition. The genus *Endothiodon* is atypical among dicynodonts because of its dentition pattern. Cox (1964) showed that the upper and the lower jaw teeth of *E. bathystoma* possess opposing serrations. The species had a single row of functional teeth and shows different modes of tooth replacement in the upper and the lower jaws. King (1990) described the upper jaw teeth of *Endothiodon* as widely spaced, circular in cross section with no serrations on the crown. The lower jaw teeth are relatively smaller, arranged in multiple rows and very closely spaced. Latimer *et al*. (1995) showed that the lower jaw teeth of *Endothiodon* are arranged into oblique 'zahnreihen' or replacement waves. They also suggested that the rate of replacement of the upper jaw teeth was much slower than that of the lower jaw where teeth replacement continued throughout life.

The present study shows that the upper jaw of *E. mahalanobisi* is characterized by a single row of teeth placed medially, on either side of the palate. Each crown is slightly posteriorly inclined with the anterior edge bearing distinct serrations. The lower jaw teeth are arranged in oblique replacement waves. Each crown bears serrations on its distal edge. Small, subtriangular wear facets are present on the lingual and buccal sides of the upper and lower jaw teeth respectively. Similar wear facets on the teeth are also reported from other *Endothiodon* species (King 1990; Latimer *et al*. 1995). The dental occlusion was bilateral as seen in extant reptiles with the left and right jaw teeth occluding at the same time. The upper jaw teeth occluded lateral to the lower jaw teeth. During propalinal action of the lower jaw, the upper jaw teeth occluded with the horn-covered lateral grooves of the dentary whereas the lower jaw teeth occluded with the horn-covered palatines resulting in a shearing motion. The occlusal surface of the palatines is much shorter and posteriorly placed than the tooth-bearing region of the lower jaw. As a result, effective occlusion for shearing between the opposing serrations was only possible when the lower jaw was in a retracted position.

Discussion of Endothiodon *feeding mechanism*. The feeding mechanism of *Endothiodon*, as evidenced from the jaw articulation and musculature, does not vary much from that of the typical dicynodonts. The forces exerted by the jaw muscles are considered here as proportional to the bulk (Crompton and Hotton 1967; King 1990) and are resolved into three components. The horizontal component runs parallel to the longitudinal axis of the lower jaw, the vertical component runs perpendicular to the same axis and the lateral component also normal to the longitudinal axis but in a horizontal plane.

The external adductors originating from the enlarged temporal fenestra and zygomatic arch and inserted into the anterolateral sides of the dentary had a distinct horizontal component, which moved the lower jaw

backward during adduction. In contrast the contraction of the pterygoideus muscles had a forward pull on the lower jaw. The combined action of these muscles resulted in the antero-posterior movement of the lower jaw, a characteristic feature of the dicynodont feeding mechanism.

An additional feature of *Endothiodon* is the possibility of the masseter-like muscle, not noted in any other dicynodonts. A prominent, posteroventrally directed boss at the anterior end of the zygomatic arch is considered to be the site of origin of the much reduced and undivided masseter-like muscle. It extended backward, downward and inward to the posterolateral surface of the jaw ramus and had distinct upward and lateral components. It is a powerful elevator of the lower jaw (Dubrul 1996) and enhanced the greater bite force of the tooth rows. The masseter and the pterygoideus muscles help in elevation and mediolateral movement of the lower jaw of the herbivorous mammals (Smith 1993). In the diademodontids the presence of a masseter muscle added new possibilities and helped in accurate occlusion (King 1996). Similarly in *Endothiodon* the lateral components of the masseter-like muscle and the pterygoideus probably resulted in a slightly transverse movement of the lower jaw. The oblique, subtriangular wear facets of the lower and upper jaw teeth give further evidence of this type of jaw movement. Thus the primitive condition of tetrapod dental occlusion with essentially no contact between the upper and lower jaw teeth does not seem to exist and *Endothiodon* records a partial tooth-to-tooth contact.

The close fit of the quadrate-quadratojugal complex on the concave articular facet in the retracted position did not allow the lower jaw to move laterally. When the quadrate-quadratojugal complex rested on the convex part of the articular the asymmetric Z-shaped profile of the complex due to the plate-like lateral condyle probably imparted some flexibility in the movement of the lower jaw. So in spite of being isognathous, the lower jaw could move laterally either in the plane of the left jaw ramus or in the plane of the right jaw ramus. The lateral movement of the endothiodont lower jaw was also suggested by Cox (1998), though he attributed the movement to the loose attachment of the quadrate to the squamosal.

Thus, the feeding mechanism in *Endothiodon* shows a divergence from the general dicynodont pattern. It involved two types of jaw movements. The fore and aft movement when the upper and lower jaw teeth occluded with the horn-covered areas of the mouth and resulted in shearing and grinding action, and the slightly transverse orthal movement when the long tooth rows moved against one another in the plane of their long axes, leading to more extensive slicing.

All the species of *Endothiodon* in comparison to other dicynodonts have quite a narrow snout with a deep median anterior notch and correspondingly sharp and pointed dentary symphysis. The anterior part of the snout and the pointed dentary symphysis were probably covered with keratinized epithelium. This resulted in a small mouth with a sharp and pointed lower beak for powerful beak bite, needed for precise slicing by the browsers. Though Cox (1964) considered *Endothiodon* to be grazers, Latimer *et al.* (1995) pointed out that as the external nares are situated just behind the tip of the lower jaw, 'mud grubbing' would be extremely difficult. They considered *Endothiodon* to be specialized browser while Cox (1998) suggested that they depended mainly on conifer cones.

The members of *Endothiodon* were unique among dicynodonts and possessed a complicated masticatory process as discussed above. The small mouth with the vaulted secondary palate and pointed lower beak was used as a food gathering mechanism, cropping plant matter for food followed by oral processing prior to swallowing. The latter mechanism mainly involved shearing of the food matter by the antero-posterior movement of the lower jaw and also slight lateral movement of the lower jaw allowing partial contact between the upper and the lower jaw tooth rows, enhancing the slicing action of *Endothiodon* feeding mechanism.

In adult forms, the lower jaw teeth are pear-shaped, posterolaterally compressed with serrated distal margins whereas the upper jaw teeth have serrated mesial edges. The partial lower jaws of the juvenile *E. mahalanobisi* (ISI R349 and ISI R360) are quite small with a slender dentary symphysis in comparison to the adults. The dorsal surface of the dentary consists of a single functional tooth row with either five or six teeth. It is bordered laterally by a longitudinal groove. The individual teeth in these juveniles are relatively small, conical, pointed and procumbent or anteriorly inclined. An oblique wear facet on the buccal side is present in one of the unbroken teeth. On the distal edge incipient serrations are seen. Thus, the crown of the tooth is much simpler than that of the adult *E. mahalanobisi* and more similar to a carnivorous or omnivorous tooth. An ontogenetic change in the diet may be inferred from this differing tooth morphology

as postulated by Parks (1969; cf. DeMar and Bolt 1981). Adaptation to herbivory depends on relatively large body size and this results in rapid and indiscriminate feeding of a large amount of low calorie plant matter. Thus, as herbivory is related to body size, diet must change with growth (Cowen 1995) as seen in most extant amphibians and reptiles. Among the living forms, small and young iguanas are carnivorous or omnivorous while the adults are mostly herbivorous. An ontogenetic change in diet was also inferred in the extinct *Trilophosauraus* by DeMar and Bolt (1981). Similarly, diet in *E. mahalanobisi* possibly changed from omnivory or insectivory in the juvenile forms to herbivory in the adult forms.

Hearing

The reflected lamina of *Endothiodon* extending well below the ventral border of the lower jaw is relatively thin and bears a median depression. It forms the lateral border of a deep angular cleft. The question of the location of the tympanum still remains open (Watson 1953; Allin 1975, 1986; King 1981; Kermack 1982; Kermack and Mussett 1983) but it may be considered as attached to the reflected lamina. However, possibly as in other dicynodonts (Kemp 1982), the reflected lamina and the depressor mandibulae (Lombard and Hetherington 1993) of *Endothiodon* also took part in the reception of sound waves, mainly ground vibrations.

The middle ear region of *Endothiodon* has been studied from the holotype skull (ISI R201), two slightly distorted occiputs (ISI R217 and ISI R219) of *E. mahalanobisi* and a large floor of the braincase (ISI R203) showing the internal otic meatus of *E. uniseries*. It consists of a prominent stapes (the tympanic bone of Broom 1905) which is stouter than that in *Dicynodon* and *Oudenodon*. The shaft of the stapes is short and robust with a deep notch in its posteroventral surface (Text-fig. 6A). As mentioned earlier, the proximal end of the shaft is highly expanded relative to the distal end. The proximal end, or the footplate of the stapes lying attached to the fenestra ovalis, is convex and conical in shape. The distal end is blunt and abuts against the concave medial face of the quadrate. The robustness of the stapes indicates that it is unlikely to vibrate as an entity for sound transmission but possibly propagated sound waves through it, similar to the pelycosaurs (Watson 1953). Camp and Welles (1956) also opined that the stapes was used to brace the quadrate and support the hyoid bones.

Olfaction

The anterior end of the external surface of snout of *E. mahalanobisi* is covered with large number of minute foramina which were earlier considered as indicating the presence of vibrissae (Brink 1956). However, later workers such as Kemp (1982) and King (1981, 1988, 1990) suggested that the snout was covered with tough keratinized epithelium in the form of a beak or an upper lip as in the genus *Endothiodon*.

The anterolateral margin of the external nares formed by the premaxilla is interrupted by a prominent groove in ISI R220. This groove runs from the anteroventral margin of the external naris to the lateral edge of the upper jaw. Cluver (1971) suggested that a muscular flap was present in this region to close the external nares in *Lystrosaurus*. Latimer *et al.* (1995) suggested three possible functions of this groove: the recycling of condensed, exhaled water vapour; the tract of a gland secreting a pheromone; or the duct of a salt gland. The functions suggested here are mostly speculative and the role of this groove in the anteriormost region of the snout is yet to be understood clearly.

Although the snout of *E. mahalanobisi* bears a prominent, broad and longitudinally running nasofrontal ridge dorsally, the inner surface (ISI R220) is smooth without any ridges. The nasal cavity of *E. mahalanobisi* laterally leads to an extensive cavity (Text-fig. 5C). The anterolateral and posterolateral walls of the cavity are formed by the maxilla and jugal respectively. This maxillary-jugal cavity is bounded dorsally by the lacrimal. Watson (1960) and Cluver (1971) termed this maxillary-jugal cavity as the 'maxillary antrum'. Watson (1960) considered it to be an air-filled diverticulum of the main air passage, situated much above the level of the internal nostrils. Cluver (1971) felt that the maxillary antrum was unlikely to house any important glandular tissue or large tusks since it may or may not be present in the dicynodonts. King (1981) doubted whether this maxillary-jugal cavity is homologous with the mammalian maxillary antrum. Following Watson's view, she also suggested that this cavity acted as an accessory olfactory surface, though quite isolated from the main olfactory area.

In comparison to the total skull length, the snouth of *E. mahalanobisi* is quite short and narrow. The similarly short and narrow snout of *Dicynodon trigonocephalus* enabled King (1981) to suggest a poor olfactory sense. Hence, by comparison with *D. trigonocephalus* it may be inferred that *E. mahalanobisi* also had a reduced olfactory sense.

Sight

In fossil forms nothing much can be said about the soft part anatomy of eye. The shape, size and the position of the orbit which supports the eye, associated muscles, blood vessels and other facial soft parts, with respect to the total skull size and comparison with the extant animals, help in arriving at certain broad conclusions regarding vision in extinct reptiles.

The orbital cavity of *E. mahalanobisi* (ISI R201) is quite large (along long axis 37 mm) in comparison to a skull length of about 160 mm, subrounded and anterolaterally positioned. The boundary surrounding this cavity is well defined and raised to form a prominent rim. This orbital rim is also common in other *Endothiodon* species. The presence of such a large orbit indicates that vision was important in *Endothiodon* but this large size does not afford a basis for distinguishing between diurnal and nocturnal habits (Gans and Parsons 1970). Also the field of view is largely dependent on the position of the eyes in the head. In vertebrates, the field of view of each eye is about 170 degrees, though the amount of overlap varies among the different groups (McFarland 1991). Overlapping of the two visual fields results in binocular vision and is generally large for predators, which permits more accurate depth perception and judgement of distance, whereas it is often small for prey species. The latter group in fact has a wider field of view, which helps them to be vigilant for approaching predators. The binocular hemifield of a squirrel is around 30 deg. while the monocular crescent is 120 deg. This binocular hemifield has been calculated for *E. mahalanobisi* to be around 40–45 deg. (Text-fig. 14) and the monocular crescent varies between 125 and 130 deg. Therefore, it is inferred that the *E. mahalanobisi* possibly had relatively less binocular vision but a greater field of view and the large eyes were used for vigilance so as to detect predators quite early.

STRATIGRAPHICAL SIGNIFICANCE

The Kundaram vertebrate fauna consists of *Endothiodon* (*E. mahalanobisi* sp. nov and *E. uniseries* Owen 1879), *Cistecephalus*, *Emydops*-like forms, *Pristerodon* and ?*Oudenodon*. The only non-dicynodont
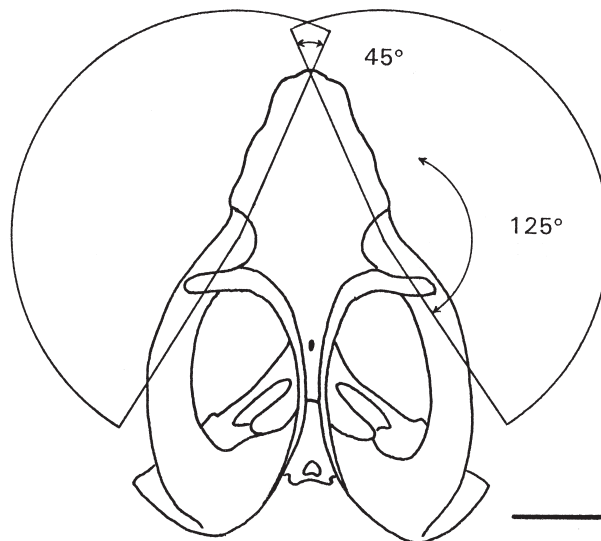
TEXT-FIG. 14. Probable monocular crescent of *E. mahalanobisi*. Scale bar represents 50 mm.

member is a captorhinid. Though the study of this fauna is far from complete, it is of stratigraphic importance because the Kundaram Formation contains the only Late Permian reptilian fauna in India. The fauna bears an overall similarity to the Late Permian dicynodont fauna of the Beaufort Group of South Africa but a precise correlation with the South African biozones is not possible at the present state of our knowledge. In the *Tropidostoma* Assemblage Zone of the Beaufort Group of South Africa *Endothiodon* predominates whereas *Cistecephalus* occurs very infrequently (Rubidge 1995). In contrast *Endothiodon* persists as a rare fossil in the *Cistecephalus* Assemblage Zone. This zone also records the first appearance of *Oudenodon*. The Kundaram fauna shows a preponderance of *Endothiodon* amounting to about 30 individuals with two or three partial skulls of *Cistecephalus* (Ray 1999). Though King (1992) suggested a probable *Oudenodon*, the dominance of *Endothiodon* and the presence of *Cistecephalus* in the Kundaram fauna indicate a broad correlation with the *Tropidostoma* and/or *Cistecephalus* Assemblage Zones of the Beaufort Group of South Africa. This suggests a Late Permian, probable Tatarian age for the Kundaram Formation. On the basis of its vertebrate faunal content, the formation is also correlated with the basal beds of the Madumabisa Mudstones of Zambia, the Ruhuhu and lower part of the Kawinga Formation of Tanzania and the Morro Pelado Member of the Rio do Rasto Formation of Brazil.

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APPENDIX

Abbreviations used in the figures

a	angular		pa	prearticular
a e l	lateral external adductor muscle		pl	palatine
a e m	medial external adductor muscle		pf	pineal foramen
a pt	anterior pterygoideus muscle		pil ant	pila antotica
ar	articular		pm	premaxilla
bo	basioccipital		po	postorbital
bs	basisphenoid		pp	preparietal
d	dentary		prf	prefrontal
dm	depressor mandibulae		pr	proötic
ds	dorsum sellae		ps a	posterior adductor muscle
ec	ectopterygoid		ps pt	posterior pterygoideus muscle
ep	epipterygoid		pt	pterygoid
eo	exoccipital		pt f	post-temporal fenestra
f	frontal		q	quadrate
fpa	facet for proatlas		qj	quadratojugal
fm	foramen magnum		q r pt	quadrate ramus of pterygoid
fo	fenestra ovalis		r a pro	retroarticular process
ic	foramen for internal carotid artery		r lam	reflected lamina
io	internal opening of internal otic meatus		s	stapes
j	jugal		sa	surangular
jf	jugular foramen		sm	septomaxilla
l	lacrimal		so	supraoccipital
l con	lateral condyle		sp	splenial
ld	lacrimal duct		sq	squamosal
m	maxilla		st	sella turcica
ma	maxillary antrum		v	vomer
m con	medial condyle		V	trigeminal nerve
mf	meckelian fenestra		VII	facial nerve
ms	masseter-like muscle		IX	glossopharyngeal nerve
n	nasal		X	vagus nerve
op	opisthotic		XI	accessory nerve
p	parietal		XII	hypoglossal nerve