FRESHWATER OSTRACODES FROM LATE TRIASSIC COPROLITE IN CENTRAL INDIA

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ABSTRACT—Freshwater ostracodes are present in a presumably reptilian coprolite collected in the Upper Triassic Maleri Formation, of the continental Gondwana Group of central India. The ostracodes belong to the families Darwinulacea and ?Cytheracea, and because of poor preservation they are discussed and illustrated in open nomenclature. These ostracodes suggest, as do vertebrate fossils, that India had closer connections with Eurasia than with the southern continents (Africa, Australia, Antarctica) during Late Triassic time. India did not drift as an island continent from the Permian to the Late Cretaceous because no endemic family of ostracodes or tetrapods is known from this subcontinent, and those vertebrates that are not cosmopolitan are most nearly similar to North American and Eurasian forms. The genus *Darwinula*, whose stratigraphic range is Pennsylvanian through Holocene, has not been reported from Australia, and the fossil vertebrates show least similarities with Australian and Antarctic forms. The available record does not support the plate tectonic models showing that the eastern margin of India was connected with Australia or Antarctica. The ultrastructure of the shell of *Darwinula stevensoni* (Brady and Robertson, 1870), the type-species of the nominate genus of the superfamily, is illustrated for the first time to show that it differs from the presently known ultrastructure of the cypridacean *Cypridopdis vidua* (Müller, 1776).

INTRODUCTION

THE MALERI Formation, a part of the continental Gondwana Group in the Pranhita-Godavari Valley of central India, is well known for its great variety of fossil vertebrates (Table 1). The floral record is poor, mainly preserved as fragments of petrified wood of *Dadoxylon* Endlicher, 1847, *Araucarioxylon* Kraus, 1870 and *Mesembrioxylon* Seward, 1919 (Pascoe, 1959, p. 976). The solitary invertebrate known to date is a unionid, *Tikhia* Sahni and Tewari, 1958. In this context, the unusual preservation of an ostracode faunule in a coprolite from the Maleri Formation provides our first definite knowledge of the occurrence of freshwater Triassic ostracodes in India. The ostracodes and the vertebrates listed on Table 1 suggest a closer relationship to the fossils known from Eurasia than to those known from Africa and Australia.

In most of the reconstructions of Gondwanaland, the position of the Indian subcontinent is controversial. There is a general consensus about the fit between Africa and South America and between Antarctica and Australia in Gondwanaland reconstructions, but when India comes into the picture there is great disagreement. Current ideas based on plate tectonic theory postulate that India rifted from Gondwanaland and drifted as an island continent during some part of the Mesozoic until it collided with Asia to give rise to the Himalayas in late Cretaceous or early Tertiary time (Dewey and Bird, 1970; Dietz and Holden, 1970; Smith and Hallam, 1970; Molnar and Tapponnier, 1977 and many others).

Counterarguments that India had been part of Asia since Proterozoic or earlier time have been voiced (Meyerhoff and Meyerhoff, 1974; Mantura, 1972; Quereshy, 1969; Saxena, 1972; Crawford, 1974; Fuchs, 1975 and others). This hypothesis is supported by Gondwana vertebrates in India. Many of the vertebrates of the Maleri Formation, e.g., parasuchians, metoposaurs, and aetosaurs are only known from northern continents. Indian forms such as *Metoposaurus* Lydekker, 1890, *Parasuchus* Lydekker, 1885 and *Typothorax* Cope, 1875 are congeneric with North American forms. The fossils that indicate connections between Africa and India, e.g., dicynodonts, advanced theriodonts, and capitosaurs, now seem to be cosmopolitan in distribution, occurring with comparable frequencies north and south of the Equator (Chatterjee and Roy Chowdhury, 1974). Cox (1973) compared Indian Triassic vertebrates with contemporary tetrapods, and found that the index of faunal similarity (at a family level, using Simpson's index) is highest for India-Europe, around 81.

TABLE *1*—The Maleri vertebrates (from Chatterjee, 1978).

FAUNAL LIST	STRATIGRAPHIC AFFINITIES
Fish	
Ceratodontidae—*Ceratodus hunterianus* Oldham, 1859	Mesozoic
Xenacanthidae—similar to *Pleuracanthus* Agassiz, 1843	Upper Devonian to Upper Triassic
Amphibian	
Metoposauridae—*Metoposaurus maleriensis* Roy Chowdhury, 1965	Upper Triassic (Carnian through middle Norian)
Reptiles	
Rhynchosauridae—*Paradapedon huxleyi* (Lydekker, 1885)	Upper Triassic (Carnian through middle Norian)
Parasuchidae—*Parasuchus hislopi* Lydekker, 1885	Upper Triassic (Carnian to lower Norian)
Aetosauridae—similar to *Typothorax* Cope, 1875	Upper Triassic
Traversodontidae—similar to *Exaeretodon* Cabrera, 1944	Upper Triassic
Thecodontosauridae	Upper Triassic
Coeluridae	Upper Triassic

Not only in the Triassic, but also in the Cretaceous, the dinosaur fauna of India appears very similar to those of North America and Asia. Charig (1973) found that the index of faunal similarity (at a family level, using Simpson's index) between Indian and North American dinosaurs in the Late Cretaceous is 100.

If the widely accepted view (Dietz and Holden, 1970) that India was an island continent from the Late Triassic to the Late Cretaceous were correct, one would expect genetic isolation and independent radiation among Indian vertebrates, much in the style of the Tertiary radiation of mammals in Australia. But from Permian to Cretaceous time, no endemic family is known from India, and those vertebrates that are not cosmopolitan are most nearly similar to Asian, European, and North American forms.

The ostracodes reported in this paper also suggest northern affinities. The affinity of the ?cyprid specimens in India with an Early Triassic species in southwestern Asia indicates geographic proximity. The recorded range of *Darwinula* is Pennsylvanian to Holocene (Sohn, 1976), and the genus is cosmopolitan in distribution; however, all the known species are from Europe, Asia, North and South America and Africa, but none are known from Australia (Henry, 1924, p. 268), and Antarctica. According to Sohn (1968, p. 47) the Triassic species recorded in Australia is *Darwinula*(?) *australis* Chapman, 1909, which is not a *Darwinula,* and may be an inorganic fragment (*fide* P. J. Jones *in* Sohn, 1968, p. 37).

GEOLOGIC SETTING

The Maleri Formation is a fluviatile, poorly sorted red-bed formation which comprises three distinct lithologies: bright red silty clay, poorly sorted fine-grained white sandstone, and lime-pellet rocks. The red clay is the dominant lithology, usually structureless and unlithified, and contains abundant fossil vertebrates (Chatterjee, 1967, p. 38). The paleoclimatic condition, as revealed by sediments and fauna, is probably of monsoon type, marked by high rainfall with alternate wet and dry seasons (Robinson, 1971). The metoposaur-parasuchid assemblage indicates a Late Triassic age for the formation, probably from late Carnian to early Norian.

The presence of coprolites in the Maleri Formation was first recorded by Oldham (1859) who described some fish teeth and two coprolites from the village of Maleri. Later collections in the Geological Survey of India, particularly by Mr. A. K. N. Aiyenger in 1935, were described by Matley (1939). These coprolites were spirally marked, fusiform, average length 50 to 55 mm, width about half the length and oval in cross-section. Matley attributed them to the lungfish *Ceratodus* Agassiz, 1843, a common member in the biota of the Maleri Formation. The chemical composition of these coprolites (Matley, 1939, p. 532) is 29.28 percent calcium phosphate ($Ca_3P_2O_8$) and 25.63 percent CaO; the remaining constitutents were not determined.

A second type of coprolite was found more recently by the Geology Unit, Indian Statistical Institute near Achlapur village. Twelve

were collected; they are fairly large, heavy, rounded, oval or ellipsoidal, average length from 7 to 10 cm, width from 50 to 80 mm. They were possibly dropped on the ground, as a few specimens show surface cracks of a type that indicates shrinkage and drying in the sun. Most of the coprolites show a rounded initial end and a tapering terminal end. Flattening of some could be due to spreading of the plastic mass after deposition, rather than to distortion after burial. These coprolites cannot be attributed to specific animals, but their large size makes it clear that they came from large forms. A few rhynchosaur bones were found near them. Rhynchosaurs were the most abundant vertebrate in the Maleri ecosystem and an adult attained the size of a cow. They lived in flood plains or marshy environments, as shell eaters, feeding mainly on mussels (Chatterjee, 1974). These or similar reptiles probably produced the coprolites.

The coprolite containing ostracodes (ISIC1) has a thin white outer rim, about 4 mm wide, encircling the yellowish groundmass (Pl. 1, figs. 4, 5). Veins of calcite and barite, the latter identified by X-ray analysis (P. J. Dunn, pers. comm., 1977), are in the groundmass. Microprobe analysis indicates a high percentage of calcium and phosphate in the bulk composition, and the presence of iron, silica, and clay (E. Jarosewich, pers. comm., 1977). Possibly unaltered organic matter is also preserved.

Half the coprolite was dissolved in formic acid, and the residue picked for ostracodes, which unfortunately are very poorly preserved (Pls. 1, 2). As rhynchosaurs relied heavily on mussels as diet, and similar reptiles could have eaten water plants, possibly ostracodes were ingested accidentally along with the food. The coprolite that we studied was excreted on dry land as indicated by the shrinkage cracks. It was covered by sediments, and later replaced by the minerals that preserved the ostracode shells.

SYSTEMATIC PALEONTOLOGY

Class OSTRACODA Latreille, 1802, emend, 1804

The category assigned to the Ostracoda in the Crustacea is still under discussion. Sohn (1977, p. 10, table 3) showed the history of classification of the Crustacea and the Ostracoda. McKenzie (1977) elevated the Crustacea to phylum rank, the Ostracoda to subphylum rank, and the Order Podocopida to class rank. Pending further study, we prefer to retain the previous classification.
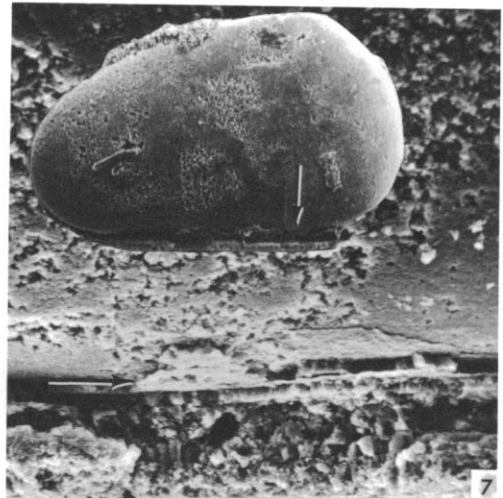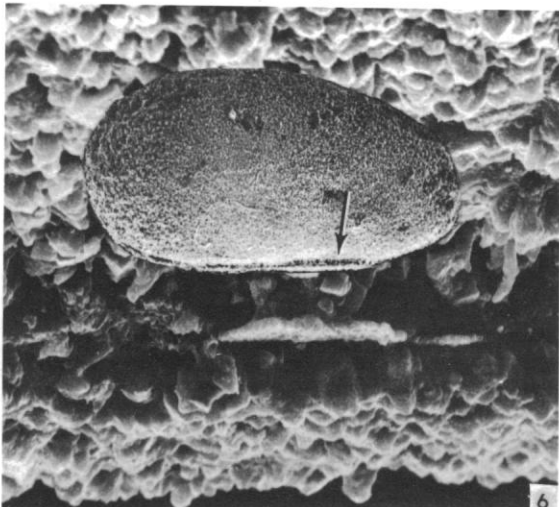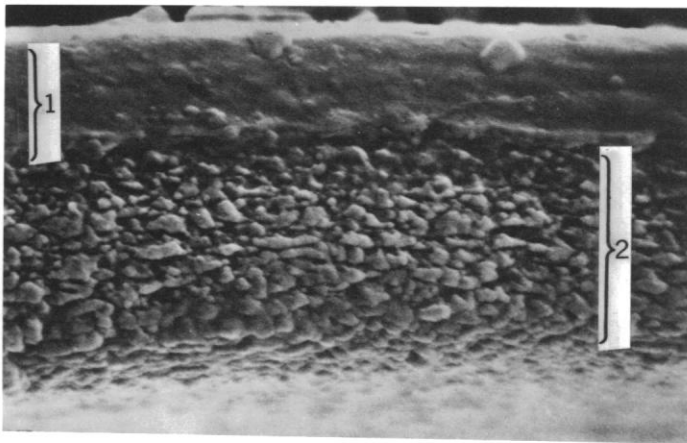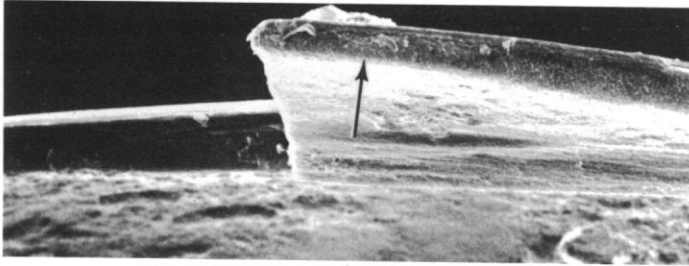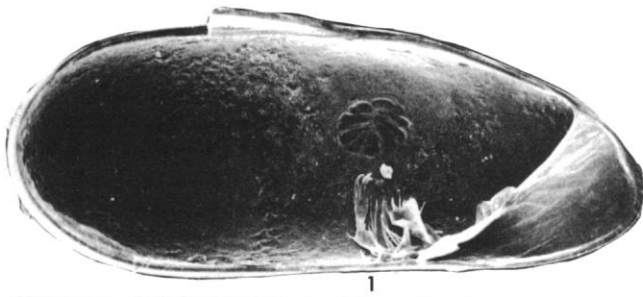
Order PODOCOPIDA Müller, 1894
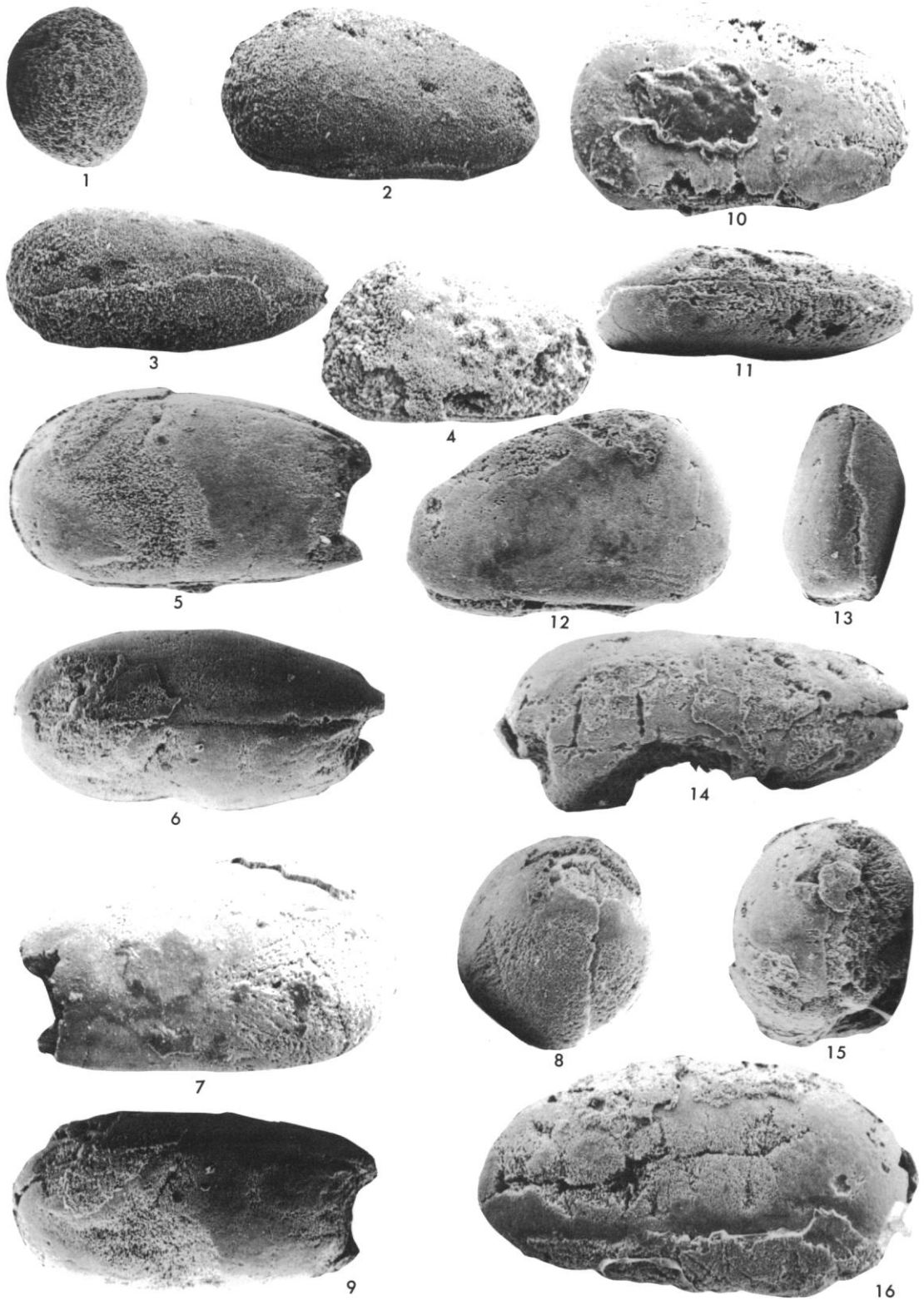### ?Superfamily CYPRIDACEA Swain, 1961

The ultrastructure of the wall of cypridacean ostracodes was described and illustrated

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with scanning electron and transmission electron micrographs by Bate and East (1972). A scanning electron micrograph of a poorly preserved carapace obtained from the coprolite is illustrated on Plate 1, fig. 7. The detail of the ultrastructure approximately ×500 is interpreted as follows: The smooth surface directly below the carapace (illustrated at approximately ×75) is the top of the endocuticle (Bate and East, 1972, p. 185, fig. 6), and the smooth, slightly higher surface (horizontal arrow) represents the exocuticle. The thicker part below that represents the endocuticle of the overlapping right valve. Although the proportion of the thickness of the exocuticle to that of the endocuticle is similar to that in the Cypridacea (Bate and East, 1972, p. 188, fig. 9), the adductor muscle attachment scar pattern is not preserved in the specimens on hand; consequently, the superfamilial designation is questioned. The ultrastructure of *Darwinula stevensoni* Brady and Robertson, 1870 from the Holocene of England is illustrated (Pl. 1, figs. 1–3) for comparison.

Family unknown
Genus indet. sp. 1
Pl. 1, fig. 7; Pl. 2, figs. 4, 10–13

Remarks.—The specimens on hand differ in lateral and dorsal outlines from any of the known freshwater ostracode genera. They are most like the Early Triassic species *Darwinuloides lii* Schleipher, 1966, and *Darwinuloides*(?) *avrovi* Schleipher, 1966, described and illustrated from the Transcaspian depression. Schleipher's species (1966, p. 127, 128, Pl. 3, figs. 7–11) may not belong to *Darwinuloides* Mandelstam, 1956, because the type-species, *Darwinula oviformis* Mandelstam,
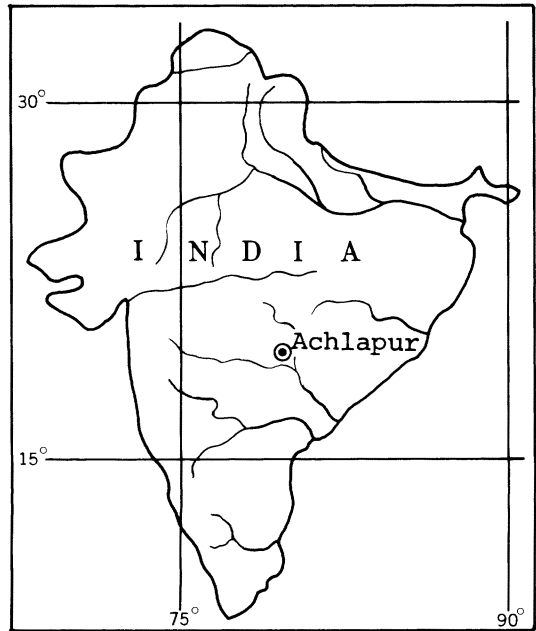
TEXT-FIG. *1*—Outline map of India showing the coprolite locality near the village Achlapur.

1947, has the anterior margin higher than the posterior margin, whereas Schleipher's specimens have the posterior margin higher than the anterior margin, as do the specimens on hand. Our specimens differ from Schleipher's species in having straighter sides in dorsal outline and in having the greatest height nearer the posterior margin in lateral outline. The ultrastructure of the shell in our specimens resembles more that described for the Cypridacea than that illustrated here for the Darwinulacea (compare Pl. 1, fig. 7 with Pl. 1, figs. 3, 6).

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EXPLANATION OF PLATE 2

FIGS. *1–3*—*Darwinula* sp. Posterior, right, and ventral (anterior to right) views of abraded carapace. Same specimen as Pl. 1, fig. *6*.

　　　　4—Gen. indet. sp. 1. Right view of abraded or exfoliated (steinkern) carapace approximately ×75. Figured specimen USNM 248119. Same collection as above.

　　　　5–9—*Darwinula* sp. Right, dorsal (anterior to right), left, posterior, and right oblique views of a steinkern with anterior part missing approximately ×75. Figured specimen USNM 248207. Same collection as above.

　　10–13—Gen. indet. sp. 1. Right, dorsal (anterior right), left and posterior views of abraded carapace approximately ×75. Figured specimen USNM 248120. Same specimen as Pl. 1, fig. 7.

　　14–16—*Darwinula* sp. Dorsal (anterior to right), posterior and left views of a badly abraded carapace approximately ×75. Figured specimen USNM 248208. Same collection as above.

TABLE 2—Measurements of specimens.

MEASUREMENTS (in mm):	GREATEST LENGTH	GREATEST HEIGHT	GREATEST WIDTH
Fig. specimen (USNM 248120)	0.7	0.4	0.2
Fig. specimen (USNM 248119)	0.6	0.39	0.16
Measured specimen (USNM 248204)	0.7	0.46	0.2
Measured specimen (USNM 248205)	0.71	0.43	0.25

Because the specimens are all abraded, and part of the outside of the shell is missing, all the measurements (Table 2) are smaller by an increment.

Superfamily DARWINULACEA Brady and Norman, 1889
Family DARWINULIDAE Brady and Norman, 1889
Genus DARWINULA Brady and Robertson, 1885

Type-species.—*Polycheles stevensoni* Brady and Robertson, 1870, Holocene, England.

Remarks.—The Genus *Darwinula* is basically a nonswimming freshwater species found in the mud substrate. Sohn (1968, p. 46–51) recorded 45 species and 19 additional taxa in open nomenclature, either as "aff." or as "sp." in the Triassic. This study was completed in 1965, and at least 29 additional species have been described to 1977. Although the type-species has the right valve larger and overlapping the left, left-over-right overlap has been described in both living (*D. pagliolii* Pinto and Kotzian, 1961) and Triassic (*D. dubia* Starozhilova *in* Lipatova and Starozhilova, 1968) species. Some of the fossil species described in the genera referred by Hartmann and Puri (1974, p. 53) to the Darwinulidae and/or the subgenera in *Darwinula (Darwinuloides)* Mandelstam, 1965, *Gerdalia* Belousova, 1965, *Suchonella* Spizharsky, 1936, differ from *Darwinula* in reversal of overlap, but, as stated above, species in *Darwinula* also show reversal of overlap. Consequently, in fossil forms, the reversal in overlap may not be a valid criterion for differentiation on the generic level.

The ultrastructure of the Darwinulacea is illustrated here for the first time (Pl. 1, figs. 1–3). The shell of *Darwinula stevensoni* (Brady and Robertson, 1870), the type-species of the nominate genus, consists of an amorphous exocuticle (1 on Pl. 1, fig. 3) that is about ⅓ the entire thickness of the shell, and a granular endocuticle (2 on Pl. 1, fig. 3). The *Darwinula* ultrastructure differs from that of *Cypridopsis vidua* (Müller, 1776) in that the exocuticle is thicker in relation to the total thickness of the shell than in *Cypridopsis* as shown by Bate and East (1972, p. 188, fig. 9). The endocuticle of the Triassic specimen (Pl. 1, fig. 6) consists of coarse crystals on the bottom of the picture that represent part of the overlapping left valve, above this is a smooth surface (below the arrow) that is interpreted to represent the exocuticle of the right valve beneath the overlapping left valve. This and the other specimens in the collection are referred to *Darwinula* because they have the characteristic size and shape of the genus.

DARWINULA spp.
Pl. 1, fig. 6; Pl. 2, figs. 1–3, 5–9, 14–16

Remarks.—The best preserved specimen is shown on Pl. 1, fig. 6 and Pl. 2, figs. 1–3, and even on this specimen, the outer surface has not been preserved. Plate 2, figs. 5–9 illustrate a steinkern with the anterior missing, and figs. 14–16 illustrate a steinkern with one of the valves partly missing. Because of the poor preservation, we do not known whether

TABLE 3—Measurements of specimens.

MEASUREMENTS (in mm):	GREATEST LENGTH	GREATEST HEIGHT	GREATEST WIDTH
Fig. specimen (USNM 248206)	0.73	0.4	0.33
Fig. specimen (USNM 248207)	0.8+	0.45	0.4
Fig. specimen (USNM 248208)	0.84	0.45	0.2 (one valve)

the specimens are conspecific. Because many of the described *Darwinula* species from the Triassic are inadequately illustrated, these specimens are not formally named.

Because the specimens are abraded and because parts of some are missing, all the measurements (Table 3) are smaller by an increment.

CONCLUSIONS

Based on Mesozoic fossil evidence we conclude:

1) Many of the Indian vertebrates are present only in the "northern" continents, but are conspicuously absent in the "southern" continents. This suggests that India was close to Eurasia, possibly connected by a filter bridge in the approximate area of Kashmir, allowing tetrapods to migrate between the two landmasses.

2) Indian fossils show least similarities with Australian and Antarctic forms. Although our knowledge of Antarctic fossils is still poor, the available record does not support the plate tectonic models showing that the eastern margin of India was connected with Australia or Antarctica. The presence of *Darwinula* in India and its absence in Australia and possibly in Antarctica throughout geologic time are additional evidence.

3) Although India shares faunal similarities with Africa, only a fraction of the exotic tetrapods of Africa is represented in India. This suggests there may have been some sort of filter preventing migration of many of the tetrapods between Africa and India.

4) India was not an island continent from the Permian to the Late Cretaceous because no endemic family is known from this subcontinent, and those vertebrates that are not cosmopolitan are most nearly similar to North American, European and Asian forms.

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