

# Maastrichtian and Danian Echinoids from Northwestern Madagascar\*

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## Introduction

As a part of palaeontological reconnaissance survey in Madagascar by the National Science Museum, Tokyo, the Majunga area was surveyed by UJIIÉ and KANIE in 1973 and OBATA and KANIE in 1975, and the Antonibe area by UJIIÉ and KANIE in 1973. In the course of the survey numerous fossil echinoids were collected.

A large number of echinoid species have been reported from the Maastrichtian to Danian strata at various localities in northwestern Madagascar (see BESAIRIE, 1972). Recently OBATA and KANIE (1978) reported a Danian nautiloid from the Majunga area, and discussed the Danian of Madagascar as a whole. Subsequently TASHIRO (1978) described the Maastrichtian to Danian bivalve fauna of northwestern Madagascar; appended to his paper were geological notes on the bivalve localities by UJIIÉ and others (1978).

In this report we describe and discuss echinoid species collected from two areas in northwestern Madagascar. The basic field work was carried out by the junior authors (OBATA and KANIE) and the laboratory work primarily by the senior author (TANAKA).

The specimens studied are to be registered as a part of the collections of the National Science Museum, and will eventually be returned to the Malagasy Republic.

We express our sincere gratitude to Professor Hiroshi UJIIÉ of University of the Ryukyus for his kind partnership during field work in 1973 and to Dr. William James KENNEDY of Oxford University for critical rephrasing of the English. We are also indebted to Dr. Jean ROMAN of the Muséum National d'Histoire Naturelle, Paris,

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### Localities of Echinoid Specimens

Continuous marine sequences of Cretaceous to Tertiary age occur widely in northwestern Madagascar. In the Majunga area, echinoids were collected from the chalky sediments of Formation C<sup>9</sup> (Maastrichtian) and Formation C<sup>10</sup> (Danian) along the national route No. 4 about 20 to 40 km southeast of Majunga (Fig. 1). A schematic columnar section with echinoid localities is shown in Fig. 2, and a list of echinoid species associated with other marine invertebrates in the area has been given by OBATA and KANIE (1978) and UJIIÉ and others (1978).

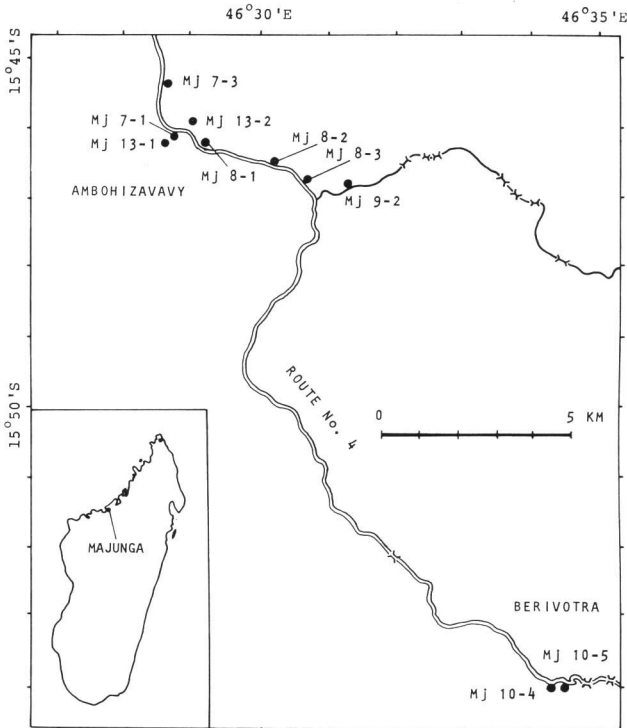


Fig. 1. Localities of echinoid species in the Majunga area.

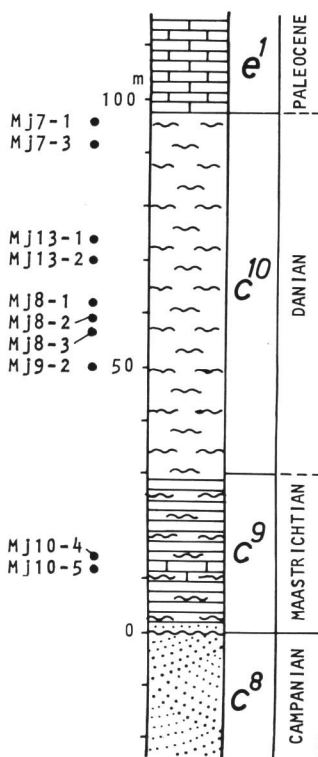


Fig. 2. Schematic columnar section along the Route No. 4 between Ambohizavavy and Berivotra. See Fig. 1 for the fossil localities.

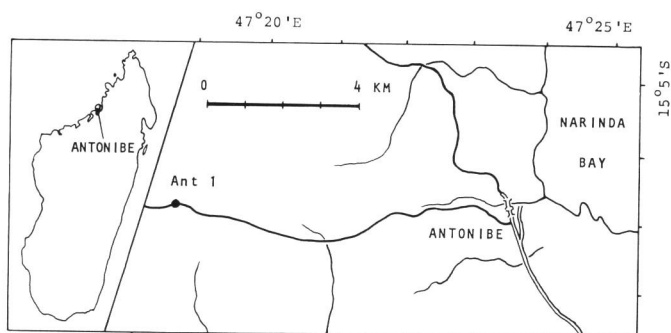


Fig. 3. Locality of echnoid species in the Antonibe area.

In the Antonibe area, we collected echnoids only from one locality, though LAMBERT (1933) reported them from various localities in Formations F and G. This echnoid locality is indicated as Ant 1 in Fig. 3.

### Notes on the Echinoid Assemblages

Most of the echinoid specimens examined came from the Majunga area; accordingly, a discussion of echinoid assemblages in conjunction with palaeoenvironmental interpretation is restricted to the Maastrichtian to Danian strata of this region (Fig. 1). The faunas are listed at generic level below, an asterisk indicating the common species at each locality.

From the top downwards

Formation C<sup>10</sup>

- Mj 7-1 *Hemiaster*\*, *Linthia*\*
- Mj 7-3 *Phymosoma*, *Linthia*\*
- Mj 13-1 “*Cidaris*”, *Phymosoma*, *Hemiaster*\*, *Linthia*
- Mj 13-2 *Hemiaster*\*, *Abatus*?, *Linthia*\*
- Mj 8-1 *Phymosoma*, *Hemiaster*\*, *Linthia*\*
- Mj 8-2 *Hemiaster*\*, *Diplodetus*
- Mj 8-3 *Phymosoma*, *Hemiaster*, *Linthia*\*
- Mj 9-2 *Linthia*, *Diplodetus*

Formation C<sup>9</sup>

- Mj 10-4 *Linthia*\*
- Mj 10-5 *Gauthieria*, *Hemiaster*, *Linthia*

Some of the echinoids from the Majunga section are regular, but many others are irregular Spatangoida. The Maastrichtian and Danian echinoid faunas are dominated by *Hemiaster* and *Linthia*. Of the echinoid species identified here, *Linthia* (*Linthia*) *inconstans* (LAMBERT) is the most abundant, followed by *Hemiaster* (*Bolbaster*) *hawkinsi* LAMBERT and *Hemiaster* (*Mecaster*) *majungensis* TANAKA sp. nov. in order of decreasing numbers. *Linthia* (*Linthia*) *inconstans*, among others, occurs commonly at various localities. The two dominant species, *Linthia* (*Linthia*) *inconstans* and *Hemiaster* (*Bolbaster*) *hawkinsi*, both show a similar stratigraphic variation of abundance.

According to our present knowledge, the regular forms, “*Cidaris*”, *Phymosoma* and *Gauthieria*, lived free on the sea floor, the first inhabiting wave-washed bottoms and the second and the third living at moderate depths. *Hemiaster* and *Linthia*, irregular forms with fascioles, were mud-dwellers living at moderate depths (sublittoral to bathyal zone). *Linthia* was a burrower as probably was *Hemiaster*. With respect to the substrates into which these echinoids burrowed, the marl and chalk constituting Formations C<sup>9</sup> (Maastrichtian) and C<sup>10</sup> (Danian) respectively are of mud grain size.

Echinoids as well as molluscs vary in abundance from horizon to horizon within the Majunga section (see OBATA and KANIE, 1978, Fig. 4). The lower part of Formation C<sup>9</sup>, which rests unconformably on Formation C<sup>8</sup> (Campanian), is devoid of echinoids, being characterized by the almost exclusive occurrence of ostreids (mainly *Pycnodonte*) suggesting a littoral environment. The middle part of Formation C<sup>9</sup> (Mj 10-5, 10-4) yields scarce echinoids (e.g. *Linthia* and *Hemiaster*), and represents

deeper water deposition. In Formation C<sup>10</sup>, echinoids are represented chiefly by *Linthia* and *Hemiaster* genera which are entirely absent below. These, together with bivalves, increase in abundance in the middle and upper parts of the unit. It is possible that the lower part of Formation C<sup>10</sup>, which yields no macrofossils other than living chamber-preserved *Hercoglossa*, may have been deposited under a deeper environment than the middle part of Formation C<sup>9</sup> or the middle to upper parts of Formation C<sup>10</sup>.

In the upper part of Formation C<sup>10</sup> (Mj 13-2, 13-1, 7-3, 7-1), echinoids are commonly associated with a bivalve fauna dominated by *Pholadomya* and *Modiolus*. As to the ecology of Recent forms, *Pholadomya* is a deep burrower in sandy mud substrates chiefly in the lower sublittoral zone, though its habitat varies in depth according to group. *Modiolus* lives in the littoral to sublittoral (even to upper bathyal) zone. As will be seen from Fig. 4, in middle to upper C<sup>10</sup> (middle to upper Danian) the stratigraphic variation in abundance of substrate-burrowing echinoids (*Linthia* and *Hemiaster*) shows a marked negative correlation with that of *Modiolus* and also with that of *Pholadomya*. There is no definite correlation between *Modiolus* and *Pholadomya* in respect to stratigraphic variation in abundance. However, palaeo-

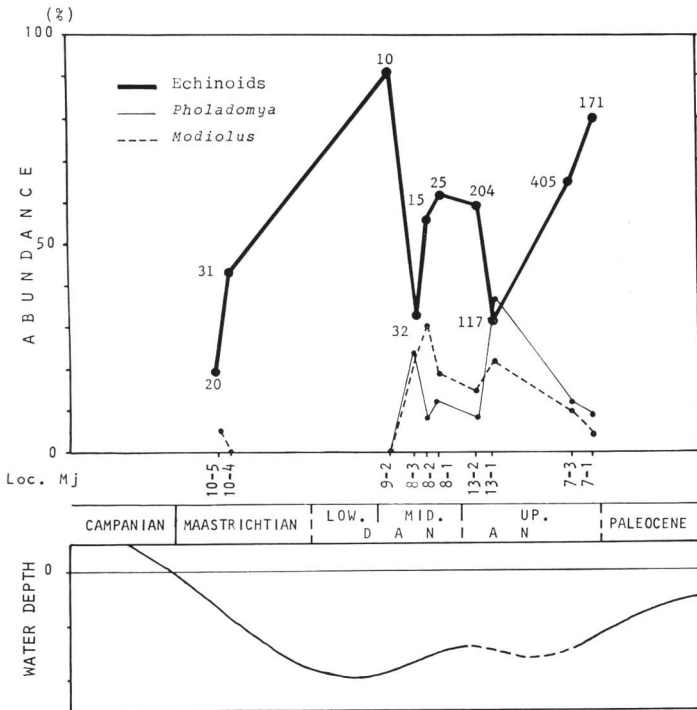


Fig. 4. Stratigraphic variation of echinoid-bivalve association along the Majunga section with the inferred water depth curve. Numerals indicate the number of echinoid specimens at individual localities.

environmental interpretation of these situations must be reserved for further study. Furthermore, ostreids dominated by *Gryphaeostrea* are found at various levels within middle to upper C<sup>10</sup>, though not commonly. *Gryphaeostrea* is small-sized and thinner-shelled than the *Pycnodonte* abounding in lower C<sup>9</sup> (lower Maastrichtian). From this we conclude that middle to upper C<sup>10</sup> were deposited in deeper water than lower C<sup>9</sup>.

From the stratigraphic change of echinoid-bivalve associations in Formations C<sup>9</sup> to C<sup>10</sup>, it is suggested that the deposition was in the littoral zone for lower C<sup>9</sup> (lower Maastrichtian) and in the neritic zone for the succeeding sequence, with a maximum depth (lower neritic or upper bathyal zone) in lower C<sup>10</sup> (lower Danian), followed by a general shallowing trend probably with some oscillations (Fig. 4). Support for this suggestion may also be found in the occasional occurrence of *Pholadomya* in middle to upper C<sup>10</sup> (middle to upper Danian). On the other hand, "*Cidaris*" is scarce in the lower part of upper C<sup>10</sup>.

### Systematic Descriptions

Subclass PERISCHOECHINOIDEA M'COY, 1849

Order CIDAROIDA CLAUS, 1880

Family Cidaridae GRAY, 1825

Subfamily Cidarinae GRAY, 1825

Genus *Cidaris* LESKE, 1778

"*Cidaris*" *majungensis* LAMBERT

Pl. 1, fig. 1a-c

*Cidaris majungensis* LAMBERT, 1933, p. 11-12, pl. 1, figs. 4-7.

*Remarks.* The only specimen available is characterized by an absence of horizontal and vertical sutural grooves, sinuate ambulacra with uniserial, horizontal and nonconjugate pore pairs, comparatively high interambulacral plates, each with a primary tubercles, and deep, well-separated areoles. The primary tubercles are noncrenulate, but two of those on the aboral surface are subcrenulate. The genus *Cidaris*, represented only by Recent forms, is characterized by the presence of end teeth on the large and small globiferous pedicellariae (FELL in MOORE, ed., 1966). In spite of this feature being unrecognizable in the present species, it has in practice been referred to this genus in the broad sense.

The specimen measures 23.0 mm across and 15.5 mm high.

*Occurrence.* Loc. Mj 13-1, Majunga area, upper part of Formation C<sup>10</sup>, Danian, chalk.

Subclass EUECHINOIDEA BRONN, 1860  
 Superorder ECHINACEA CLAUS, 1876  
 Order PHYMOSOMATOIDA MORTENSEN, 1904  
 Family Phymosomatidae POMEL, 1883  
 Genus *Phymosoma* HAIME, 1853

*Phymosoma archiaci* (COTTEAU)  
 Pl. 1, fig. 2a–c

*Diplopodia archiaci*, DESOR, 1856, p. 77.

*Pseudodiadema archiaci*, COTTEAU, 1864, p. 505–507, pl. 1121, figs. 11–13.

*Cyphosoma archiaci*, COTTEAU, 1865, p. 615–618, pl. 1149, figs. 1–9.

*Remarks.* COTTREAU (1908) described a “variety” of *Phymosoma archiaci* (p. 165–166 [21–22], pl. 15 [3], fig. 1, 1a–b, text-fig. 12) from the Maastrichtian of Madagascar. The slightly sunken region between the two series of primary tubercles in each adapical interambulacral area is granulated in this “variety”, whereas in the specimens available as well as in those described by COTTEAU (1864, 1865) it is naked.

Most of the specimens measure between 24 mm and 25.5 mm across and between 11 mm and 13 mm high.

*Occurrence.* The present species occurs in Danian chalk at the following localities in the Majunga area: Mj 7–3, upper part of Formation C<sup>10</sup>; Mj 8–1 and 8–3, middle part of Formation C<sup>10</sup>; Mj 13–1, upper part of Formation C<sup>10</sup>.

Genus *Gauthieria* LAMBERT, 1888

*Gauthieria* sp.  
 Pl. 1, fig. 3a–b

*Description.* The only specimen available is fragmentary. The test is low and slightly flattened above. The ambulacral plates are compound, with five pore pairs, and the pore zones are simple throughout and undulated, with pore pairs in a single series. The primary tubercles are in two regular series in each interambulacral area, having fine radiating striae in the areoles. They are crenulate and imperforate.

*Remarks.* The specimen, though fragmentary, appears similar to *Gauthieria menuthiae* (LAMBERT et SAVIN) (LAMBERT and THIÉRY, 1911, p. 221–222, pl. 6, figs. 1–4) from the Danian of Madagascar in the general features of the test. However, the specific identity of the present form with that species is impossible because of the poor preservation.

*Occurrence.* Loc. Mj 10–5, Majunga area, middle part of Formation C<sup>9</sup>, Maastrichtian, marl.

Superorder ATELOSTOMATA ZITTEL, 1879  
 Order SPATANGOIDA CLAUS, 1876  
 Suborder Hemiasterina FISCHER, 1966

## Family Hemiasteridae CLARK, 1917

Genus *Hemiaster* AGASSIZ, 1847Subgenus *Bolbaster* POMEL, 1869*Hemiaster (Bolbaster) hawkinsi* LAMBERT

Pl. 1, fig. 4a-d; Text-figs. 5-8

*Hemiaster (Leucaster) lamberti*, COTTREAU, 1908, p. 173-174, pl. 17, fig. 3, 3a, text-fig. 15.*Hemiaster hawkinsi* LAMBERT, 1933, p. 22-23, pl. 4, fig. 19.

*Remarks.* This species is characterized by the subglobular shape of the test, the faint frontal depression disappearing near the ambitus, lacking of an anterior notch, and by the small petals. Therefore, according to LAMBERT and THIÉRY'S (1924; section), MORTENSEN'S (1950; section), and FISCHER'S (in MOORE, ed., 1966; subgenus) classifications of the genus *Hemiaster*, the present species is to be placed in the subgenus *Bolbaster*. LAMBERT and THIÉRY (1924) and MORTENSEN (1950) maintained that the pores of all the petals were round, and took this as one of the characters of *Bolbaster*. However, in the specimens available, the pores are generally round in the frontal ambulacrum, whereas they are oblong in the paired petals, the anterior petals having somewhat shorter pores in the anterior poriferous zones than in the posterior. Similar features were described by COTTREAU (1908). It should also be noted that the apical system, not mentioned by previous authors, is ethmophract and the posterior genital plates are not separated by the madreporite.

*Hemiaster (Bolbaster) hawkinsi* is closely similar to *H. (B.) madagascariensis* COTTREAU to be described below, but can be separated from that species by its lower, less globular test. The former species has nearly the same test outline, i.e. nearly the same ratio of width to length of the test as, but a lower ratio of height to length or width of the test than the latter species (Text-figs. 6-8). Moreover, there is a minor but distinct difference in peripetalous fasciole between the two. The peripetalous fasciole has rounded course in *H. (B.) hawkinsi*, but is lozenge-shaped (polygonal) in *H. (B.) madagascariensis*.

The largest specimen is 16.3 mm long, 15.2 mm wide and 12.0 mm high.

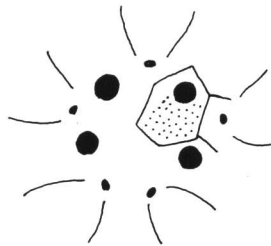


Fig. 5. Apical system of *Hemiaster (Bolbaster) hawkinsi* LAMBERT from loc. Mj 7-1, Majunga area,  $\times 15$ .



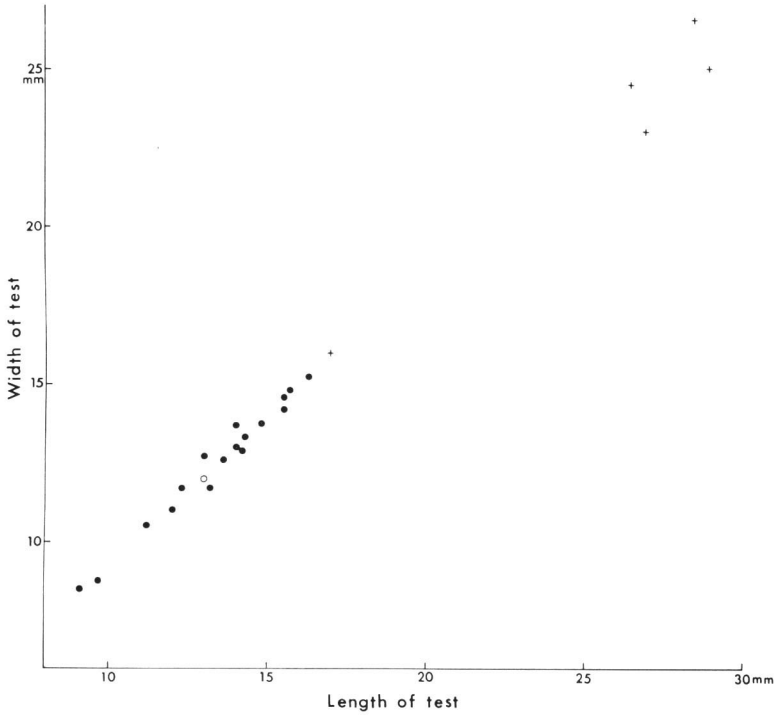


Fig. 6. Relation between the length and the width of the test in *Hemiaster (Bolbaster) hawkinsi* LAMBERT and *H. (B.) madagascariensis* COTTREAU.

Solid circle: *Hemiaster (Bolbaster) hawkinsi*, specimens examined.

Open circle: ditto, COTTREAU, 1908.

Cross: *H. (B.) madagascariensis*, COTTREAU, 1922; LAMBERT, 1903, 1906.

*Occurrence.* The present species occurs in Danian chalk at the following localities in the Majunga area: Mj 7-1, upper part of Formation C<sup>10</sup>; Mj 8-1 and 8-2, middle part of Formation C<sup>10</sup>; Mj 13-1 and 13-2, upper part of Formation C<sup>10</sup>.

*Hemiaster (Bolbaster) cf. madagascariensis* COTTREAU  
Pl. 1, fig. 5

*Compare.*

*Hemiaster* sp., LAMBERT, 1903, p. 87, pl. 3, figs. 6-8.

*Hemiaster* sp., LAMBERT in BOULE and THEVÉNIN, 1906, p. 53, pl. 2, fig. 6, 6a-b.

*Hemiaster madagascariensis* COTTREAU, 1922, p. 118-120, pl. 14, figs. 1-8.

*Hemiaster madagascariensis*, LAMBERT, 1936a, p. 28.

*Remarks.* The specimens available are small and poorly preserved, but are characterized by a rounded ovate test outline, very faint frontal sinus, disappearing near the ambitus, lacking of an anterior notch, and the development of a peripetalous fasciole



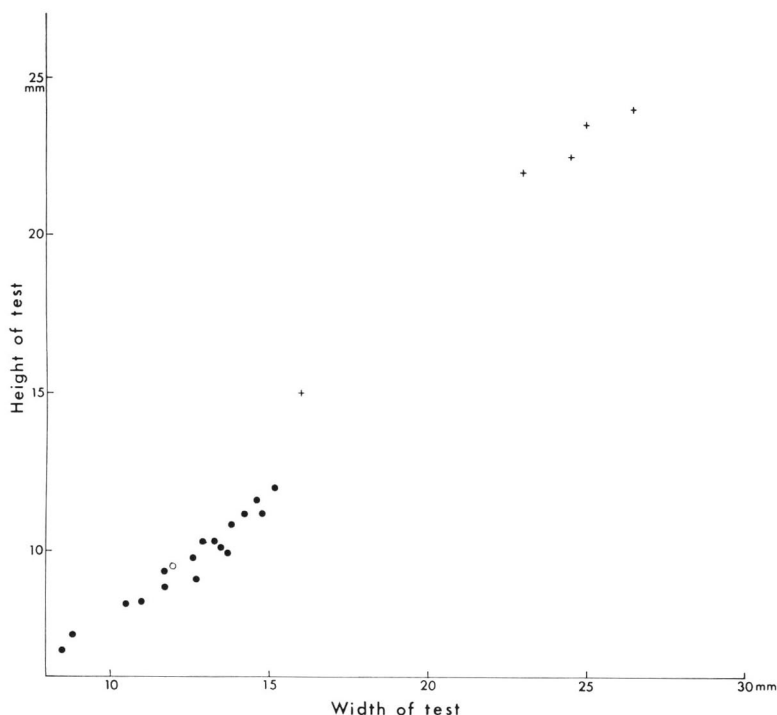


Fig. 8. Relation between the width and the height of the test in *Hemiaster (Bolbaster) hawkinsi* LAMBERT and *H. (B.) madagascariensis* COTTREAU. Symbols as in Fig. 6.

Maastrichtian, marl.

Subgenus *Mecaster* POMEL, 1883

*Hemiaster (Mecaster) boulei* COTTREAU

Pl. 3, fig. 7

*Hemiaster boulei* COTTREAU, 1908, p. 171–173, pl. 15, fig. 8, 8a.

*Remarks.* The test, though deformed, appears to have a subpentagonal outline, the frontal sinus is fairly conspicuous, and the petals are subequal in length and somewhat flexuous. Accordingly, the specimen belongs to the subgenus *Mecaster* (FISCHER in MOORE, ed., 1966), designated as a section of *Hemiaster* by LAMBERT and THIÉRY (1924) and MORTENSEN (1950). In the present specimen the four gonopores are arranged in a trapezoidal form and approach each other in a longitudinal direction, as indicated in the original specific diagnosis (COTTREAU, 1908). However, the poor preservation of the apical system makes it impossible to ascertain whether the madreporite extends as far back as to separate the posterior genital plates

and touches the posterior ocular plates, as is characteristic of the subgenus.

*Occurrence.* Loc. Mj 13-1, Majunga area, upper part of Formation C<sup>10</sup>, Danian, chalk.

*Hemiaster (Mecaster) majungensis* TANAKA sp. nov.

Pl. 1, fig. 6a-d; Pl. 2, fig. 1; Text-fig. 9

*Type specimens.* Holotype, NSM.PA 11994 from Mj 13-1; paratype, NSM.PA 11995 from Mj 8-1.

*Description.* Test medium-sized, rather roundly subovate, as wide as long, widest point somewhat anterior to the midpoint, relatively low; frontal depression moderately deep, becoming shallower near the ambitus; anterior notch indistinct. Aboral surface gradually sloping anteriorly, abruptly truncated posteriorly; oral surface nearly flat, plastronal region slightly inflated. Apical system posterior, ethmophract; four gonopores arranged in a trapezoidal form, approaching each other in a longitudinal direction; madreporite extending as far back as to separate the posterior genital plates, touching the posterior ocular plates. Frontal ambulacrum moderately deeply sunken, semipetaloid; pores minute, round, oblique; pores of each pair separated by a granule. Paired ambulacra well sunken, having relatively short



Fig. 9. Apical system of *Hemiaster (Mecaster) majungensis* TANAKA sp. nov. from loc. Mj 8-1, Majunga area,  $\times 15$ .

and somewhat flexuous petals, slightly depressed between the distal end of the petals and near the ambitus; pores elongate or slitlike, conjugate; posterior petals considerably shorter than, and 0.5 to 0.6 the length of the anterior ones. Periproct longitudinally oval, placed high up on the posterior truncate surface; peristome anterior. Peripetalous fasciole well developed, running in a straight line between the end of the petals; no other fascioles. Tubercles conspicuously larger on the oral surface than on the aboral surface.

*Measurements (in mm).*

	Length	Width	Height
Holotype NSM.PA 11994	38.3	38.8	23.8

The specimens are 37 mm to 42 mm in length.

*Remarks.* In *Hemiaster (Mecaster) majungensis* sp. nov. the madreporite extends as far back as to separate the posterior genital plates, and touches the posterior ocular plates. This feature of the apical system was considered to be mere intraspecific

variation in *Hemiaster* by LAMBERT and THIÉRY (1924), but later MORTENSEN (1950) maintained that it is one of the characters of *Mecaster*, a section of *Hemiaster*. The above feature of the apical system combined with the relatively low test, moderately deep frontal sinus and somewhat flexuous paired petals may make it possible to assign the species to the subgenus *Mecaster* of FISCHER's classification (MOORE, ed., 1966). On the other hand, the rather roundly subovate outline of the test and the paired petals of unequal length (the posterior petals considerably shorter than the anterior) are not in accordance with the subgeneric diagnosis of *Mecaster*. In spite of this, and if one attaches importance to the characters of the apical system, one may refer the species to the subgenus *Mecaster*.

This new species is easily distinguishable from *Hemiaster* (*Mecaster*) *boulei* COTTREAU described above. In *Hemiaster* (*Mecaster*) *majungensis* the frontal sinus becomes shallower near the ambitus, the anterior notch thus being indistinct. But in *H. (M.) boulei* the frontal depression is distinct throughout, forming a conspicuous notch at the anterior margin of the test. Moreover, the former species has a more rounded test outline and much shorter petals than does the latter species.

*Occurrence.* Locs. Mj 8-1 and 8-3, Majunga area, middle part of Formation C<sup>10</sup>, Danian, chalk; loc. Mj 13-1, Majunga area, upper part of Formation C<sup>10</sup>, Danian, chalk. Some specimens probably identifiable with the present species are found at loc. Mj 8-2, in the same area, where the middle part of Formation C<sup>10</sup> is exposed.

*Hemiaster* (s.l.) sp.

Pl. 2, fig. 2

*Description.* Test roundly subovate; frontal sinus becoming shallower near the ambitus; anterior notch indistinct. Apical system eccentric behind. Frontal ambulacrum sunken; paired ambulacra sunken, petaloid; posterior petals somewhat shorter than the anterior ones. Well developed peripetalous fasciole running in a straight line between the end of the petals; no other fascioles.

*Remarks.* The only specimen available, though deformed and poorly preserved, is assigned to *Hemiaster* on the basis of the general features of the test. Subgeneric determination is not possible because of the poor preservation.

*Occurrence.* Loc. Mj 10-5, Majunga area, middle part of Formation C<sup>9</sup>, Maastrichtian, marl.

Family Schizasteridae LAMBERT, 1905

Genus *Abatus* TROSCHEL, 1851

*Abatus* ? sp.

Pl. 2, fig. 3a-d; Text-fig. 10a-b

*Description.* Test roundly heart-shaped, as wide as long; frontal sinus deep, forming a conspicuous notch in the anterior edge of the test. Aboral surface

uniformly convex, highest posteriorly, gradually sloping anteriorly, abruptly truncated posteriorly, with a weak carina in the posterior interambulacrum; oral surface rather inflated. Apical system deplacd anteriorly, ethmolytic, with three gonopores, the one in the madreporite lacking. Anterior ambulacrum deeply sunken throughout its length, subpetaloid; pores minute, round, the pores of each pair separated by a granule. Paired ambulacra well sunken, petaloid; anterior petals slightly flexuous, both poriferous zones about equal in width, with elongate pore pairs; posterior petals shorter than the anterior. Peristome anterior; periproct oval, vertically elongate, placed high up on the posterior truncated surface. Peripetalous fasciole well marked more or less embayed between the anterior and posterior petals, in contact with the end of the anterior petals; no other fascioles.

*Measurements (in mm).*

Length	Width	Height
21.4	21.7	14.0

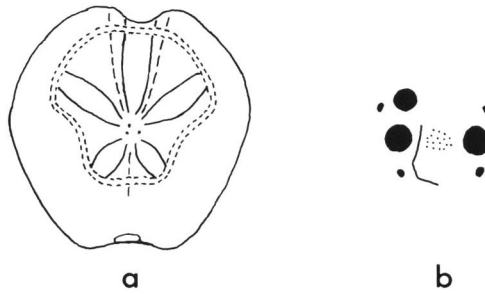


Fig. 10. *Abatus?* sp. from loc. Mj 13-2, Majunga area. a, Aboral view,  $\times 1.5$ . b, Apical system,  $\times 11$ .

*Remarks.* In the genus *Abatus*, the lateroanal fasciole is more or less rudimentary or even totally lacking in the adult (MORTENSEN, 1951; FISCHER in MOORE, ed., 1966). The only specimen available, though well preserved, show no lateroanal fasciole. The present form is of small size, having about twenty pore pairs in the anterior petals. Nevertheless, it is difficult to determine whether it is adult or not. Lack of information on the lateroanal fasciole, whether present or lacking, makes it impossible to determine the exact generic position of the species. However, it is characterized by the deep frontal depression forming a conspicuous notch in the frontal edge of the test. These features prevent us from placing the present form in the allied genus *Tripylus*. Such being the case, it is provisionally referred to the genus *Abatus* on the basis of the general features of the test, and that the anterior petals reach the peripetalous fasciole, this being one of the characters distinguishing *Abatus* from *Tripylus*. The two species of *Tripylus* from the Danian of Madagascar, *T. pseudoviviparus* LAMBERT (1933, p. 27-28, pl. 4, figs. 1-7) and *T. antonibensis* LAMBERT (1933, p. 28, pl. 4, figs. 12-14),

according to MORTENSEN (1951) and FISCHER (in MOORE, ed., 1966), are placed with some doubt in the genus *Abatus*, and with this we agree. The specimen described here resembles these two species in many respects. The former, however, has three gonopores as against two in the latter. Because of this significant difference, together with *Abatus* being a Recent genus, the present form, if assigned to *Abatus*, may represent a new species clearly distinct from the two species mentioned above. It appears similar to *Linthia (Linthia) inconstans* (LAMBERT) in the general features of the test, but the number of gonopores is immediately distinctive.

*Occurrence.* Loc. Mj 13-2, Majunga area, upper part of Formation C<sup>10</sup>, Danian, chalk.

Genus *Linthia* DESOR, 1853  
Subgenus *Linthia* DESOR, 1853

*Linthia (Linthia) inconstans* (LAMBERT)  
Pl. 2, figs. 4a-d, 5a-d; Pl. 3, fig. 1; Text-fig. 11a-c

*Periaster inconstans* LAMBERT, 1933, p. 25-26, pl. 4, fig. 15.

*Remarks.* The original specific diagnosis (LAMBERT, 1933) applies to the specimens available except for the structure of the apical system. MORTENSEN (1951) doubted that the present species belongs to the genus *Periaster* as designated by LAMBERT (1933), because the frontal sinus is deep and the petals are more distinctly sunken. We agree with him, taking into consideration the conspicuous notch in the frontal edge of the test. A matter of more significance is that the structure of the apical system is revealed to be ethmolytic, a feature clearly observable in many specimens. The ethmolytic apical system has four gonopores, the madreporite separating the posterior ocular plates. The character of the apical system described above, among others, makes it possible to identify the present species with the genus *Linthia* rather than *Periaster*. Moreover, the species is placed in the subgenus *Linthia (Linthia)* because it has more or less anteriorly situated apical system and vertically elongate periproct.

In *Linthia (Linthia) inconstans*, the peripetalous fasciole is distinct, but the lateroanal fasciole is variable in continuity from individual to individual, as is the case with fossil *Linthia* and Recent forms (MORTENSEN, 1951). Thus the continuity of the lateroanal fasciole in this species is to be classified into four basic types, A, B, C and D as follows:

- Type A. lateroanal fasciole developed completely so as to join with the peripetalous fasciole at its extremity a short distance behind the distal ends of the anterior petals.
- Type B. lateroanal fasciole nearly complete, not joining with the peripetalous fasciole.
- Type C. lateroanal fasciole incomplete, the anterior half of its lateral segment

lacking.

Type D. lateroanal fasciole much more incomplete so as to be restricted below the periproct.

Type A is seen in about half of the total individuals examined. The continuity of the lateroanal fasciole sometimes differs between the left and the right sides of the test. It is usually greater at the left than at the right (Table 1) with only one exception. This is considered to be related partly with some asymmetric disposition of the internal organs (e.g. the intestinal tract). Frequency of the types of lateroanal fasciole relative to the length of the test is shown on Table 2. On this table the types of lateroanal

Table 1. Asymmetrical development at the left/right side of test of the lateroanal fasciole in *Linthia* (*Linthia*) *inconstans* (LAMBERT)  
Numerals are the number of individuals.

Continuity type				
A/B	A/C	B/C	C/D	D/None
2	1	2	5	1

Table 2. Relation between the development of lateroanal fasciole and the length of test in *Linthia* (*Linthia*) *inconstans* (LAMBERT)  
Numerals are the number of individuals, with percentage in parentheses.

Continuity type	Length of test in mm		
	15-25	25-35	>35
A	6 (28.6)	28 (49.1)	8 (80.0)
B	—	5 (8.8)	1 (10.0)
C	3 (14.3)	15 (26.3)	—
D	10 (47.6)	9 (15.8)	1 (10.0)
None	2 (9.5)	—	—
Total	21 (100.0)	57 (100.0)	10 (100.0)

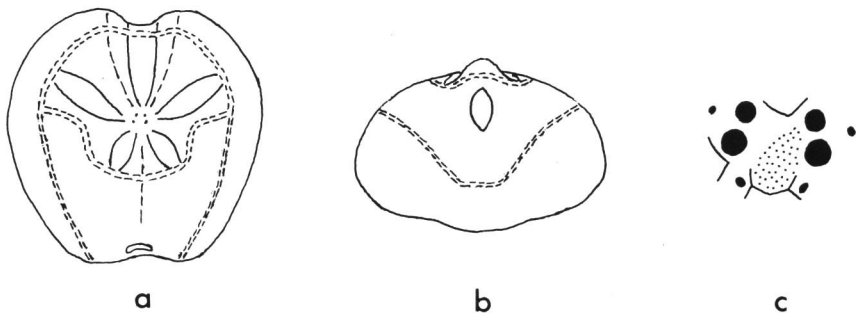


Fig. 11. *Linthia* (*Linthia*) *inconstans* (LAMBERT). a, Aboral view,  $\times 1$  (Loc. Mj 9-2, Majunga area); b, Posterior view of the same,  $\times 1$  c, Apical system,  $\times 12$  (Loc. Mj 7-1, Majunga area).



fasciole, when showing an asymmetrical difference between the two sides of the test, refer to the left-side type concerned which is usually, though not always, better developed. The lateroanal fasciole has a tendency to become complete as the length of the test increases. The larger the test, the larger frequency of type A fasciole. In smaller individuals, on the other hand, the continuity of the lateroanal fasciole varies greatly, thus no one particular type of continuity appearing predominant. It should be noted that the two specimens without any trace of lateroanal fasciole (even its anal segment) are smaller (about 2 cm in length). From the observation noted above it is suggested that the lateroanal fasciole originates below the periproct, then developing forwards so as to form its lateral segment.

*Linthia (Linthia) inconstans* resembles *L. (L.) madagascariensis* sp. nov. to be described below and *L. (L.) sindensis* DUNCAN et SLADEN (1882, p. 18–20, pl. 4, figs. 1–11) from the Paleocene of India. However, *L. (L.) inconstans* is distinctly separated from *L. (L.) madagascariensis* by its rather parallel-sided frontal sinus, narrower anterior notch, narrower anterior petals, shorter and narrower posterior petals, and its more distal junction of lateroanal and peripetalous fascioles. In the present species the posterior petals are about half the length of the anterior petals, whereas in *L. (L.) sindensis* they are about two-thirds the length. The posterior interambulacrum of *Linthia (Linthia) inconstans* is distinctly carinate in comparison with that of *L. (L.) sindensis*. The periproct is placed higher up on the posterior truncated surface in the former species than in the latter. Moreover, in the present form the lateroanal fasciole extends from the lateral to the anal segment in a straight line, but in the Indian species an embayment is seen between the lateral and the anal segments.

*Measurements (in mm).*

	Length	Width	Height
Largest specimen	36.0	36.1	23.3
Smallest specimen	15.3	14.6	10.3

*Occurrence.* The present species occurs in Danian chalk at the following localities in the Majunga area: Mj 7–1 and 7–3, upper part of Formation C<sup>10</sup>; Mj 8–1, 8–3 and 9–2, middle part of Formation C<sup>10</sup>; Mj 13–2, upper part of Formation C<sup>10</sup>. Moreover, specimens probably identical with this species were collected from Danian chalk at loc. Mj 13–1 (upper part of Formation C<sup>10</sup>) in the Majunga area, and also from Danian calcareous mudstone at loc. Ant 1 in the Antonibe area. The species is also found in Maastrichtian marl at loc. Mj 10–4 (middle part of Formation C<sup>9</sup>) in the Majunga area, though less commonly than the coexisting *Linthia (Linthia) madagascariensis*.

*Linthia (Linthia) madagascariensis* TANAKA sp. nov.

Pl. 3, figs. 2a–d, 3, 4; Text-fig. 12a–c

*Type specimens.* Holotype, NSM.PA 11996 from Mj 10–4; paratypes, NSM.PA 11997 and 11998 from Mj 10–4.

*Description.* Test medium-sized, roundly heart-shaped, as wide as long, relatively low; frontal sinus deep, widening distinctly towards the ambitus, forming a broad and deep notch at the frontal margin of the test. Aboral surface uniformly convex, highest somewhat behind the center, gradually sloping anteriorly, abruptly truncated posteriorly, with a more or less prominent carina in the posterior interambulacrum; oral surface rather inflated. Apical system slightly anterior, ethmolytic, with four gonopores; madreporite separating the posterior ocular plates. Frontal ambulacrum broad, deeply sunken throughout its length, subpetaloid; pores minute, round; pores of each pair separated by a granule. Paired ambulacra straight, well sunken, petaloid; petals unequal in length, rather broad; anterior petals longer than the posterior, much more divergent; posterior petals two-thirds the length and nearly as wide as the anterior; pores elongate, conjugate. Peristome anterior, transversely oval. Periproct oval, vertically elongate, placed high up on the posterior truncated surface. Peripetalous fasciole distinct, rather narrow, bending more or less deeply inwards between the anterior and posterior petals; lateroanal fasciole much narrower, much less distinct than the peripetalous fasciole, joining with the latter at its extremity a short distance behind the distal ends of the anterior petals and at some distance towards the apex, continuing straight back; continuity variable.

*Measurements (in mm).*

	Length	Width	Height
Holotype NSM.PA 11996	31.6	31.6	20.2

The specimens measure between about 27 mm and about 35 mm in length.

*Remarks.* In the holotype (Pl. 3, fig. 2a–d) the posterior truncated surface is nearly vertical, as a result of deformation. This new species appears similar to *Hemiasster latesulcatus* LAMBERT (1936, p. 206, pl. 24, figs. 3–4) from the Maastrichtian of Madagascar, especially in the general outline of the test, the wide frontal sinus and the distinct anterior notch at the frontal margin of the test. It is not known, however, whether the apical system of this species is ethmophract or ethmolytic, and this makes

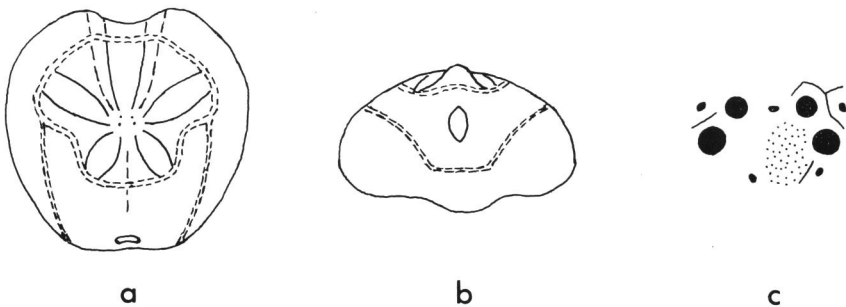


Fig. 12. *Linthia (Linthia) madagascariensis* TANAKA sp. nov. from loc. Mj 10–4, Majunga area (Holotype, NSM. PA 11996). a, Aboral view,  $\times 1$ . b, Posterior view,  $\times 1$ . c, Apical system,  $\times 15$ .

it difficult to assign the species to *Hemiaster*, even though no fascioles other than the peripetalous (understood as such from the LAMBERT's description) are present. The material available is as small as 14 mm long so that the possibility exists that the development of a peripetalous fasciole only is a matter of intraspecific variability. In this connection, it should be noticed that in *Linthia (Linthia) inconstans* (LAMBERT), described above, continuity of the lateroanal fasciole varies greatly between individuals. In that species the lateroanal fasciole tends to become incomplete with decreasing size of the test, and we have an individual without lateroanal fasciole, about 20 mm long, one of the smallest specimens available. In *Linthia (Linthia) madagascariensis*, on the other hand, there are no comparably small specimens. Most of the individuals of the present species have a completely developed lateroanal fasciole. Even in the case of the worst development of the lateroanal fasciole, only the anterior half of the lateral segment is lacking; this situation refers to the type C lateroanal fasciole in *Linthia (Linthia) inconstans*. Under these circumstances, it is very likely that *Hemiaster latesulcatus* and *Linthia (Linthia) madagascariensis* are one and the same species, the former being no more than the much smaller (younger) form of the latter species. Notwithstanding, the specific identity of the present material with *Hemiaster latesulcatus* is not possible because the exact generic position of the latter species is doubtful.

This species closely resembles *Linthia (Linthia) inconstans* (LAMBERT), described above, in the general features of the test. One of the most distinct differences between the two species is that in *L. (L.) madagascariensis* the frontal sinus expands uniformly and distinctly towards the ambitus and in *L. (L.) inconstans* it is nearly parallel-sided for the anterior two-thirds. Thus, the anterior notch is wider in the former species than in the latter. *Linthia (Linthia) madagascariensis* also has wider paired petals when compared with *L. (L.) inconstans*. In the new species the posterior petals are as wide as the anterior ones and are relatively long (two-thirds the length of the anterior), whereas in *L. (L.) inconstans* they are narrower and only one-third to one half the length. The lateroanal fasciole joins with the peripetalous fasciole more proximally in *L. (L.) madagascariensis* than in *L. (L.) inconstans*.

There are also similarities to *Linthia (Linthia) sindensis* DUNCAN et SLADEN (1882, p. 18–20, pl. 4, figs. 1–11) from the Paleocene of India in the relatively weak development of the posterior interambulacral carina, wide paired petals and relatively long posterior petals. The present form differs, however, from that Indian species in that the frontal sinus is deep and expands towards the frontal margin of the test and in the lateroanal fasciole, the lateral segment extends back to the anal segment in a straight line.

*Occurrence.* Locs. Mj 10–4 and 10–5, middle part of Formation C<sup>9</sup>, Maastrichtian, marl.

*Linthia (Linthia)?* sp.  
Pl. 3, fig. 6; Text-fig. 13

*Description.* The two specimens available are poorly preserved and secondarily

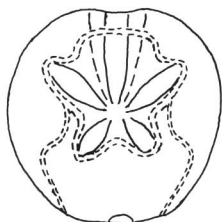


Fig. 13. Aboral view of *Linthia* (*Linthia*)? sp. from loc. Ant 1, Antonibe area,  $\times 1$ .

depressed. The frontal sinus is comparatively deep, and the anterior notch very shallow. The apical system is slightly anterior, the anterior ambulacrum sunken and the paired ambulacra sunken and petaloid. The periproct is vertically elongate. The peripetalous fasciole is distinct and deeply embayed between the petals; the lateroanal fasciole is narrower than the peripetalous and deeply embayed.

*Remarks.* These specimens are probably referable to *Linthia* (*Linthia*) on the basis of the general features of the test, although the structure of the apical system is uncertain. This species is clearly distinguished from *Linthia* (*Linthia*) *inconstans* (LAMBERT) and *L. (L.) madagascariensis* TANAKA sp. nov. described above. In the present species the anterior notch is very shallow and the peripetalous fasciole is deeply embayed between the petals. In *L. (L.) inconstans*, on the other hand, the anterior notch is deep and the peripetalous fasciole is less deeply embayed between the anterior and posterior petals and moreover not embayed between the frontal ambulacrum and the anterior petals and between the posterior petals. In the present form the lateral segment of lateroanal fasciole is deeply embayed, whereas in *Linthia* (*Linthia*) *inconstans* and *L. (L.) madagascariensis* it is straight. Furthermore, the lateroanal fasciole joins with the peripetalous fasciole more proximally in the present species than in the two others.

*Occurrence.* Loc. Ant 1, Antonibe area, Danian, calcareous mudstone.

Suborder Micrasterina FISCHER, 1966  
Family Micrasteridae LAMBERT, 1920  
Genus *Brissopneustes* COTTEAU, 1887

*Brissopneustes decaryi* LAMBERT  
Pl. 3, fig. 8a-b

*Brissopneustes decaryi* LAMBERT, 1933, p. 19, pl. 3, figs. 9-10

*Remarks.* The poorly preserved specimens available are characterized by, among other features, the presence of a subanal fasciole and a mesamphisternous plastron. These characters, together with many other features of the test, make it possible to identify these specimens with *Brissopneustes decaryi* LAMBERT, although the structure

of the apical system is not known.

The specimens measure between 21.5 mm and 25.0 mm long, between 19.5 mm and 22.5 mm wide, and between 13.0 mm and 14.0 mm high.

*Occurrence.* Loc. Ant 1, Antonibe area, Danian, calcareous mudstone.

Family Brissidae GRAY, 1855

Genus *Diplodetus* SCHLÜTER, 1900

Subgenus *Protobrissus* LAMBERT, 1907

*Diplodetus (Protobrissus) cf. gauthieri* COTTREAU

Pl. 3, fig. 5

*Compare.*

*Diplodetus gauthieri* COTTREAU, 1908, p. 174–175, pl. 15, fig. 7, 7a–b.

*Remarks.* The poorly preserved specimens available are characterized by having a peripetalous fasciole which is somewhat diffuse and more or less embayed between the adjoining petals, a subanal fasciole, and an ultramphisternous plastron. From these features, in conjunction with many others, one may refer these specimens to *Diplodetus gauthieri* COTTREAU, although the structure of the apical system is not known.

MORTENSEN (1951) maintained that *Diplodetus gauthieri* of COTTREAU (1908) belongs rather to the genus *Protobrissus*, which, in turn, is included in the genus *Diplodetus* as a subgenus by FISCHER (in MOORE, ed., 1966). Actually, in the present form the test is small and the petals are about equal in length; these features are those that distinguish *Protobrissus* from *Diplodetus* (s. s.). According to FISCHER (in MOORE, ed., 1966), it is also a characteristic of *Protobrissus* that the anterior petals diverge laterally from the anteriorly placed apex. However, the anterior petals are not as divergent in the present species as in the type species of the subgenus.

The specimens are generally about 3 cm long and are slightly longer than wide.

*Occurrence.* Locs. Mj 8–2 and 9–2, Majunga area, middle part of Formation C<sup>10</sup>, Danian, chalk.

### Concluding Remarks

The echinoid faunas studied came mostly from the Danian of the Majunga area, and only a few from the Maastrichtian of this area and the Danian of Antonibe. Among them eight genera and fourteen species are identified. They are listed below, common occurrence being indicated by an asterisk.

Majunga area

Maastrichtian *Gauthieria* sp.

*Hemiaster (Bolbaster) cf. madagascariensis* COTTREAU

*Hemiaster* (s.l.) sp.

- Linthia (Linthia) madagascariensis* TANAKA sp. nov.  
*Linthia (Linthia) inconstans* (LAMBERT)  
 Danian “*Cidaris*” *majungensis* LAMBERT  
*Phymosoma archiaci* (COTTEAU)  
*Hemiaster (Bolbaster) hawkinsi* LAMBERT\*  
*Hemiaster (Mecaster) boulei* COTTREAU  
*Hemiaster (Mecaster) majungensis* TANAKA sp. nov.  
*Abatus?* sp.  
*Linthia (Linthia) inconstans* (LAMBERT)\*  
*Diplodetus (Protobrissus)* cf. *gauthieri* COTTREAU
- Antonibe area  
 Danian *Linthia (Linthia)* cf. *inconstans* (LAMBERT)  
*Linthia (Linthia)?* sp.  
*Brissopneustes decaryi* LAMBERT

Among the above species, two are new and one known species is transferred from *Periaster* to *Linthia*.

In Madagascar a large number of echinoid species occur in Maastrichtian and Danian strata (BESAIRIE, 1972). Many of the species described here as well as many others are restricted either to the Maastrichtian or to the Danian. On the other hand, *Linthia (Linthia) inconstans* (LAMBERT) occurs not only in the Danian but also in the Maastrichtian. Such is the case with “*Cidaris*” *beaugeyi* LAMBERT, *Phymosoma archiaci* (COTTEAU), *Hemiaster (Bolbaster) hawkinsi* LAMBERT, *H. (B.) madagascariensis* COTTREAU and *Cyclaster pfenderae* LAMBERT, plus *Tripylus pseudoviviparus* LAMBERT and *T. antonibensis* LAMBERT, whose generic determination is doubtful. Thus, it may well be said that the Danian echinoid fauna of Madagascar is not clearly distinguished from the Maastrichtian one.

*Linthia (Linthia) sindensis* DUNCAN et SLADEN from the Paleocene of India and *L. (L.)* aff. *sindensis* have been reported from the Danian of Madagascar (LAMBERT, 1933; BESAIRIE, 1972). Closely allied to the former species is *Linthia (Linthia) inconstans* (LAMBERT), one of the commonest of the Malagasy Danian echinoids. *Hemiaster (Mecaster) cristatus* STOLICZKA from the upper Senonian of India is also known to occur in the Danian of Madagascar (BESAIRIE, 1972). The above facts suggest some affinity between the Malagasy and the Indian echinoid faunas.

The echinoid fossils from the Maastrichtian to Danian of the Majunga area are assigned chiefly to fasciole-bearing *Hemiaster* and *Linthia* species. Echinoids occur in common association with molluscs dominated by *Pholadomya* and *Modiolus* in the middle to upper Danian. From the echinoid-bivalve association, combined with other available data, it is suggested that the lower Maastrichtian was of littoral deposition and that the succeeding sequence was deposited under neritic conditions, with a maximum depth (lower neritic or upper bathyal zone) in the lower Danian yielding *Hercoglossa*, followed by a general shallowing trend.

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## Explanation of Plates

### Plate 1

- Fig. 1. "*Cidaris*" *majungensis* LAMBERT  
1a, Aboral view,  $\times 1$ . 1b, Oral view,  $\times 1$ . 1c, Lateral view,  $\times 1$ . Loc. Mj 13-1, Majunga area, upper part of Formation C<sup>10</sup>, Danian.
- Fig. 2. *Phymosoma archiaci* (COTTEAU)  
2a, Aboral view,  $\times 1$ . 2b, Oral view,  $\times 1$ . 2c, Lateral view,  $\times 1$ . Loc. Mj 8-1, Majunga area, middle part of Formation C<sup>10</sup>, Danian.
- Fig. 3. *Gauthieria* sp.  
3a, Oral view,  $\times 1$ . 3b, Lateral view,  $\times 1$ . Loc. Mj 10-5, Majunga area, middle part of Formation C<sup>9</sup>, Maastrichtian.
- Fig. 4. *Hemiaster* (*Bolbaster*) *hawkinsi* LAMBERT  
4a, Aboral view,  $\times 1.5$ . 4b, Oral view,  $\times 1.5$ . 4c, Lateral view,  $\times 1.5$ . 4d, Posterior view,  $\times 1.5$ . Loc. Mj 7-1, Majunga area, upper part of Formation C<sup>10</sup>, Danian.
- Fig. 5. *Hemiaster* (*Bolbaster*) cf. *madagascariensis* COTTREAU  
Aboral view,  $\times 1.5$ . Loc. Mj 10-5, Majunga area, middle part of Formation C<sup>9</sup>, Maastrichtian.
- Fig. 6. *Hemiaster* (*Mecaster*) *majungensis* TANAKA sp. nov.  
6a, Aboral view,  $\times 1$ . 6b, Oral view,  $\times 1$ . 6c, Lateral view,  $\times 1$ . 6d, Posterior view,  $\times 1$ . Holotype, NSM. PA 11994. Loc. Mj 13-1, Majunga area, upper part of Formation C<sup>10</sup>, Danian.

### Plate 2

- Fig. 1. *Hemiaster* (*Mecaster*) *majungensis* TANAKA sp. nov.  
Aboral view,  $\times 1$ . Paratype, NSM. PA 11995. Loc. Mj 8-1, Majunga area, middle part of Formation C<sup>10</sup>, Danian.
- Fig. 2. *Hemiaster* (s.l.) sp.  
Aboral view,  $\times 1$ . Loc. Mj 10-5, Majunga area, middle part of Formation C<sup>9</sup>, Maastrichtian.
- Fig. 3. *Abatus?* sp.  
3a, Aboral view,  $\times 1.5$ . 3b, Oral view,  $\times 1.5$ . 3c, Lateral view,  $\times 1.5$ . 3d, Posterior view,  $\times 1.5$ . Loc. Mj 13-2, Majunga area, upper part of Formation C<sup>10</sup>, Danian.
- Fig. 4. *Linthia* (*Linthia*) *inconstans* (LAMBERT)  
4a, Aboral view,  $\times 1$ . 4b, Oral view,  $\times 1$ . 4c, Lateral view,  $\times 1$ . 4d, Posterior view,  $\times 1$ . Loc. Mj 9-2, Majunga area, middle part of Formation C<sup>10</sup>, Danian.
- Fig. 5. *Linthia* (*Linthia*) *inconstans* (LAMBERT)  
5a, Aboral view,  $\times 1$ . 5b, Oral view,  $\times 1$ . 5c, Lateral view,  $\times 1$ . 5d, Posterior view,  $\times 1$ . Loc. Mj 13-2, Majunga area, upper part of Formation C<sup>10</sup>, Danian.

## Plate 3

- Fig. 1. *Linthia (Linthia) inconstans* (LAMBERT)  
Aboral view,  $\times 1$ . Loc. Mj 10-4, Majunga area, middle part of Formation C<sup>9</sup>, Maastrichtian.
- Fig. 2. *Linthia (Linthia) madagascariensis* TANAKA sp. nov.  
2a, Aboral view,  $\times 1$ . 2b, Oral view,  $\times 1$ . 2c, Lateral view,  $\times 1$ . 2d, Posterior view,  $\times 1$ .  
Holotype, NSM. PA 11996. Loc. Mj 10-4, Majunga area, middle part of Formation C<sup>9</sup>, Maastrichtian.
- Fig. 3. *Linthia (Linthia) madagascariensis* TANAKA sp. nov.  
Aboral view,  $\times 1$ . Paratype, NSM.PA 11997. Loc. Mj 10-4, Majunga area, middle part of Formation C<sup>9</sup>, Maastrichtian.
- Fig. 4. *Linthia (Linthia) madagascariensis* TANAKA sp. nov.  
Aboral view,  $\times 1$ . Paratype, NSM.PA 11998. Loc. Mj 10-4, Majunga area, middle part of Formation C<sup>9</sup>, Maastrichtian.
- Fig. 5. *Diplodetus (Protobrissus) cf. gauthieri* COTTREAU  
Aboral view,  $\times 1$ . Loc. Mj 8-2, Majunga area, middle part of Formation C<sup>10</sup>, Danian.
- Fig. 6. *Linthia (Linthia)?* sp.  
Aboral view,  $\times 1$ . Loc. Ant. 1, Danian.
- Fig. 7. *Hemiaster (Mecaster) boulei* COTTREAU  
Aboral view,  $\times 1$ . Loc. Mj 13-1, Majunga area, upper part of Formation C<sup>10</sup>, Danian.
- Fig. 8. *Brissopneustes decaryi* LAMBERT  
8a, Aboral view,  $\times 1.5$ . 8b, Oral view,  $\times 1.5$ . Loc. Ant 1, Danian.

