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Small Permian dicynodonts from India

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Abstract. The Lower Gondwana Kundaram Formation of the Pranhita-Godavari valley records the sole occurrence of Permian amniotes in India. The horizon has yielded various dicynodonts, mainly represented by medium-sized *Endothiodon*. This assemblage also contains several small dicynodonts belonging to the family Pristerodontidae and Emydopidae. *Pristerodon* (*P. mackayi* Huxley, 1868), *Emydops* (*E. platyceps* Broom and Haughton, 1917) and *Cistecephalus* (*C. microrhinus* Owen, 1876) are described here. This is the first detailed description of these genera from outside Africa. The older name *Emydops* in place of *Emydoses* is retained and the Indian specimens of *Pristerodon*, *Emydops* and *Cistecephalus* are compared with those from the Beaufort Group, Karoo Supergroup of South Africa. Based on its vertebrate fauna, the Kundaram Formation is broadly correlated with the *Tropidostoma* and *Cistecephalus* Assemblage Zones of the Beaufort Group, Karoo Supergroup, South Africa, the basal beds of the Madumabisa Mudstones of Zambia, the Ruhuhu and the lower part of the Kawinga Formation of Tanzania and the Morro Pelado Member of the Rio do Rasto Formation of Brazil. It suggests a Late Permian Tatarian age for the Kundaram Formation. The distribution of the Kundaram dicynodonts in the other Gondwanan countries indicates the close proximity of the continents during that period and a lack of endemism or provinciality.

Key words: Dicynodont, Gondwana, Kundaram, Pranhita-Godavari valley

Introduction

Permian dicynodonts have been reported from the Kundaram Formation, a Lower Gondwana horizon of the Pranhita-Godavari valley, one of the several Gondwana basins in India (Kutty, 1972; Ray, 1997). The formation is underlain by the coal-bearing Barakar Formation and overlain by the sand-dominant Kamthi Formation (Table 1). The fluvial sediments of the Kundaram Formation comprise red mudstone, sandstone, sandstone-mudstone alternations and ferruginous shale (Ray, 1997).

The extensive red mudstone ground of the Kundaram Formation contains abundant fossils of Permian dicynodonts, which have been collected from the two localities near Golet (Figure 1) in the northwestern part of the Pranhita-Godavari valley (Kutty, 1972). Most of the specimens were encrusted with a hard iron matrix, resulting in the masking of the original shapes and forming oblate and spherical nodules. These were collected *in situ* as isolated skulls with and without lower jaws and other cranial fragments. The separated skulls and lower jaws are mainly preserved with their dorsal sides up. Those skulls with associated lower jaws are found lying on their sides with their lateral sides up. Postcranial elements are relatively rare though a few in the form of rolled vertebrae and broken limb ends are present and show signs of rolling, abrasion and rounding.

Fossil material prepared mechanically with a dental vibrotool reveals the preponderance of medium-sized *Endothiodon* (superfamily Endothiodontoidea). There are at present two species of *Endothiodon*, *E. uniseries* and *E. mahalanobisi* (Ray, 2000). The former has a skull length (SL) around 300 mm while in the latter it is around 160 mm. In addition, the assemblage contains some very small dicynodonts (SL 50 mm approx.) characterised by a broad intertemporal bar relative to the interorbital region. The aim of this paper is to describe the small and varied dicynodonts of the Kundaram Formation. These dicynodonts are known mainly from Africa and those mentioned here are the first forms from outside Africa to be described in detail. The paper also discusses the biostratigraphic and palaeobiogeographic implications of this unique fauna.

Systematic palaeontology

Infraorder Dicynodontia Owen, 1859

Superfamily Pristerodontoidea Cluver and King, 1983

Family Pristerodontidae King, 1988

Genus **Pristerodon** Huxley, 1868

Table 1. Lower Gondwana succession of the Pranhita-Godavari valley, India.

Formations	Main lithologies	Fossils	Age
Kamthi	Sandstone and siltstone	?dicynodont	Permo-Triassic
Kundaram	Mudstone, sandstone and ferruginous shale	dicynodonts, captorhinid	Late Permian
Barakar	Sandstone, carbonaceous shale and coal	*Glossopteris* flora	Early to Late Permian
Talchir	Tillite, greenish shale, sandstone		Early Permian

Type species.—*Pristerodon mackayi* Huxley, 1868 (subsequent designation by Keyser, 1993).

Pristerodon mackayi Huxley, 1868

Figures 2A–E, 3–4

Pristerodon mackayi Huxley, 1868, p. 204–205, pl. 12; King, 1988, p. 113; Keyser, 1993, p. 47 (see for prior synonymies).

Holotype.—BMNH R1810, skull and lower jaw from East London, Cape Province, South Africa; *Cistecephalus* Assemblage Zone, Late Permian.

Diagnosis.—Small dicynodonts with or without maxillary tusks; broad intertemporal region; wide parietal exposure; palatine large, leaf-like; postcanine teeth in an oblique, anteriorly converging row; long interpterygoidal vacuity extending to the rear of the vomer; median interpterygoid ridge continues anteriorly on the ventral surface of the anterior pterygoid process; deep dentary sulcus, prominent lateral dentary shelf (Cluver and King, 1983; King, 1988; Keyser, 1993).

Material.—ISIR 209, anterior part of a laterally compressed skull and lower jaw; ISIR 369, anterior part of skull; ISIR 370, distorted skull with lower jaw, ISIR 372, occiput.

Repository.—The specimens are housed in the Geology Museum, Indian Statistical Institute, Calcutta.

Locality and horizon.—Near Golet, Pranhita-Godavari valley, India; Kundaram Formation, Late Permian.

Description.—The Indian material includes a well preserved but laterally compressed, small, anterior half of a skull with associated lower jaw (ISIR 209). Its total length measured along the dorsal midline is inferred to be about 50.6 mm. The morphology of the skull and lower jaw follows the typical dicynodont pattern and the description of individual bones is not repeated here.

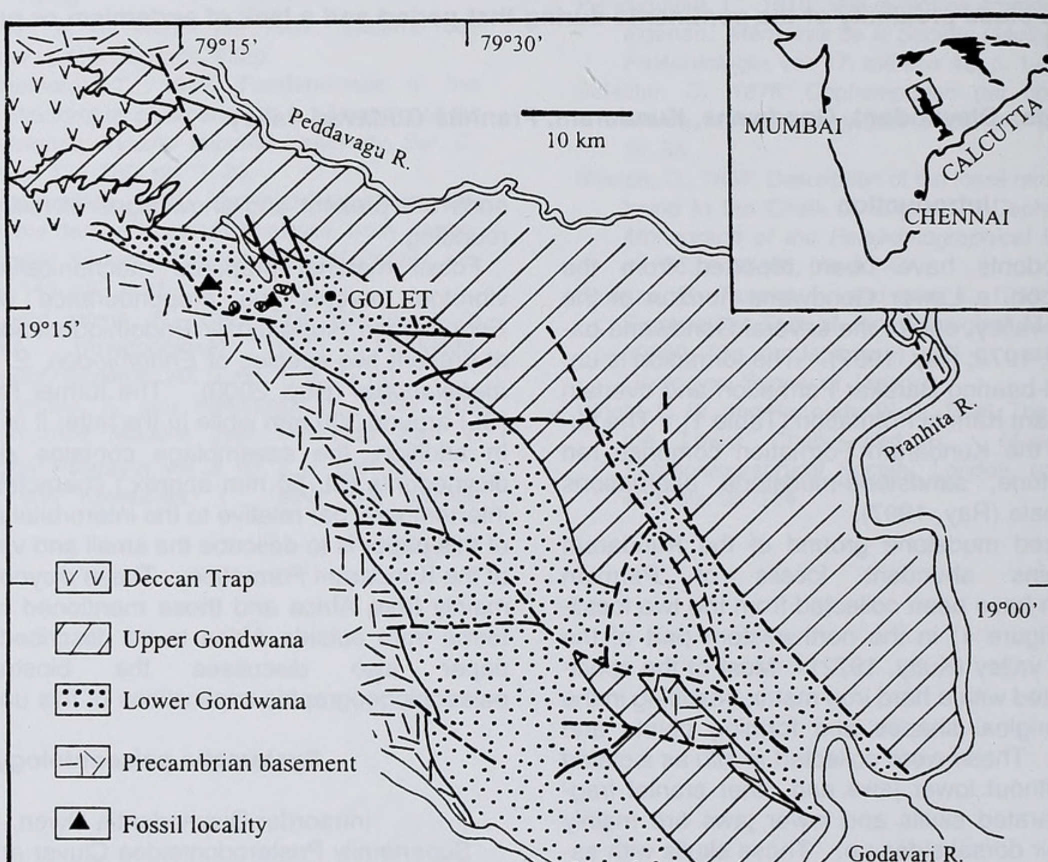

Figure 1. Geological map of the Pranhita-Godavari valley, India (after Kutty *et al.*, 1987) showing the fossil localities. Inset: Major Gondwana basins of India.

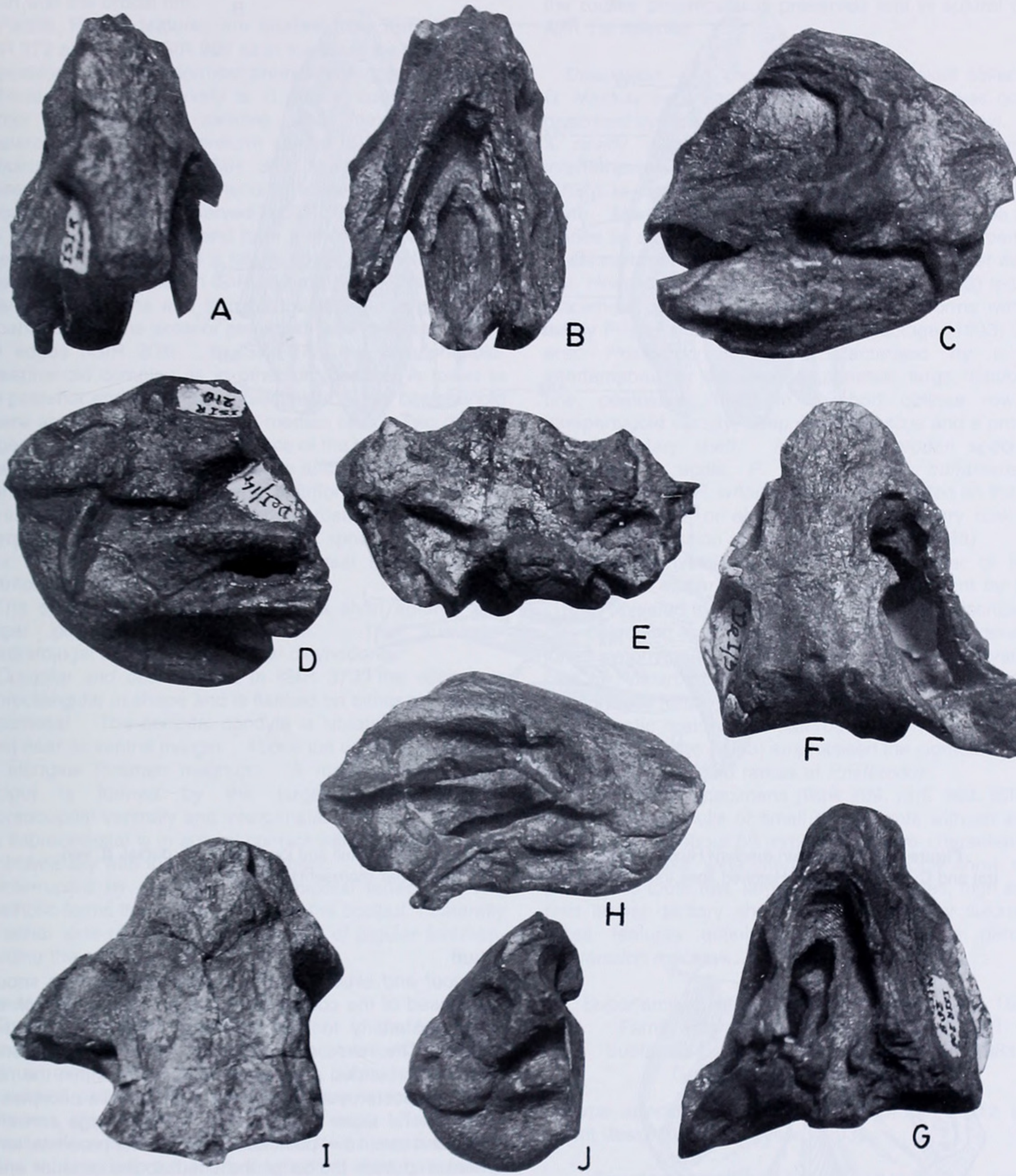

Figure 2. A–E. *Pristerodon mackayi* Huxley, 1868. A–D. ISIR 209. Partial skull with attached lower jaw in **A**, dorsal, **B**, ventral, **C**, right lateral, **D**, left lateral views. ×1.1. **E**. ISIR 372. Partial occiput in posterior view. ×1.3. **F–H**. *Emydops platyceps* Broom and Haughton, 1917. ISIR 208. Skull and lower jaw in **F**, dorsal, **G**, ventral, **H**, right lateral views. ×1. **I–J**. *Cistecephalus microrhinus* Owen 1876. ISIR 210. Partial skull and lower jaw in **I**, dorsal view. ×1.3. **J**, left lateral view. ×0.8.

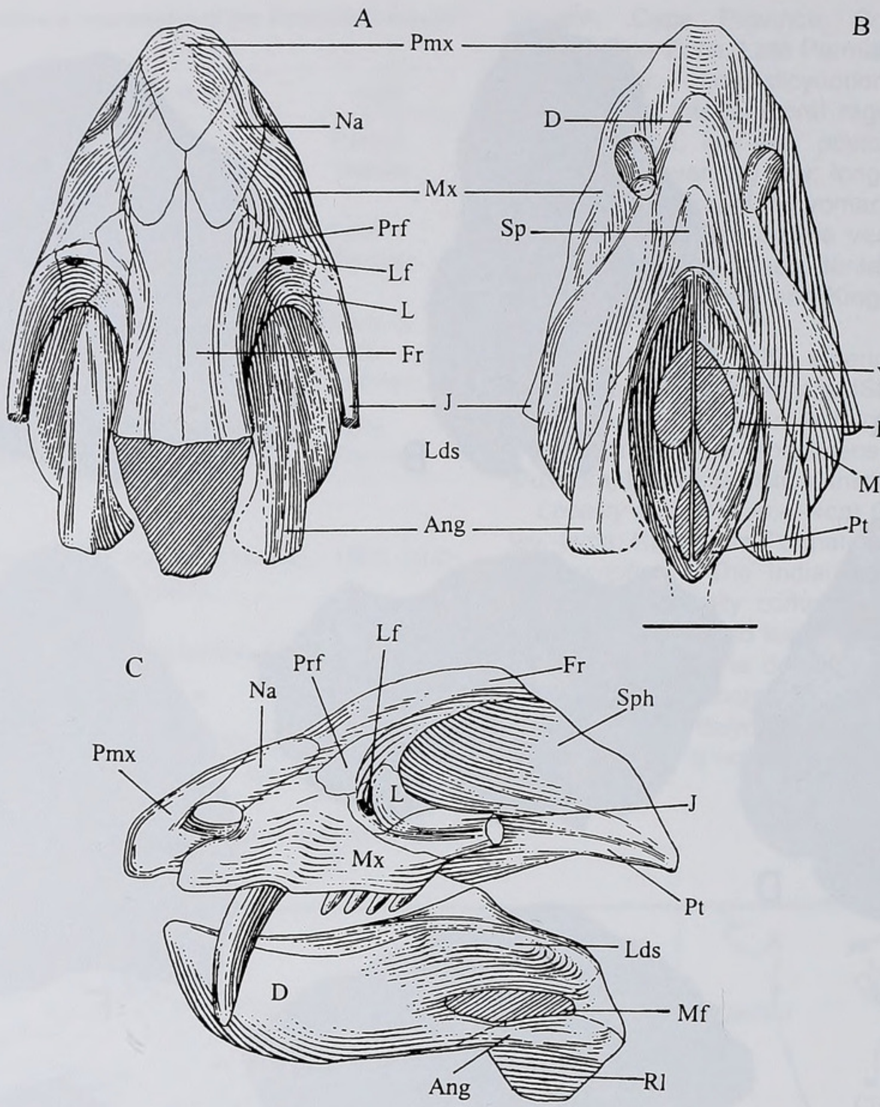

Figure 3. *Pristerodon mackayi* Huxley, 1868. ISIR 209. Restored partial skull and lower jaw in **A**, dorsal, **B**, ventral and **C**, lateral views. Hatched lines indicate broken surfaces. Scale bar represents 10 mm.

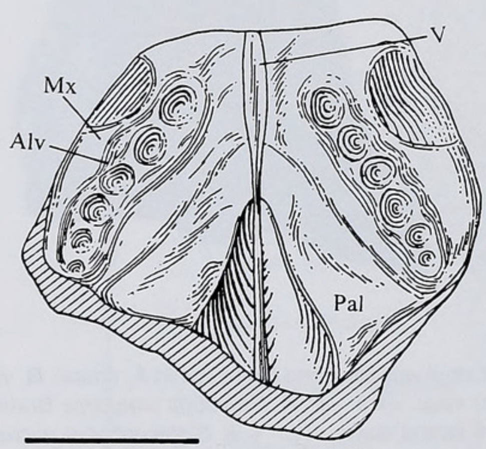

Figure 4. *Pristerodon mackayi* Huxley, 1868. ISIR 369. Anterior part of skull in ventral view. Scale bar represents 10 mm.

Skull

Snout and skull roof. The narrow and tapering snout is composed of the completely fused premaxillae, which continue posteriorly to form a wedge between the external nares. The nares open near the extremity of the snout. Small, subrounded septomaxilla, recessed within the naris, forms its posteroventral margin. The maxilla occupies the anterolateral sides of the skull and bears large caniniform tusks and about 3–4 postcanine teeth. The preorbital length (measured from the tip of the snout to the anterior end of orbit) is 16.6 mm. It is covered by the elongated, paired nasals mostly, followed by the frontals posteriorly. Only the anterior part of the orbit is preserved, well defined by a narrow rim. The preserved part of the interorbital region is broad (9 mm), flat and formed by the relatively extensive frontal. Anterolaterally the orbital rim consists of the subtriangular prefrontal, which is rather large in comparison to the more ventrally placed subrounded lacrimal and slender jugal. The lacrimal bears a prominent foramen just flush with the orbital rim.

Palate. Palatal features are studied from ISIR 369 and ISIR 372 along with ISIR 209 as in the latter the lower jaw is in position. The anteriormost premaxilla forms a sharp peripheral rim and posteriorly is in sutural contact with the vomer medially and palatine and maxilla laterally. Posteromedial to the caniniform tusk in ISIR 209 or to the subcircular alveolus in ISIR 369, the maxilla bears a uniserial, short tooth row, tending to converge anteriorly. Though teeth are not preserved in ISIR 369, the apertures of the alveoli are confluent and form a short, shallow groove. The margin of this groove is raised above the surface of the maxilla. The palatines in ISIR 369 are broad, leaf-shaped, bearing undulations and forming the lateral margin of the choanal slits. The anterior pterygoid rami have sharp ventral edges (ISIR 209). In ISIR 372, the parasphenoid-basisphenoid complex as in other dicynodonts is fused to the posterior end of the pterygoidal plate. The basiphenoid tubera are separated by a deep median cleft. Two distinct ridges run along the anterior surface of the tubera while their faces are laterally oriented, concave and consist of the foramen ovalis. In ISIR 209, the cultriform process of the parasphenoid extends as a slender rostrum between the interpterygoid vacuity. Anteriorly the sphenethmoid complex stands in a groove on the dorsal surface of the cultriform process.

The epipterygoid is L-shaped with a short anterior and longer posterior quadrate ramus. The quadrate-quadratojugal complex is typical of dicynodonts.

Occipital and otic regions. In ISIR 372, the occiput is subrectangular in shape and is flanked on either side by the squamosal. The occipital condyle is situated medially almost near its ventral margin. Above the condyle is situated an elongate foramen magnum. A major portion of the occiput is formed by the large, medially placed supraoccipital ventrally and interparietal dorsally. Laterally the supraoccipital is in sutural contact with the tabulars and ventrolaterally with the rodlike opisthotic. This latter suture is interrupted by a distinct post-temporal fenestra. The opisthotic forms the ventral margin of the occiput. Laterally on either side of the condyle is a pair of jugular foramen, piercing the exoccipitals.

Lower jaw

The portion of the lower jaw anterior to the Meckelian fenestra is preserved in ISIR 209. The relationships of the various elements of the lower jaw follow the normal dicynodont pattern. The anterior dentary symphyseal end is narrow, slender and forms a cutting edge. Though the dorsal surface is hardly visible as the lower jaw is attached to the skull, a deep but short, longitudinal dentary sulcus is discerned, which is for occlusion with the upper jaw teeth. Laterally the jaw ramus bears a distinct and high dentary shelf just above and anterodorsal to the Meckelian fenestra, which is quite long and elliptical. The dentary extends up to the posterodorsal end of the fenestra while the angular forms its ventral margin. The subrounded reflected lamina of the angular extends well below the ventral margin of the lower jaw. A small, elongated splenial medially forms the anteroventral margin of the lower jaw. The anterior end of the rodlike prearticular is preserved and in sutural contact with the splenial.

Discussion.—An imperfect 'lacertilian' skull collected by G. Mackay from East London, South Africa was originally described by Huxley (1868) as *Pristerodon mackayi.* It was a nearly complete skull with a posteriorly widening intertemporal bar. The skull was considered by Seeley (1895) to be an endothiodont because of its postcanine teeth. Many diverse dicynodonts bearing little or no resemblance to each other except for the postcanine teeth were traditionally placed under Endothiodontidae. Later works by Van Hoepen (1934) and Cluver and King (1983) led to the placement of *Pristerodon* and its related forms within the family Pristerodontidae. King and Rubidge (1993) considered *Pristerodon* to be characterised by a broad intertemporal bar with exposed parietals, large, leaflike palatine, postcanine teeth in a short oblique row, long interpertygoid vacuity, deep dentary sulcus and a prominent lateral dentary shelf. All the *Pristerodon* species (*P. mackayi*, *P. agilis*, *P. boonstrai*, *P. buffaloensis*, *P. vanhoepeni and P. whaitsi*) were differentiated on the bases of the presence or absence of the maxillary tusk, nasal bosses and position of the alveolus (King, 1988).

However, investigation of a large number of toothed dicynodonts earlier considered as endothiodont by Keyser (1993) revealed that the vast majority of the described species belonging to *Pristerodon* and various other genera are junior synonyms of *Pristerodon mackayi*, the only valid species of *Pristerodon.* He further suggested that the crista oesophagea forming ridges on the anterior pterygoid rami is a diagnostic feature of *Pristerodon.* On the other hand, King and Rubidge (1993) emphasised the sigmoidal curve of the anterior pterygoid ramus of *Pristerodon.*

All the Indian specimens (ISIR 209, ISIR 369, ISIR 370, ISIR 372) are skulls of small dicynodonts with an average skull length of about 50 mm. These are characterised by caniniform tusks, wide intertemporal regions, short, oblique postcanine tooth row, large, leaflike palatines, high and distinct lateral dentary shelf and deep dentary sulcus. All these features definitely show that these pertain to *Pristerodon mackayi.*

Superfamily Diictodontoidea Cluver and King, 1983
Family Emydopidae Cluver and King, 1983
Subfamily Emydopinae Cluver and King, 1983
Genus ***Emydops*** Broom, 1912

Type species.—*Emydops minor* Broom, 1912 (subsequent designation by Keyser, 1993).

Emydops platyceps Broom and Haughton, 1917

Figures 2F–H, 5–6, 7E–F

Emydops platyceps Broom and Haughton, 1917, p. 125: King, 1988, p. 116.
Emydops tener Keyser, 1993, p. 49, fig. 5.1.

Holotype.—SAM-PK-2667, skull from Dunedin, Beaufort West, South Africa; *Cistecephalus* Assemblage Zone, Late Permian.

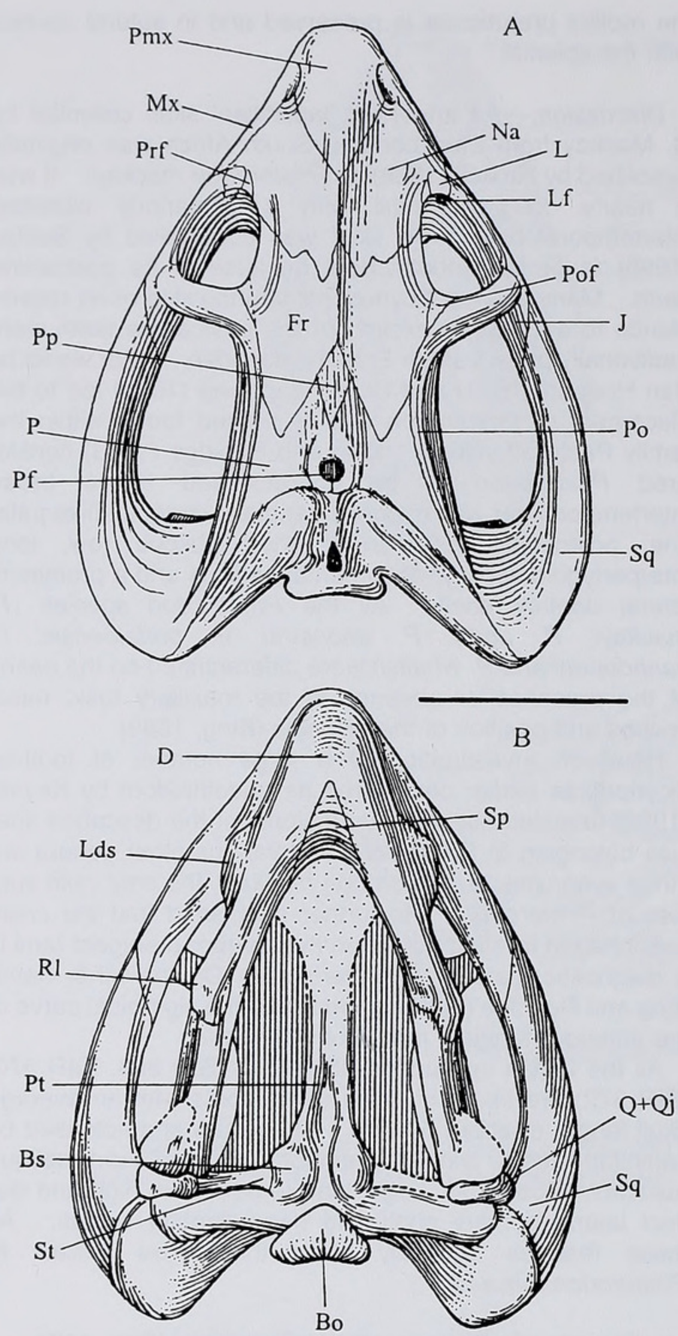

Figure 5. *Emydops platyceps* Broom and Haughton, 1917. ISIR 208. Restored skull and lower jaw in **A**, dorsal and **B**, ventral views. The stippled area indicates matrix covering. Scale bar represents 20 mm.

Revised diagnosis.—Small dicynodonts with or without caniniform tusks; prominent lacrimal foramen; wide intertemporal region with parietal exposure; median premaxillary ridge on palate bordered by grooves on either side, irregularly placed maxillary and dentary teeth; small palatal embayment just anterior to caniniform process; flat, squarish palatine with notched medial and concave posterior margins; straight anterior pterygoid process, prominent lateral dentary shelf; dentary symphysis drawn up into a sharp cutting edge.

Material.—ISIR 208, a complete, slightly distorted skull with attached lower jaw.

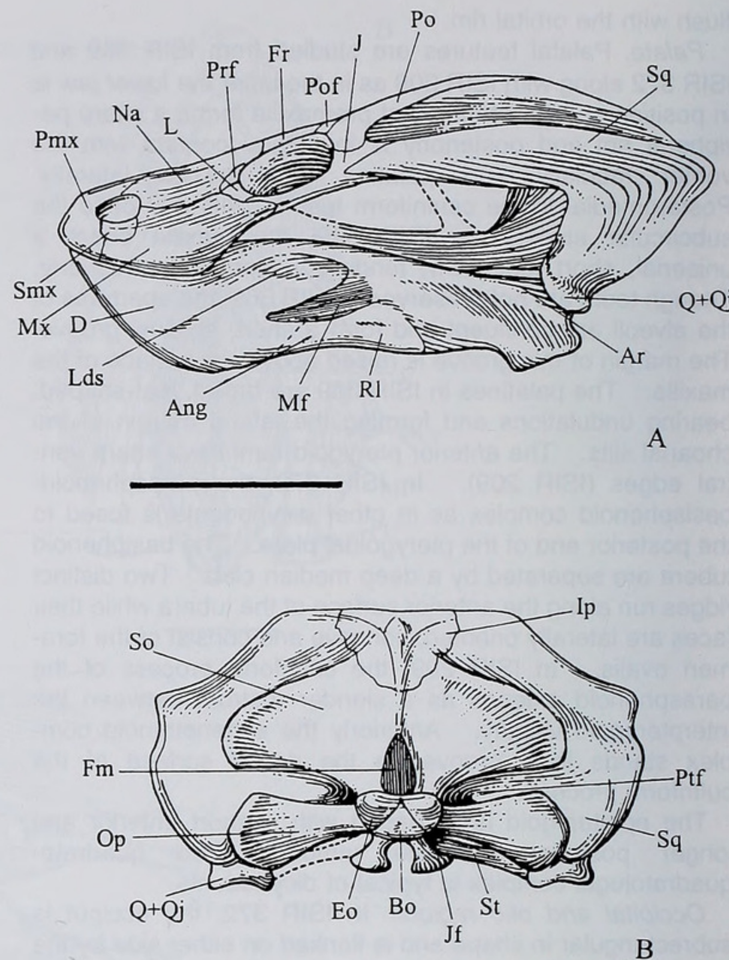

Figure 6. *Emydops platyceps* Broom and Haughton, 1917. ISIR 208. Restored skull and lower jaw in **A**, lateral and **B**, occipital views. Scale bar represents 20 mm.

Repository.—The specimen is housed in the Geology Museum, Indian Statistical Institute, Calcutta.

Locality and horizon.—The specimens were collected near Golet (Figure 1), Adilabad district, Andhra Pradesh, India from the Late Permian Kundaram Formation, Gondwana Supergroup.

Description.—

Skull

General features. The small and triangular skull measures 47.8 mm along the dorsal midline. The snout is narrow, tapering anteriorly and quite short (preorbital length is 10 mm). Measurements of the skull are given in Table 2. The elliptical nostril is situated close to the midline at the extremity of the snout. It is bordered by the premaxilla anterodorsally, nasals posterodorsally and the maxilla posteriorly and ventrally. The orbit is relatively small, subrounded (diameter 10 mm approx.) and anterodorsally positioned. The interorbital region is flat, quite broad and about 15.5 mm. Beyond the orbit, the zygomatic arch flares out and meets the occipital plane at a high angle. The temporal fenestra is large, elongated and extended beyond the level of the occipital condyle. The intertemporal region is much wider than the

Table 2. Measurements of the skull (ISIR 208) of *Emydops platyceps*. All measured in mm.

Parameters	*Emydops platyceps* (ISIR 208)
Skull length	
a. Measured along the dorsal midline	47.8
b. Over squamosal wings	58.4
c. At palatal midline	–
Preorbital snout length	10
Postorbital snout length	25
Length from anterior edge of premaxilla to anterior edge of pineal foramen	37
Skull width across squamosal	44.5
Diameter of pineal foramen	2.8
Interorbital width	15.5
Intertemporal width	28
Snout width	16.7
Length of temporal fenestra	31.6
Width of temporal fenestra	14.3
Greatest width of occiput	41.3
Width of occipital condyle	13.8
Least squamosal width of the occiput	28
Occipital height	25.5

interorbital bar (Table 2) and gradually widens posteriorly. A small, circular pineal foramen is situated medially on a slightly raised area at the posterior end of the skull. The skull roof is relatively flat but gently sloping anteriorly. The occiput is trapezoid in shape with a large, elliptical occipital condyle situated medially near its ventral margin.

Snout and skull roof. The anteriormost premaxilla separates the nostrils dorsally and forms a wedge-shaped contact with the paired nasals posteriorly. Posterolaterally it is in contact with the maxilla, a major element on the anterolateral sides of the skull. The maxilla borders the nasal openings ventrally and posteriorly. The septomaxilla is slightly exposed along the posteroventral border of the nasal cavity. In dorsal view, posterior to the premaxilla is a pair of large nasals. This is followed posteriorly by the frontal occupying most of the skull roof anterior to the temporal fenestra. Posterolaterally the nasal is bordered by a small elongated prefrontal. The latter, along with the relatively large, subrounded lacrimal, form the anterior margin of the orbit. There is a distinct lacrimal foramen. Dorsally and posterodorsally the circumorbital rim is formed by the frontal and a small, triangular postfrontal respectively. Ventrally the orbit is bordered by the jugal. The slender, rodlike postorbital forms the narrow anteromedial border of the temporal fenestra. Characteristically the intertemporal region comprises mostly the widely exposed parietals. Medially at the frontoparietal junction is a large, rhomboidal preparietal, which lies entirely in front of the pineal foramen. The circular pineal foramen is situated on a slightly raised area, at the posterior end of the skull roof and is bounded by the parietals. Posterior to the pineal foramen is a single, large interparietal, which occupies a dorsomedial position on the occiput. The squamosal is the posteriormost element in dorsal view and divisible into three parts as is typical of dicynodonts. Attached to the anterior face of the squamosal is a small quadratojugal.

Palate. The anterior part of the palate cannot be partly seen because of matrix covering and as the lower jaw is in position. Posteriorly the pterygoid bone is narrow with a poorly developed pterygoidal crest.

The parasphenoid-basisphenoid complex is fused to the posterior end of the pterygoidal plate. The basisphenoid consists of two anteriorly converging tubera separated by a narrow and deep median cleft. The faces of the tubera are laterally oriented, concave and house the foramen ovalis.

The quadrate is strongly fused with the more laterally placed quadratojugal, though there is deep groove between them. The palatal face of the quadrate, as in other dicynodonts, is composed of a broad, medial and a lateral condyle separated by a shallow groove. Lying between the medial face of the quadrate and the fenestra ovalis is a thin, long, rodlike, imperforate stapes with slightly expanded ends.

Occipital and otic regions. In posterior view, the occiput is trapezoid in outline. It bears a prominent, elliptical occipital condyle medially, which is composed of the paired exoccipitals and the basioccipital. Above the condyle is an elongated, triangular foramen magnum. The dorsal margin of the foramen magnum is formed by the supraoccipital, which also forms the roof of the braincase. The interparietal, situated on the dorsal side of the supraoccipital, is characterised by a median ridge tapering ventrally. Ventrolateral to the condyle is a jugular foramen, piercing the exoccipital and the rodlike opisthotic, which expand laterally overlapping the squamosal. A large posttemporal fenestra is present near the occipital condyle at the sutural contact between the opisthotic and the dorsally placed supraoccipital. Laterally the occiput is margined by the winglike flanges of the squamosal. The anterior face of the occiput bears a pair of small, flat prootics, which along with the opisthotics form the anterior and posterior walls, respectively of the otic capsule.

Lower jaw

The lower jaw is attached to the skull. The anterior end is relatively slender and is drawn up into a sharp cutting edge. The dentary symphysis is strongly fused. Laterally the jaw ramus bears a distinct, high dentary shelf and a large Meckelian fenestra. The anteriormost element of the lower jaw, the dentary, extends posteriorly as far as the posterior end of the Meckelian fenestra. It is bounded posteriorly by the surangular and posteroventrally by the angular. Presence or absence of teeth cannot be determined as the lower jaw is in position. The reflected lamina of the angular is quite small and is in line with the ventral margin of the lower jaw. The transversely widened posterodorsal surface of the articular forms lateral and medial condyles separated by a low ridge as found in the dicynodonts. It slopes downward posteriorly to form the retroarticular process.

Discussion.—

On the genus *Emydops*

A small dicynodont skull, about 45 mm in length, was first described by Broom (1912) from Kuilspoort, Beaufort West, South Africa as a new genus and species *Emydops minor*. It is tuskless with a wide intertemporal region, a large median preparietal forming the anterior margin of the pineal foramen, a slender postorbital arch and a feeble beak. Broom (1913) redefined *Emydops* as a small tuskless form with a few unserrated postcanine teeth. Subsequently, a number of *Emydops* species, collected from the Permian part of the Beaufort Group of South Africa, were described by Broom (1913, 1921). These species were distinguished based on the shapes and arrangements of the bones of the frontal and parietal regions. Broom and Haughton (1917) described another new species of *Emydops*, *E. platyceps* based on a tusked skull from Dunedin, Beaufort West, South Africa.

Broom (1921) created a new genus *Emydopsis* (the type species is *Emydopsis trigoniceps*), characterised by the presence of only three or four posteriorly serrated teeth. Toerien (1953) stated that the number and size of the teeth alone cannot be used to differentiate between *Emydops*, *Emydopsis* and *Pristerodon*, then considered to be closely related to the former two genera. He further concluded that *Emydops* may be differentiated from *Pristerodon* on the basis of the size of the palatine and the absence of the palato-premaxillary contact in *Pristerodon*.

The holotypes of the type species of *Emydops*, *E. minor* (AMNH 5525; Figure 7A) and *Pristerodon*, *P. mackayi* (BMNHR 1810; Figure 7B) were again examined by Cluver and King (1983). They stated that in both specimens, few characters of taxonomic importance are visible. They supplemented the generic diagnoses of *Emydops* and *Pristerodon* from the information accumulated from other species of the two genera. According to them, the characteristic features of *Emydops* include: small dicynodonts with wide intertemporal region and exposed parietals (Figure 7C), platelike palatine with concave posterior border, quite short interpterygoidal vacuity, presence of embayment in the palatal rim and weak interpterygoidal crest, prominent lateral dentary shelf, dentary symphysis drawn up into sharp cutting edge and shallow groove on the dorsal edge of the dentary.

Keyser (1993) while reviewing the small dicynodonts of South Africa transferred most of the holotypes of *Emydops* species to *Pristerodon mackayi*. According to him, *Emydops minor*, the type species of *Emydops*, displays no distinctive features-a view also shared by Cluver and King (1983). Keyser (1993) found *E. minor* to be similar to *Pristerodon mackayi* and considered *Emydops minor* as *nomen dubium*. He suggested that *E. platyceps* is the only valid species, characterised by large and square palatines which are perforated by foramina. He renamed *Emydops* in part as *Emydoses* (Keyser, 1993, p. 48) and assigned two species to the genus, namely *Emydoses tener* (Figure 7D) and *Emydoses platyceps* (*Emydops platyceps* of Broom and Haughton, 1917; holotype SAM-PK-2667; Figure 7E).

However, King and Rubidge (1993) considered *Emydops* to be well characterised. *Emydops* is differentiated from the other toothed dicynodonts (*Eodicynodon*, *Pristerodon* and *Robertia*), based on such features of the palate and lower jaw as the size and shape of the palatine, arrangement of the postcanine teeth, lateral dentary shelf and dorsal surface of the lower jaw (King and Rubidge, 1993; p. 141, table 2).

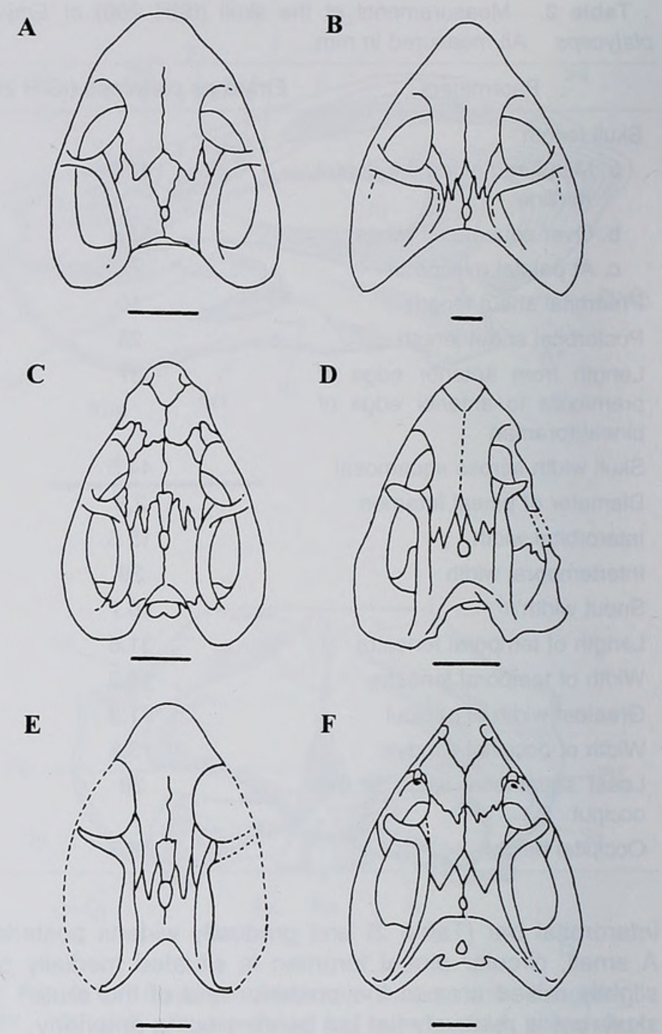

Figure 7. Skulls in dorsal view. **A**. *Emydops minor*, holotype AMNH 5525 (after Cluver & King, 1983). **B**. *Pristerodon mackayi*, holotype BMNHR 1810 (after Cluver and King, 1983). **C-F**. *Emydops platyceps*, **C**, SAM-PK-11060 (after Cluver & King 1983); **D**, SAM-PK-K10170 (syntype, *Emydoses tener* of Keyser, 1993); **E**, holotype SAM-PK-2667, **F**, ISIR 208. Scale bars represent 10 mm.

From the above review, it is evident that a disagreement persists regarding the nomenclature of the genus *Emydops*. Though Keyser (1993) in effect renamed *Emydops* as *Emydoses* because most of the earlier described species, including the type species of the formers, had in his view become junior synonyms of *Pristerodon mackayi*, the generic diagnosis remains nearly the same for *Emydops* and *Emydoses*. Moreover, *Emydops* is a long-accepted name in its accustomed meaning. Thus in the present study priority is given to the older name of the genus and the name *Emydops* is retained, to provide stability and avoid confusion in the nomenclature by introducing a new name.

On the species of *Emydops*

As mentioned earlier Keyser (1993) considered *E.*

Erratum

In the article by Komatsu, Saito and Fürsich (Vol. 5, No. 2), the columnar section in the upper left of Figure 7 (page 128) was partly obliterated during the printing process. Remove the corrected columnar section below and affix it to the appropriate position.

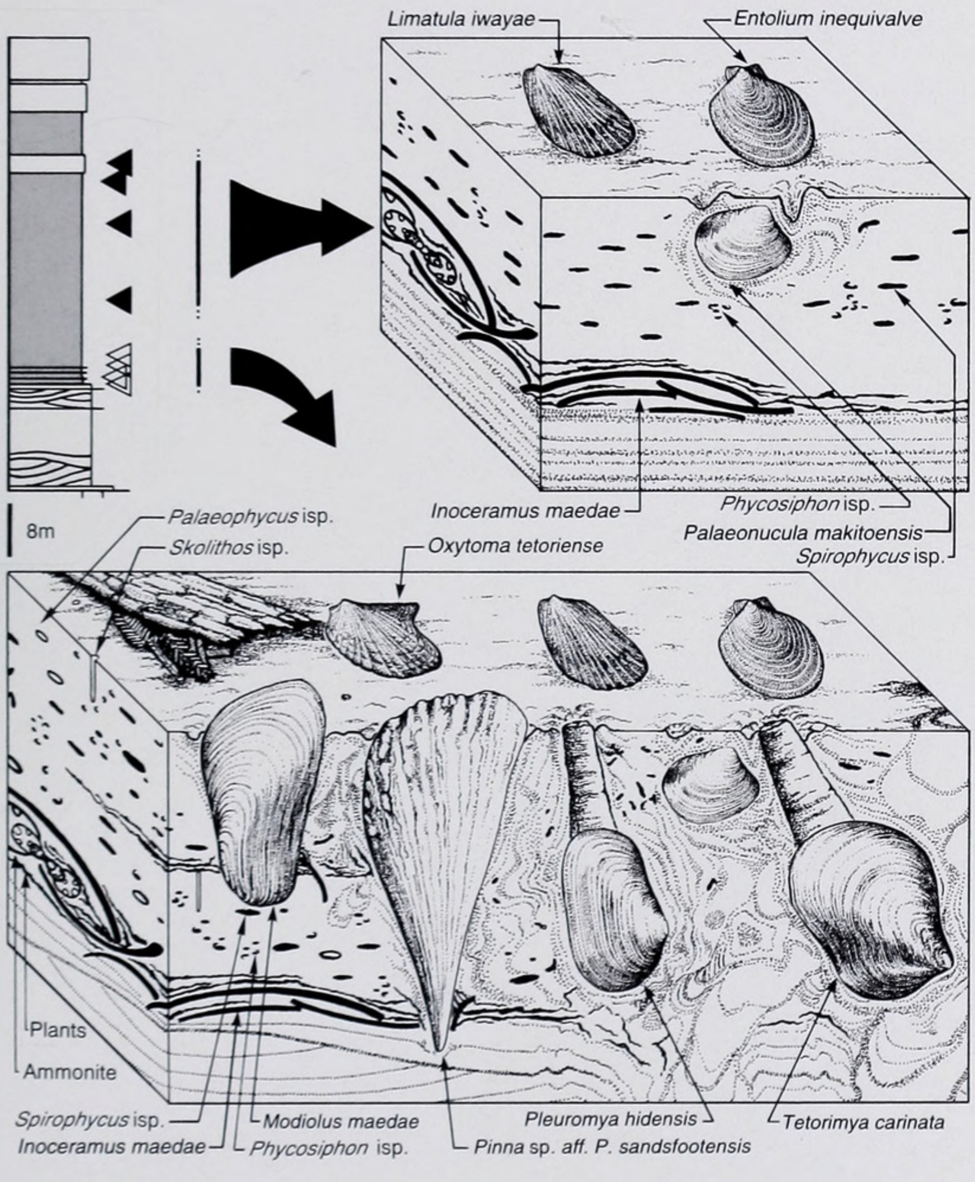

Figure 7. Ecological reconstruction of the bivalve fauna in shelf deposits of the Mitarai Formation.

Table 3. Comparative measurements of several specimens of *Emydops*. All measured in mm. Abbreviations used: SL, skull length along dorsal midline; SLsq, skull length over the squamosals, PSL, preorbital snout length; SnW, snout width, IO, interorbital width, IT, intertemporal width; TF, length of temporal fenestra; SW, skull width; OcH, occipital height; OcW, occipital width.

Specimens	Parameters									
	SL	SL sq	PSL	SnW	IO	IT	IT/IO	TF	SW	OcH	OcW
ISIR 208	47.8	58.4	10	16.7	15.5	28	1.81	31.6	44.5	25.5	41.3
SAM-PK-2667	40.58	51.9	9.75	15.68	10.69	15.69	1.48	-	34.54	-	-
SAM-PK-10170	49.33	61.36	7.97	17	10.52	19.88	1.89	32.9	47.46	18.35	39.58
SAM-PK-10148	51.06	58.72	16.26	16.28	10.96	18.38	1.68	30.2	42.88	23.66	35.34
SAM-PK-K1671	30.38	39.37	7.58	12.34	4.9	9.8	2	20.55	29.1	15.74	21.95
SAM-PK-3721	44	54.1	-	12.15	11.2	15.85	1.42	29.44	-	18.89	30.4
SAM-PK-10172	40.16	46.03	11.34	10.33	8.11	14.8	1.82	-	33.3	-	-
SAM-PK-11060	41.23	47.32	11.13	-	12	15.86	1.32	21	28.96	20.38	27.78
SAM-PK-K1517	46.69	56.64	11.58	-	15.38	19.77	1.3	17.5	30.4	22.03	30.6
SAM-PK-K5974	56.2	65.5	-	-	14.95	22.63	1.51	35.94	43.83	27	48.8
SAM-PK-K6693	47.94	59.56	12.33	16.37	12.08	18.54	1.53	25.7	44.4	18.85	33.22
SAM-PK-K6623	46.03	54.85	12.21	16.98	13.52	16.55	1.22	30.46	53.88	24.5	33.31

platyceps Broom and Haughton, 1917 and *E. tener* Keyser, 1993 as the only valid species. The former was characterised by large, squarish palatines, which are perforated by foramina and the latter by its "slender" build (Keyser 1993). The use of features like slender or delicate skull to define species is subjective (King, 1993) and avoided in the present study. A close examination of *Emydops* specimens housed at the South African Museum, Cape Town, including the holotype SAM-PK-2667 of *E. platyceps* and the syntypes (SAM-PK-10148 and SAM-PK-10170) of *E. tener* reveal that the shape of the palatines are similar in all the specimens. The palatal portion of the palatine is flat, squarish and bears a notch or palatine foramen in its medial margin. Its posterior margin is concave. Although the area between the medial margin of the palatine and the vomer along the ventral midline is covered with matrix in most of the specimens, the presence of the notch can be clearly discerned, especially in SAM-PK-10148, SAM-PK-3721, SAM-PK-K1671, SAM-PK-11060 and SAM-PK-K6623. Moreover, it appears that the syntypes of *E. tener* do not have any feature different from *E. platyceps* Broom and Haughton, 1917. It is considered here as the junior synonym of *E. platyceps* Broom, 1912. Thus, from the specimens available for study, it appears that the genus *Emydops* has only one valid species, *E. platyceps* and is now distinguished by the generic features of *Emydops*: small dicynodonts which may be tusked or tuskless, prominent lacrimal foramen flush with the orbit, wide intertemporal region with broad parietal exposure, irregularly placed maxillary and dentary teeth, small embayment on the palatal rim anterior to the caniniform process, premaxillary ridge bordered by grooves on either side, flat, squarish palatine with notched medial and concave posterior margins, straight anterior pterygoid process, dentary symphysis drawn up into a sharp cutting edge and a prominent lateral dentary shelf.

Comparison between the Indian and South African forms

ISIR 208 (Figure 7F) is a small skull (47.8 mm) with broad intertemporal region and widely exposed parietal. The pterygoid bridge posterior to the choanae, though not well preserved, is quite narrow (Figure 5B). The lateral dentary shelf is very distinct and high and the dentary symphysis is drawn up into a sharp cutting edge. Thus, it is assigned to the genus *Emydops*. The anterior palatal features are not visible because of the position of the lower jaw. Table 3 gives a detailed comparison of ISIR 208 with a number of South African forms, including the holotype of *E. platyceps* (SAM-PK-2667), based on different cranial parameters. It shows that the overall skull proportions of ISIR 208 such as length, width, occipital height, occipital width and length of the temporal fenestra fall within the range of the South African forms. On the other hand, the snout length is much shorter while the interorbital and intertemporal width with respect to the skull length is much greater than that of the SAM specimens. IT/IO ratio (1.8) though again within the range, which varies from 1.22 (SAM-PK-K6623) and 2 (SAM-PK-3721), is at the higher end of the range. The interorbital (IO) and intertemporal (IT) width relative to the skull length and IT/IO ratio are found to be not reliable specific characters (Keyser, 1975; King, 1993) and are not considered here. However, in ISIR 208 the pineal foramen is situated near the end of the intertemporal bar. The preparietal lies entirely in front of the pineal foramen and does not form its anterior margin (Figure 7F). Though this feature is not found in any other *Emydops* specimens and is unique to ISIR 208, more specimens with this feature need to be discovered before it can be considered as a reliable specific character. Apart from this, ISIR 208 bears overall similarity with *E. platyceps* and is placed within *Emydops platyceps*.

Subfamily Cistecephalinae Broom, 1903
Genus ***Cistecephalus*** Owen, 1859

Type species.—*Cistecephalus microrhinus* Owen, 1876 (subsequent designation by King, 1988).

Cistecephalus microrhinus Owen, 1876

Figures 2I-J, 8-10, 11A-B

Cistecephalus microrhinus Owen, 1876, p. 63, pl. 64, fig. 4-7: King, 1988, p.118, fig. 33 (see for prior synonymies).

Holotype.—BMNH R 47066, an imperfect skull from Stylkraans, Graaff-Reinet, Cape Province, South Africa; *Cistecephalus* Assemblage Zone, Late Permian.

Diagnosis.—Small, toothless emydopids with broad or narrow intertemporal region; lacrimal foramen, postfrontal and preparietal absent; pterygoid meeting below parabasisphenoid complex; interpterygoidal vacuity absent; stapes perforated or deeply incised; prominent lateral dentary shelf (Keyser, 1973; King, 1988).

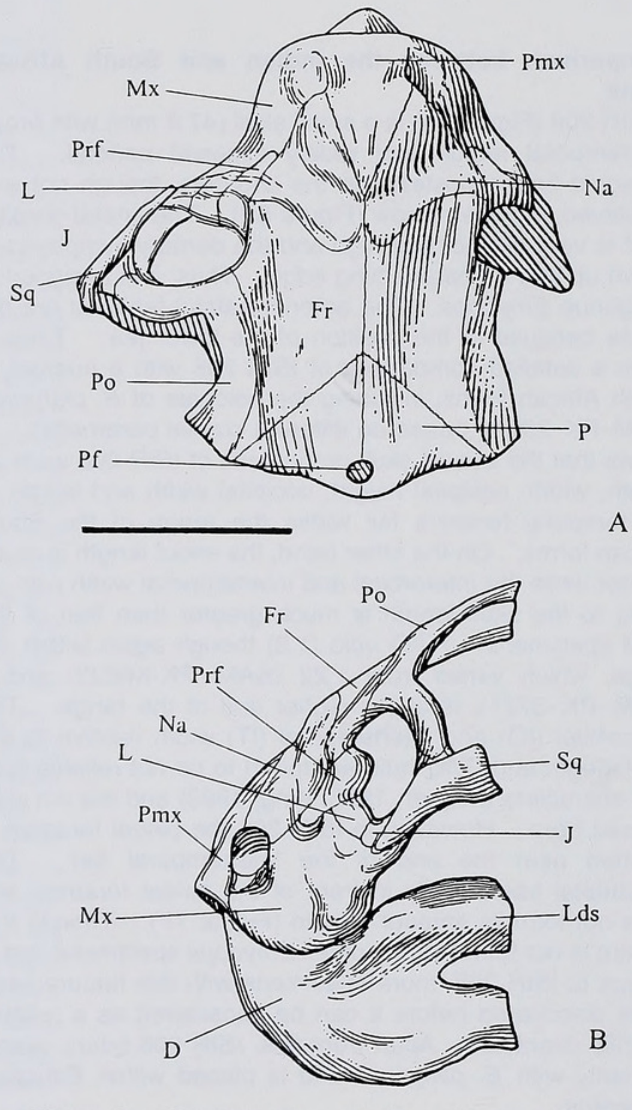

Figure 8. *Cistecephalus microrhinus* Owen, 1876. ISIR 210. Partial skull with lower jaw in **A**, dorsal and **B**, lateral views. Scale bar represents 20 mm.

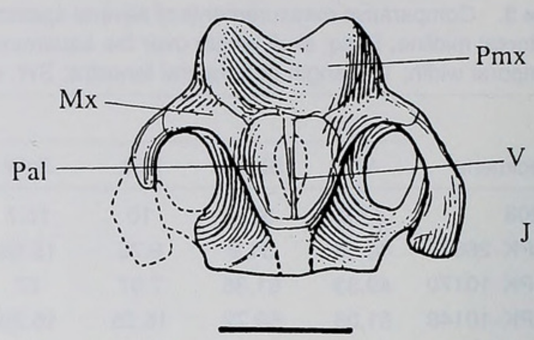

Figure 9. *Cistecephalus microrhinus* Owen, 1876. ISIR 366. Anterior part of skull in ventral view. Scale bar represents 10 mm.

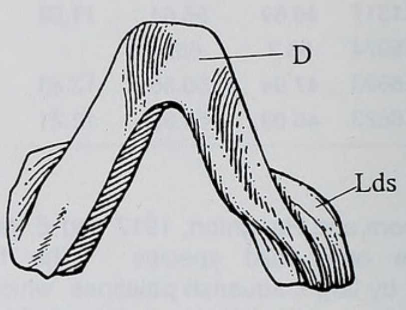

Figure 10. *Cistecephalus microrhinus* Owen, 1876. ISIR 367. Anterior part of lower jaw in dorsal view. Scale bar represents 10 mm.

Material.—ISIR 210, anterior portion of a skull with attached lower jaw, lacking the posterior part of the zygomatic arch, squamosals, occiput and postdentary bones, ISIR 365, a laterally compressed skull with attached lower jaw, ISIR 366, left portion of skull, ISIR 367, snout region, ISIR 368, anterior part of a lower jaw.

Repository.—The specimens are housed in the Geology Museum, Indian Statistical Institute, Calcutta.

Locality and horizon.—The specimens were collected near Golet (Figure 1), Adilabad district, Andhra Pradesh, India from the Late Permian Kundaram Formation, Gondwana Supergroup.

Description.—

Skull

ISIR 210 is a small, triangular skull with a slight lateral and anteroposterior distortion. Its length along the dorsal midline from the anterior end of the premaxilla to the posterior end of the pineal foramen is 41 mm while the total length is inferred to be about 52 mm. Different measurements of ISIR 210 are given in Table 4. Its snout is short, broad and tapers anteriorly with the nostrils situated close to the midline and separated by a large, swollen and wedge-shaped premaxilla. The maxilla occupies the anterolateral sides of the skull. The septomaxilla is completely recessed within the nostril. The orbits are circular, relatively small, anterodorsally placed and separated by a wide interorbital

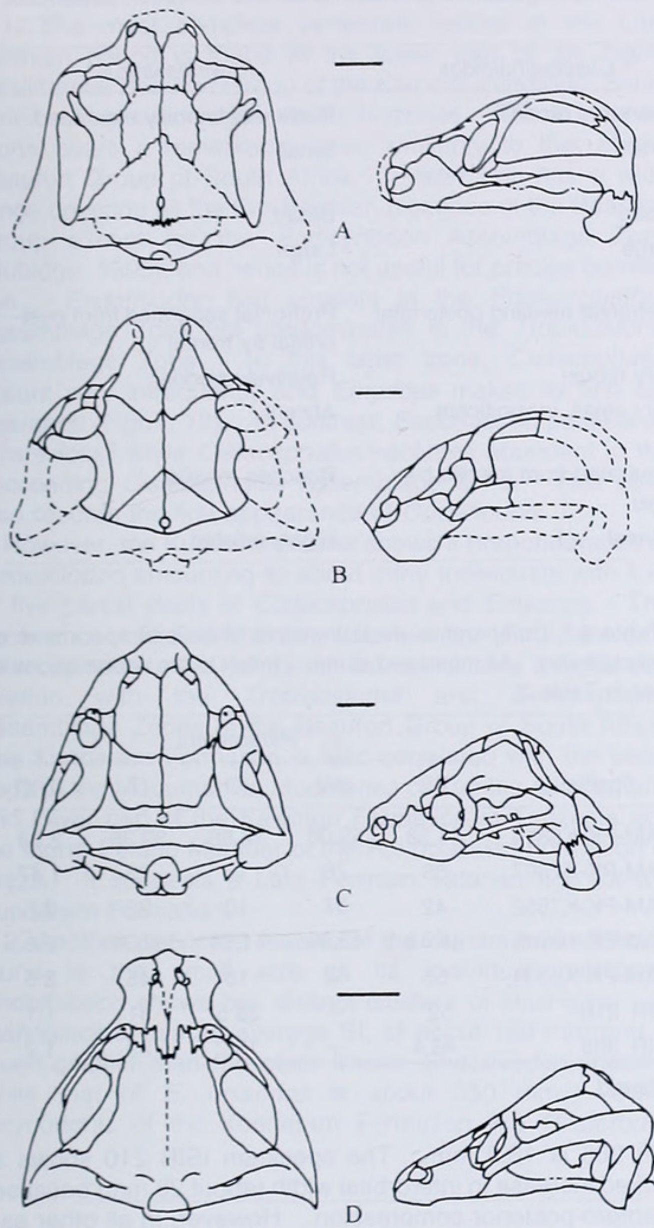

Figure 11. Skulls in dorsal and lateral views; **A**–**B**, *Cistecephalus microrhinus*. **A**, after Broili and Schroder, 1935; **B**, ISIR 210; **C**, *Cistecephaloides boonstrai* (after Cluver, 1974a); **D**, *Kawingasaurus fossilis* (after Cox, 1972). Scale bars represent 10 mm.

region. This region consists of large, paired nasals anteriorly and frontals posteriorly. The anterior part of the circumorbital rim is formed by the large, elongated prefrontal and rectangular lacrimal. The postfrontal is absent. The intertemporal region widens considerably (31 mm approx.) especially at the posterior end of the skull. A small, circular pineal foramen is situated at the far end of the skull roof. The paired parietals constituting the intertemporal bar are broad, widely exposed and laterally bordered by the slightly raised but narrow postorbital. The postorbital is separated from the prefrontal by the frontal. The preparietal is absent.

Table 4. Measurements of the skull (ISIR 210) of *Cistecephalus microrhinus*. Asterix (*) indicates inferred measurements. All measured in mm.

Parameters	*Cistecephalus microrhinus* (ISIR 210)
Skull length	52*
Preorbital snout length	17.5
Postorbital snout length	23
Length from anterior edge of premaxilla to posterior edge of pineal foramen.	41
Diameter of the pineal foramen	2
Interorbital width	28.5
Intertemporal width	31
Snout width	27.5

Beyond the pineal foramen, the posterior part of the skull and the zygomatic arches are broken.

In ISIR 210, the slender jugal is completely overlapped by the squamosal; the latter reaches the maxilla because of antero-posterior compression. The usual *Cistecephalus* feature of maxilla and squamosal separated by the jugal is preserved in ISIR 365. The palate of the specimen ISIR 210 cannot be studied as the lower jaw is in position and attached to the skull. The anterior part of the palate is studied from the specimens ISIR 365 and ISIR 367. It is edentulous and consists of a sharp palatal rim formed anteriorly by the premaxilla and posterolaterally by the maxilla. The palatines are very small and curved posteriorly. A narrow vomerine septum separates the very small internal nostrils.

Lower jaw

The lower jaw is described from the specimens ISIR 210, ISIR 365 and ISIR 368. It is short, robust and deep. The dentaries are completely fused at the symphysis and form sharp, transverse cutting edge anteriorly. Posterior to the cutting edge, the dorsal surface of the dentary is slightly raised and further posteriorly it bears a pair of ridges. Posteriorly the lower jaw is flared out laterally. Above the Meckelian fenestra is present a distinct lateral dentary shelf. The posterior ends of the specimens and the postdentary bones are not preserved in the specimens ISIR 210 and ISIR 367. In ISIR 210, the lower jaw is attached to the palate showing that the latter is much wider than the symphyseal region of the lower jaw.

Discussion. — The subfamily Cistecephalinae contains small, toothless emydopids with very broad intertemporal region lacking the postfrontal and preparietal (King, 1988). Other characteristic features of this subfamily include perforated or deeply incised stapes, vestigial or no interpterygoid vacuity, reduced palatine, premaxilla extended far back posteriorly, anterior edge of the dentary symphysis forming a sharp cutting edge and a prominent lateral dentary shelf.

This subfamily is composed of three genera, *Cistecephalus* Owen, 1876 (Figures 11A–B), *Cistecephaloides* Cluver, 1974a (Figure 11C) and *Kawingasaurus* Cox, 1972 (Figure 11D). The cranial and postcranial morphology

Table 5. Distinguishing features of *Cistecephalus*, *Cistecephaloides* and *Kawingasaurus* (sources: Broili and Schroder, 1935; Cox, 1972; Cluver, 1974a; King, 1988).

Parameters	*Cistecephalus*	*Cistecephaloides*	*Kawingasaurus*
Snout	Short and broad	Short and broad	Flattened, laterally expanded
Orbits	Large, anterolaterally placed orbits	Small	Small
Interorbital region	May be broad or narrow	Broad	Broad
Lacrimal foramen	Absent or present low down within the orbit	Large	Large
Relation between prefrontal, frontal and postorbital	Prefrontal separated from postorbital by frontal	Prefrontal meeting postorbital	Prefrontal separated from postorbital by frontal
Postorbital	Relatively slender	Very robust	Relatively slender
Pineal foramen	Circular, situated at the far end of the intertemporal bar	Very small, insignificant	Absent
Squamosal	May be separated from maxilla by jugal	Separated from maxilla by jugal	Reaches maxilla
Otic region	Normal	Normal	Highly inflated

of these taxa have been studied in detail (Seeley, 1894; Broom, 1932, 1948; Broili and Schroder, 1935; Keyser, 1973 and Cluver, 1974a, b, 1978) and show that the features like the broad, triangular skull with wide interorbital and intertemporal regions, rounded occiput and absence of the interpterygoidal vacuity are of a highly specialised animal with fossorial habits. However, *Cistecephaloides* differ from *Cistecephalus* in having a very high skull roof, sloping anteriorly and with the prefrontal in sutural contact with a robust postorbital, while *Kawingasaurus* is distinguished by the absence of the pineal foramen and an inflated otic region. The other distinctive features of *Cistecephalus* are given in Table 5.

The Indian specimens exhibit a short snout, circular orbit, absence of the postfrontal, preparietal and the lacrimal foramen, frontal separating the postorbital and prefrontal, wide intertemporal region, circular pineal foramen, transverse cutting edge of the dentary and prominent lateral dentary shelf (Figure 11B). These features clearly indicate that the specimens belong to the genus *Cistecephalus*.

A large number of *Cistecephalus* species were originally erected, distinguished by parameters such as their size differences, broad or narrow skull, and variations in the arrangement of the skull roof bones (Owen, 1876; Broom, 1932, 1948). All the fossils were collected from the Permian part of the Beaufort Group of South Africa. Keyser (1973) suggested that *Cistecephalus* species are members of a growth series and synonymised all the species with *C. microrhinus*, the latter being the only valid species of the genus. The Indian *Cistecephalus* is compared with the South African forms (SAM-PK-K6814, SAM-PK-K7667, SAM-PK-K7852, SAM-PK-K8304 and SAM-PK-10665) collected from the Late Permian part of the Beaufort Group of the Karoo Supergroup and housed in the South African Museum, Cape Town (Table 6). The total skull lengths of the African specimens studied vary between 42 mm and 63 mm. The skull length of ISIR 210 and ISIR 365 (Table 6) falls well within that range. The intertorbital width of the African specimens varies between 10 and 18 mm and that of

Table 6. Comparative measurements of several specimens of *Cistecephalus*. All measured in mm. Index to the abbreviations is given in Table 3.

Specimen	Parameters				
	SL	SW	IO	IT	IT/IO
SAM-PK-K6814	54.38	59.06	16.88	39.38	2.33
SAM-PK-K7667	63	70	17	25	1.47
SAM-PK-K7852	42	37	10	25	2.5
SAM-PK-10665	48.46	42.69	11.54	32.31	2.8
SAM-PK-K8304	55	62	18	45	2.5
ISIR 210	52*	—	28.5	31	1.1
ISIR 365	46.4	—	18.2	23	1.2

*inferred

ISIR 365 is 18.2 mm. The specimen ISIR 210 shows a marked increase in interorbital width (about 28 mm) because of antero-posterior compression. However, in all other aspects, the Indian specimens bear an overall similarity with the African forms.

Concluding remarks

The Permian in India is very poorly represented by vertebrate fossils. Apart from some palaeoniscoid fishes and temnospondyl amphibians from other Gondwana basins (Werneburg and Schneider, 1996), the Kundaram vertebrates record the sole occurrence of the Permian amniotes in India. Studies have shown that the fauna is largely represented by the two species of *Endothiodon* (Ray, 2000). The present work further strengthens this fauna with the addition of three more genera, *Pristerodon* (*P. mackayi*), *Emydops* (*E. platyceps*) and *Cistecephalus* (*C. microrhinus*). King (1992) reported the presence of *Oudenodon*. The only non-dicynodont member is a captorhinid (Kutty, 1972). Although the study of the Kundaram fauna is far from completion, it is worthwhile to mention some important aspects of the fauna.

1. The most complete vertebrate record of the Late Permian period is found in the lower part of the highly fossiliferous Beaufort Group of the Karoo Supergroup, South Africa and is subdivided into six biozones. The Kundaram fauna bears a remarkably close similarity to that of the Beaufort Group of South Africa. *Pristerodon* has a wide range covering all the five Permian biozones of the Beaufort Group except for the *Eodicynodon* Assemblage Zone (Rubidge, 1995), and hence is not useful for precise correlation. *Endothiodon* first appears in the *Pristerognathus* Assemblage Zone but predominates in the *Tropidostoma* Assemblage Zone. In this latter zone, *Cistecephalus* occurs very infrequently and *Emydops* makes its first appearance (Figure 12). In contrast, *Endothiodon* persists as a rare fossil while *Cistecephalus* becomes abundant in the succeeding *Cistecephalus* Assemblage Zone. This zone also records the first appearance of *Oudenodon*.

However, the Kundaram fauna shows a preponderance of *Endothiodon* amounting to about thirty individuals with four or five partial skulls of *Cistecephalus* and *Emydops*. The dominance of *Endothiodon* followed by *Emydops* and *Cistecephalus* in the Kundaram fauna indicates a broad correlation with the *Tropidostoma* and *Cistecephalus* Assemblage Zones of the Beaufort Group of South Africa. The Kundaram 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. It suggests a Late Permian Tatarian age for the Kundaram Formation.

2. Another distinctive feature of the Kundaram vertebrate fauna is the small size of its individual members. *Endothiodon* shows two distinct clusters of skull size. *E. mahalanobisi* has an average SL of about 160 mm and is much smaller than the other known *Endothiodon* species, while that of *E. uniseries* is about 350 mm. Other dicynodonts of the Kundaram Formation like *Pristerodon mackayi* (SL ca. 50.6 mm), *Emydops* sp. (SL ca. 47.8) and *Cistecephalus microrhinus* (SL ca. 50 mm) are also small. This smallness of size is also reflected in the captorhinid (SL ca. 50 mm).

The dominance of the small forms in the Kundaram fauna is comparable with that of the *Cistecephalus* Assemblage Zone. In this zone, more than 70% of the total faunal assemblage is composed of small forms, in marked contrast to that of the underlying *Tropidostoma* Assemblage Zone. The latter zone is characterised mainly by medium to large dicynodonts such as *Rhachiocephalus* (Rubidge, 1995). There are too many unknown parameters, to say with confidence what might have caused this size differentiation. It may be due to preservational bias, transportational sorting or palaeoclimatic and palaeogeographic influences and necessitates further study of the Permian Kundaram fauna.

3. The distribution of Kundaram dicynodonts, *Endothiodon*, *Oudenodon*, *Pristerodon*, *Emydops* and *Cistecephalus*, in the now widely separated geographic areas (Table 7) suggests that there was no apparent physical barrier between these regions. Moreover, the Pangean distribution of these dicynodont-bearing regions shows a broad and regular zone, extending from Brazil in the west to India in the east (Ray, 1999). It indicates the close proximity of the continents during that time and a lack of endemism or provinciality among these genera.

Table 7. Distribution of the five dicynodont genera (after Anderson and Cruikshank, 1978; King, 1992; Ray, 1999).

South Africa	India	Malagasy	Tanzania	Zambia	Mozambique	Brazil
Pristerodon	+		+	+		
Endothiodon	+		+	+	+	+
Emydops	+			+		
Cistecephalus	+					
Oudenodon	+	+		+		

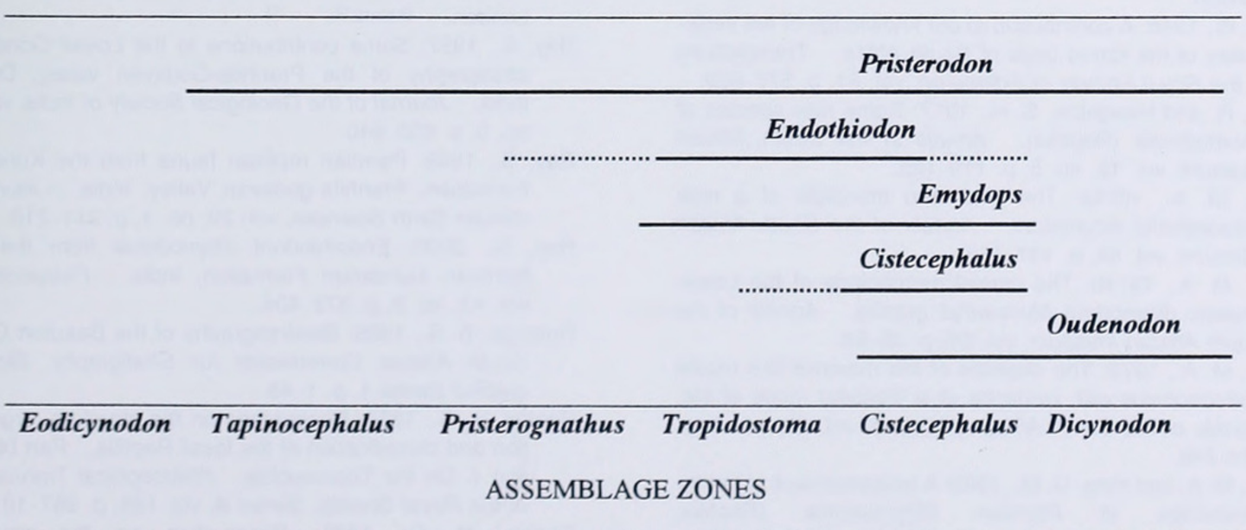

Figure 12. Ranges of the Kundaram dicynodont genera present in the Beaufort Group, Karoo Supergroup, South Africa (after Rubidge, 1995).