

**Bryozoa : Living and fossil species
of the catenicellid subfamilies
Ditaxiporinae Stach and Vasignyellinae nov.**

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ABSTRACT

The discovery of living species of the predominantly Tertiary catenicellid subfamily Ditaxiporinae on the Norfolk Ridge has necessitated a revision of the subfamily, which is characterised by biserial multizoooidal segments. The type species of the genera of Ditaxiporinae and of the related family Ditaxiporinidae were examined by scanning electron microscopy, leading to the recognition of six genera (two new) and 18 species (four new) and the incorporation of the Ditaxiporinidae into the Ditaxiporinae. The earliest occurring species is *Caberoides rockallensis* sp. nov. in the late Paleocene of the North Atlantic. There are only two living species - *Bryosartor subtilis* gen. et sp. nov. and *Plagiopora recens* Gordon, both on the northern Norfolk Ridge. A new monotypic genus, *Ahcheethamia*, is introduced for *Caberoides corniculatus* Cheetham from the British Eocene. With the exception of two species from North America, the subfamily is clustered in two centres of diversity - northwestern Europe and Australasia, the latter including *Caberoides miranda* sp. nov. and *Plagiopora alma* sp. nov., both newly recorded from the Eocene of New Zealand. Thus a Tethyan distribution of the subfamily was achieved relatively early in the Paleogene.

Just as in other catenicellids, there seem to have been parallel trends in the Ditaxiporinae in the diversification of the frontal shield from a spinocyst to a perforated gymnocyst on the one hand and with cryptocystal elements (derived from expanded shallow pore-chambers) on the other. A unique development is indicated by the genus *Vasignyella*. Hitherto

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included in the family Savignyellidae, *Vasignyella* appears to have been derived from *Ditaxiporina* or a common ancestor by reduction to unizoidal segments and the loss of ovicells. A new subfamily of Catenicellidae, Vasignyellinae, is established for this genus.

RÉSUMÉ

Bryozoa : Espèces vivantes et fossiles des sous-familles catenicellides : Ditaxiporinae Stach et Vasignyellinae nov.

La découverte, sur la ride de Norfolk, d'espèces vivantes appartenant à la sous-famille catenicellide des Ditaxiporinae, surtout répandue au Tertiaire, a conduit à la révision de cette sous-famille caractérisée par des segments à nombreux zooïdes bisériés. Les espèces type des genres des Ditaxiporinae et de la famille des Ditaxiporinidae ont été examinées au MEB. Ceci a conduit à reconnaître six genres (dont deux nouveaux) et 17 espèces (dont trois nouvelles) et à incorporer les Ditaxiporinidae dans les Ditaxiporinae. L'espèce la plus ancienne est *Caberoides rockallensis* sp. nov. du Paléocène supérieur de l'Atlantique nord. Seules deux espèces actuelles existent, *Bryosartor subtilis* gen. et sp. nov. et *Plagiopora recens* Gordon, toutes deux sur la partie nord de la ride de Norfolk. Un nouveau genre monotypique, *Ahcheethamia*, est créé pour *Caberoides corniculatus* Cheetham de l'Éocène d'Angleterre. À l'exception de deux espèces trouvées en Amérique du Nord, la sous-famille se regroupe suivant deux centres de diversification : le Nord-Ouest de l'Europe et l'Australasie, le second incluant *Caberoides miranda* sp. nov. et *Plagiopora alma*, récemment trouvées toutes deux dans l'Éocène de Nouvelle-Zélande. Ainsi une distribution téthysienne de la sous-famille a été réalisée relativement tôt dans le Paléogène.

De même que chez les autres catenicellides, il semble y avoir eu des tendances parallèles chez les Ditaxiporinae dans la diversification du bouclier frontal, depuis un spinocyste jusqu'à un gymnocyste perforé d'une part et avec des éléments cryptocystiques (dérivés de chambres porales peu profondes, dilatées) d'autre part. Le genre *Vasignyella* présente un développement unique. Inclus jusqu'à présent dans la famille des Savignyellidae, *Vasignyella* semble dérivé de *Ditaxiporina* ou d'un ancêtre commun, par réduction à des segments à un seul zooïde et la perte d'ovicelles. Une nouvelle sous-famille de Catenicellidae, celle des Vasignyellinae, est créée pour ce genre.

INTRODUCTION

Among the Bryozoa collected by the MUSORSTOM cruises in New Caledonian waters were some taxa of the cheilostomate superfamily Catenicelloidea that were either previously known only from the Tertiary of Victoria, Australia (*Chelidozoum*), or which have their earliest representation there (*Petalostegus*, Petalostegidae, and Ditaxiporinae) (GORDON & D'HONDT, 1991; GORDON, 1993). The latter taxon, Ditaxiporinae, is a subfamily of the Catenicellidae, a fairly widely distributed family with its greatest abundance in the Australasian region. Until recently, when a new species attributed to *Plagiopora* was discovered on the Norfolk Ridge north of Norfolk Island (GORDON, 1989a), the Ditaxiporinae was thought to be extinct. Now a new genus, with a major ancestral feature, has been discovered in the MUSORSTOM collections from New Caledonia. Its discovery provides a much-needed opportunity to revise and discuss the relationships of the whole subfamily Ditaxiporinae.

The Catenicellidae Busk, 1852 is a very distinctive and well-circumscribed family. The bushy colonial morphology is characteristic, with branches comprising long chains of uni- to multizoidal segments separated by chitinous joints. This characteristic morphology fortunately permits the classification of some very disparate zooidal morphologies in the one family (BANTA & WASS, 1979). It is this varied zooidal morphology that is the most remarkable feature of the family, comprising a range of frontal-shield types that elsewhere in the order Cheilostomatida might each have significance at the family level. Nevertheless, within the Catenicellidae it is possible to determine ancestral and derived characters and consequent polarities, permitting the construction of morphological lineages. Thus, the presence of a field of costal spines is an ancestral character, a lack of spines and a concomitant extensive gymnocyst a derived character. Similarly, any kind of cryptocystal feature is derived. Appropriately, the oldest-known catenicellid, from the Maastrichtian (Upper Cretaceous) of Jamaica (CHEETHAM, pers. comm. in BANTA & WASS, 1979 : 22) resembles *Costaticella*, a spinocystal genus, but by the early Eocene in the Indian Ocean, *Catenicella*, with an advanced morphology, is already present (LABRACHERIE & SIGAL, 1976, as *Vittaticella*).

The range of zooidal morphologies in the Catenicellidae led to the recognition of different groupings within the family. Accordingly, when BUSK (1852a) introduced the family, with two included genera, *Catenicella* and *Calpidium*, he recognised three groupings within *Catenicella* - fenestratae, vittatae, and inermes, but not as formal taxa. He continued to use these groupings (BUSK, 1852b, 1884), only changing 'inermes' to 'simplices' in the former work but abandoning the family name in the latter. In subsequent decades various authors recognised several new genera within BUSK's groupings. STACH (1933, 1934, 1935a) was the first to recognise subfamilies within the Catenicellidae, basing them primarily on the position of the ovicell within the segment. He named five subfamilies - Vittaticellinae (STACH, 1933), Scuticellinae (STACH, 1934), and Catenicellinae, Cornuticellinae, and Ditaxiporinae (STACH, 1935a). The distinction between the Vittaticellinae and Catenicellinae was artificial and based on a misunderstanding, since *Vittaticella* is a junior synonym of *Catenicella* (GORDON, 1984), and work by WASS & BANTA (1981) on catenicellid ovicell complexes has shown that the cornuticelline grouping may also be included in the Catenicellinae. Thus BANTA & WASS (1979) and WASS & BANTA (1981) accepted the distinction between the Catenicellinae, in which the ovicelled segment does not comprise the terminal segment of a branch, and the Scuticellinae, in which it does.

The remaining subfamily, Ditaxiporinae, was segregated primarily on the basis of the characteristic biseriate multizooidal segments, found in the fossil genera *Ditaxipora* MacGillivray, 1895, and *Ditaxiporina* Stach, 1935a. The chief features cited by STACH (1935a) as distinguishing these two genera were the longitudinal band on the frontal area in the former and the evenly porous shield lacking a band in the latter. STACH (1935b) noted the occurrence of multizooidal forms in the European and North American Paleogene. Because these were then the oldest-known catenicellids, he regarded them as archaic. [In the event, as mentioned above, the earliest-known catenicellid, from the Maastrichtian (mentioned above), resembles *Costaticella*, which makes the Scuticellinae the earliest-occurring subfamily.] CHEETHAM (1963) discussed the differences between *Ditaxipora* and *Ditaxiporina*, concluding that the evenly porous frontal shield and other (minor) features of the latter must preclude a close relationship. He therefore established a new family, Ditaxiporinidae, for *Ditaxiporina* and *Caberoides* Canu, 1908 (CHEETHAM, 1963). Notwithstanding having segregated the Ditaxiporinidae, he nevertheless concluded "Future investigations will probably verify the proximity of this family to the basal stock from which the Vittaticellidae [i.e., Catenicellidae] have sprung. ... However, the Vittaticellid roots should be sought amongst the archaic groups of Cheilostomata in Lower and Middle Eocene beds, not the more specialized forms of the Upper Eocene and Oligocene" (CHEETHAM, 1963 : 489). However, at that time, pre-Miocene scuticellines and catenicellines had not yet been discovered.

Thus, by 1966, only the three biseriate-multizooidal genera, *Ditaxipora*, *Ditaxiporina*, and *Caberoides*, segregated in two families, had been recognised. Subsequently, the discovery of a new species of *Plagiopora* MacGillivray at 831 m depth northwest of Norfolk Island (GORDON, 1989a) indicated that this multizooidal genus ought also to be included in the Ditaxiporinae. Previously known only from a single Middle Miocene species, this genus had been included by MACGILLIVRAY (1895) in the now-abandoned (and unrelated) family Lepraliidae.

The recognition of a new, living, genus of Ditaxiporinae in the MUSORSTOM samples from the northern Norfolk Ridge, plus the discovery of new ditaxiporine species in the New Zealand Eocene, prompted a reconsideration of all the multizooidal genera, especially based on scanning-electron-microscopic examination of type species.

LIST OF STATIONS

New Caledonia.

BIOCAL : station DW 70, 4.9.85, 23°24.70' S, 167°53.65' E, 965 m : *Bryosartor sutilis* (+ *Bifaxaria modesta*, *Diplonotos serratus*, *Petalostegus scopulus*).

MUSORSTOM 4 : station CP 214, 28.9.85, 22°53.80' S, 167°13.9' E, 425-440 m : *Bryosartor sutilis*.

BIOGEOCAL : station DW 313, 2.5.87, 20°58.95' S, 166°59.04' E, 1640-1600 m : *Bryosartor sutilis* (+ *Bifaxaria menorah*).



FIG. 1 a-f. — *Bryosartor sutilis* gen. et sp. nov. : a, arrangement of zooids in the multizoooidal segment (x 42) ; b, ♀ zooid with ovicell (x 73) ; c, autozooid, showing the narrow costal field (x 144) ; d, proximal zooids of a young segment (x 86) ; e, dorsal view of a developing segment (x 58) ; f, interior view of costae from one side of a costal field and the irregular suture-line at their tips (x 305). (All from BIOCAL Stn DW 70.)

SYSTEMATIC ACCOUNT

Suborder ASCOPHORINA Levinsen, 1909

Infraorder CRIBRIOMORPHA Harmer, 1926

Superfamily CATENICELLOIDEA Busk, 1852a

Family CATENICELLIDAE Busk, 1852a

Subfamily DITAXIPORINAE Stach, 1935a

Genus *BRYOSARTOR* nov.

DIAGNOSIS. — Multizoidal, biseriate. Frontal shield includes a narrow costal field with several pairs of vestigial costae and a few extracostal windows; the adjacent gymnocyst with large shallow pore-chambers, 1 axial (1-2 on female zooids), 2 marginal, and another distal to the outer avicularium. Only a single avicularium on autozooids, at the outer distolateral corner; paired avicularia in female zooids. Ovicell large, with a large exposure of granular endooecium surrounded by smooth ectooecium. Dorsal zooidal surface smooth, lacking pore-chambers.

RANGE. — Holocene.

TYPE SPECIES. — *Bryosartor subtilis* sp. nov.*Bryosartor subtilis* sp. nov.

Fig. 1 a-f

MATERIAL EXAMINED. — New Caledonia. BIOCAL : stn DW 70, 965 m.

MUSORSTOM 4 : stn CP 214, 425-440 m.

BIOGEOCAL : stn DW 313, 1640-1600 m.

DESCRIPTION. — Colony erect, branching, to 31 mm high, the branches biserial with 4-6 zooids per fully formed segment; maximum segment length 4.74 mm and width 0.66 mm. All joints are single - at bifurcations the 2 distal zooids are angled away from each other, producing widely separated branches, and there is only a single zooid at the proximal end of each segment, which buds 2 daughter zooids to generate biseriality. Zooids vary in length according to position in segment - the shortest zooids (~0.34 mm) occur at the proximal end, the longest zooids (~0.64 mm) occur immediately distal to female zooids; zooidal width ~0.34 mm. The frontal side of each zooid has several components - centrally, there is a narrow, adaxially curving, costal field of about 11-19 short flattened spines with a median suture running through the field to the orifice; the distalmost costae are very broad; outside the costal field are 3-4 gymnocystal foramina. Pore-chambers are large and shallow, with 1 on the axial side and 3 on the outer, marginal, side of each zooid - the axial one is the largest, extending from just distolateral to the orifice, past an avicularium (if there is one on that side), to a position adjacent to the middle of the costal field; laterally, there is a chamber behind the outer distolateral avicularium and two larger chambers proximal to the avicularium. Zooidal orifice proportionately large, suboval, with a pair of tiny condyles about one-third the distance from the proximal rim. Avicularia 1-2, 1 at the outer distolateral corner of every zooid, with complete cross-bar and acute rostrum; a similar, less-acute, avicularium occurs opposite, adjacent to the distalmost costae, in ovicelled zooids and occasionally in other zooids. Ovicell large, about the size of the maternal zooid, occupying the complete frontal surface of the distal zooid, the ovicellular surface mostly granular endooecium with 'flaps' of smooth ectooecium distally and proximally; the orifice of fertile zooids generally a little longer than other orifices. Dorsal surface of branch segment with grooves marking the boundaries between zooids, especially along the axis,

otherwise fairly smooth with no ridges. Colony anchored to substratum by a number of rhizoids descending the proximal parts of the colony; rhizoids issue from the proximal parts of zooids dorsally. Ancestrula small, 0.32 mm long and 0.23 mm wide including the distolateral corners; resembling later zooids but the proximal half evenly narrow and claviform, supported by a rhizoid issuing from the proximal end. The postancestrular and some later segments unizoidal.

TYPES. — *Holotype* : a colony from BIOCAL Stn DW 70, 965 m, MNHN-Bry 19934.

Paratypes : fragments of mature colonies from the same station, and young attached colonies from BIOGEOCAL Stn DW 313, 1640-1600 m, MNHN-Bry 19933.

ETYMOLOGY. — The genus name is partly derived from *sartor* (Latin), a tailor, and the species name from *sutillis* (Latin), sewed together. Both names allude to the narrow costal field which gives the zooidal frontal shield a stitched appearance.

DISTRIBUTION. — Southern New Caledonia and northern Norfolk Ridge, 425-1640 m.

REMARKS. — *Bryosartor* differs from *Ditaxiporina* in several important characters, including the presence of costae and extra-costal foramina, the number and disposition of frontal pore-chambers, and the complete lack of dorsal pore-chambers. At present, *Bryosartor* is monospecific.

Genus *CABEROIDES* Canu, 1908

DIAGNOSIS. — Multizoidal, biseriate. Frontal shield with a tiny suboral costal field with a few vestigial costae; no extracostal windows; adjacent gymnocyst with large shallow pore-chambers - 1-2 axially and 1-2 laterally, with another behind the outer lateral avicularium. Avicularia single or paired. Ovicell large, with a narrow exposure of endooecium surrounded by a large area of smooth ectooecium. Dorsal zooidal surface with at least 2 pore-chambers, with one or both narrow and curved.

RANGE. — Thanetian (Upper Paleocene) to Priabonian (Upper Eocene).

TYPE SPECIES. — *Caberoides canaliculata* Canu, 1908.

CONGENERIC SPECIES. — Four other species may be included in the genus. These are :

Catenicella continua Waters, 1891 = *Caberoides continua* (Waters, 1891) comb. nov., Priabonian, northeast Italy.

Caberoides grignonensis Canu, 1908, Lutetian, near Paris, France.

Vitaticellid [*sic*], n. gen. Cheetham & Håkansson, 1972 = *Caberoides rockallensis* sp. nov., Thanetian, Rockall Plateau, Northeast Atlantic.

Caberoides miranda sp. nov., Ypresian, Chatham Island, New Zealand.

Caberoides canaliculata Canu, 1908

Fig. 2 a-d

Caberoides canaliculata Canu, 1908 : 88, pl. 11 [84, pl. 8], figs 11-12. — BASSLER, 1953 : G212, fig. 159.4. — CHEETHAM, 1966 : 81.

MATERIAL EXAMINED. — **France**. Muséum national d'Histoire naturelle : Holotype specimen R.53409, Institut de Paléontologie, CANU Collection, Orglandes, near Paris, Lutetian.

DESCRIPTION. — Segments up to 2.26 mm long and 0.97 mm wide, with up to 12 zooids per segment. Zooids alternating, 0.29-0.38 mm long and 0.31-0.39 mm wide. Frontal shield with a central Y-shaped gymnocystal area flanked by pore-chambers, with a small costal field between the arms of the Y. The pore-chamber on the axial side extends from near the distolateral corner of the orifice to the proximal third of the zooid; the marginal pore-chamber extends from the lateral avicularium to the same level; more proximally is a very narrow pore-chamber that extends partly onto the dorsal surface. This arrangement is apparent in non-ovicelled zooids (at the proximal end in fertile segments). Orifice with a broad shallow poster. Avicularia single, on the lateral margin facing laterally, or double, as in ovicelled zooids. The axial avicularia occur in a series along the

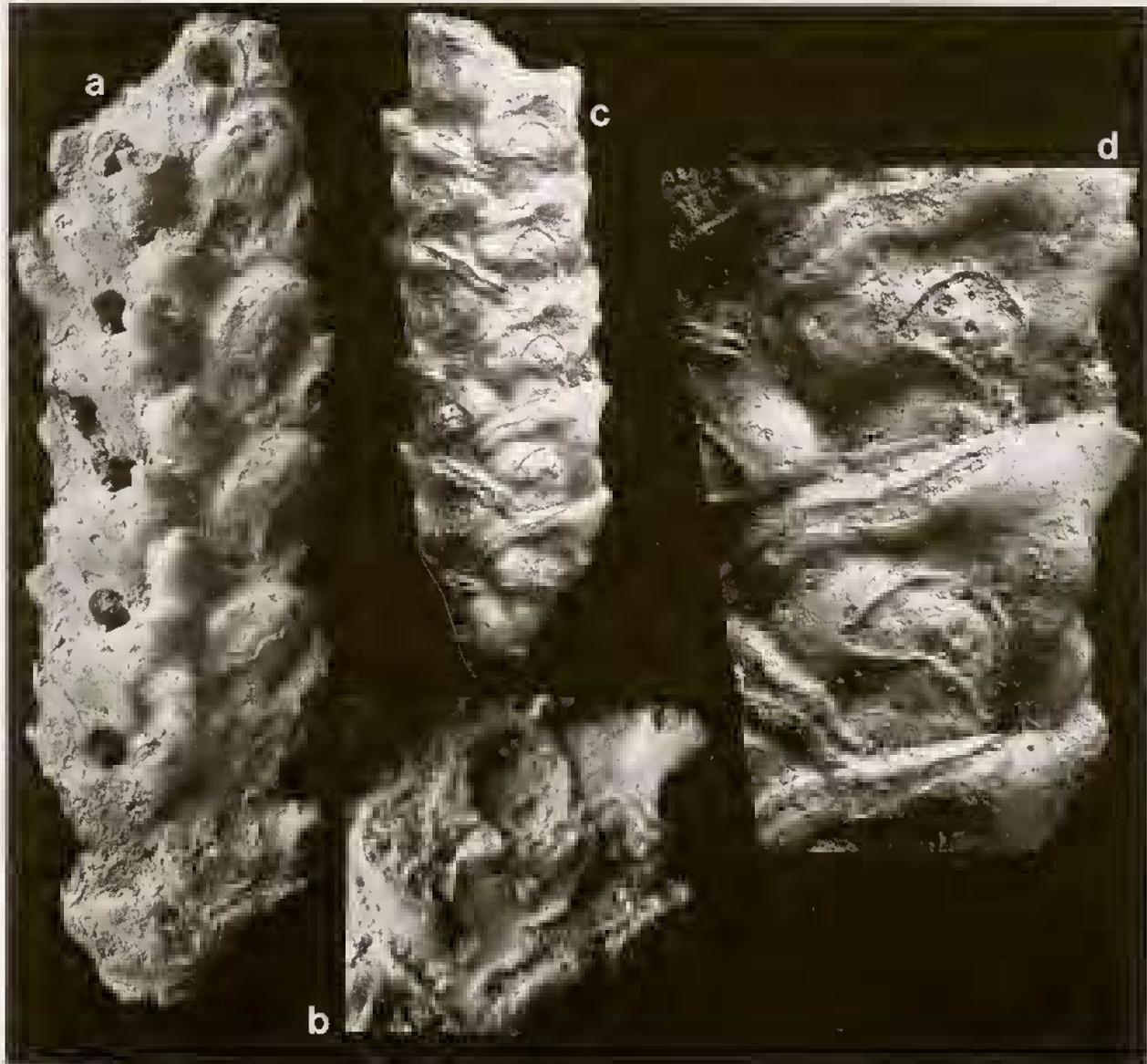


FIG. 2 a-d. — *Caberoides canaliculata* Canu : a, fertile segment with numerous ovicells (x 62) ; b, enlargement of the bottom right zooid in fig. a, showing the expanded lateral pore-chambers flanking the Y-shaped gymnocyst with small costal field (x 142) ; c, dorsal face of a segment, showing the disposition of pore-chambers (x 42) ; d, part of fig. c, magnified (x 119). [SEMs of CANU's uncoated figured specimens from Orglandes (CANU, 1908, pl. 8 (pl. 11), figs 11-12), slide R53409, Institut de Paléontologie, Muséum national d'Histoire naturelle.]

centre of the segment, with each obliquely facing the zooid which bears it; both axial and lateral avicularia with semicircular opesiaec, complete cross-bars, and acute triangular rostra; frequently the lateral avicularium is projected beyond the rostrum. Ovicell relatively large, obliquely recumbent over much of the frontal shield of the zooid distal to it; the ectooecium smooth with a narrow axial fenestra (widening proximally) and possibly a few scattered pores. Dorsal surface of segment with a distinctive arrangement of pore-chambers - a long and narrow, vibraculum-like, chamber extends from behind each lateral avicularium obliquely down and across the zooidal surface beyond the midline of the segment; thus the oblique pore-chambers on one side of the segment overlap with those on the other side. A somewhat semicircular pore-chamber, with several scattered septular pores, occurs in the centre of the dorsal wall of each zooid.

DISTRIBUTION. — Middle Lutetian (Middle Eocene), near Paris.

REMARKS. — CANU (1908) had some difficulty in interpreting this genus, not being intimately acquainted with the southern hemisphere catenicellids. He called the axial row of avicularia vibracula, presumably akin to those in the branch axils of *Scrupocellaria*, and referred to the oblique dorsal pore-chambers (like catenicellid 'vittae') as "a system of gutters containing vibracular bristles" [our translation]. Nevertheless, he recognized the obvious ascophorine nature of the genus and, while not then suggesting a family for his new genus, CANU & BASSLER (1929) later suggested the Reteporidae. CHEETHAM (1963) recognized the catenicellid affinities of *Caberooides* and *Ditaxiporina*, meanwhile establishing a new family, Ditaxiporinidae, for these two genera. Later, CHEETHAM (1966) described an apparent new species of *Caberooides* (*C. corniculatus*) from the Bartonian (upper Middle Eocene) of Sussex, England. We have examined this species by scanning electron microscopy and conclude that it is not congeneric with *Caberooides* — later in this paper, we introduce a new genus for it (*Ahcheethamia*).

Caberooides grignonensis Canu, 1908 (fig. 3 a-b) is very similar to *C. canaliculata*, differing in details of the costal field and dorsal surface and in its longer and narrower segments. Another species that may be included in *Caberooides* is *Catenicella continua* Waters, 1891 (fig. 3 c-f) from the Priabonian (late Eocene) of northeast Italy (BRAGA & BARBIN, 1988, as *Vittaticella*). WATERS's (1891) attribution of this species to *Catenicella* was based primarily on the presence of conspicuous lateral pore-chambers (vittae), like those of *Catenicella* but larger. When MACGILLIVRAY (1895) established his new genus *Ditaxipora*, he implied that *C. continua* might be included in it but this idea was not followed by later authors (e.g., WATERS, 1913; CANU & BASSLER, 1917, 1920) until the work of STACH (1935a, b), who first used the combination *Ditaxipora continua*. This is surprising, especially in the case of WATERS (1913 : 483), who allied the species with *D. internodia* when he first described *continua* (WATERS, 1891). In the event, *C. continua* must be excluded from *Ditaxipora* which lacks any trace of a costal shield and in which the dorsal surface of each zooid is mostly composed of a single large pore-chamber. On the other hand, *C. continua* shares the important characters of *Caberooides miranda* and *C. rockallensis* (see below), viz, a small costal field flanked by pore-chambers, laterally facing avicularia, and a vibraculum-like dorsal pore-chamber and may be included in the genus as a new combination, *Caberooides continua*. It is interesting that *C. continua*, occurring later in the Paleogene (Priabonian) than the other species (Thanetian to Lutetian), has much longer frontolateral pore-chambers that anticipate those in *Ditaxipora*, which may have been derived from *Caberooides*. It is to be noted that, whereas the supraavicularian pore-chamber is long and vibraculum-like in most of the species, it is the proximolateral one in *C. continua* that has this form. When more species become known it may be appropriate to divide *Caberooides* into subgenera on the basis of this character.

FIG. 3 a-b. — *Caberooides grignonensis* Canu : a, fertile segment with numerous ovicells (x 39) ; b, part of fig. a showing the distalmost ovicells. Note the small costal field in the upper left-hand zooid (x 120). (SEM of CANU's uncoated figured specimen from Grignon [CANU, 1908, pl. 8 (pl. 11), fig. 15], slide R53358, Institut de Paléontologie, Muséum national d'Histoire naturelle.)

FIG. 3 c-f. — *Caberooides continua* (Waters) : c, e, autozooidal frontal shields showing the arrangement of pore-chambers, median gymnoecyst. and small costal field (x 209 ; x 360) ; d, f, dorsal surface of segment and zooids, showing disposition of pore-chambers (x 47 ; x 128). (From Montecchio di Costozza, Italy, late Eocene ; BRAGA Collection, Dipartimento di Geologia, Paleontologia e Geofisica dell'Università di Padova.)



Caberoides miranda sp. nov.

Fig. 4 a-d

MATERIAL EXAMINED. — New Zealand. From New Zealand Geological Survey (NZGS) collection GS 14765 from the Matanginui Limestone, Ypresian (Lower Eocene), 50 m north of the mouth of Waipapa Creek, Chatham Island (locality CH/f603), collected by H.J. CAMPBELL and P.A. MAXWELL, March 1981; three other poorly preserved non-type specimens in a separate well on the same slide.

DESCRIPTION. — Segments incomplete in the present material, the largest attaining 1.20 mm long and 0.43 mm wide, comprising parts of 8 zooids. Zooids small, 0.33-0.43 mm long and ~ 0.25 mm wide, widest in the distal half, sometimes tapering narrowly in the proximal half, the median line between zooids tracing an irregular zigzag course along each segment. Zooidal orifice with a pair of small rounded condyles separating a broad anter from smaller poster - the exact shape of the latter is uncertain owing to poor preservation. The frontal area of each zooid comprises 3 components - gymnocystal and cryptocystal (of approximately equal area) and spinocystal. The spinocystal comprises a small suboral field of ~6 tapering costae whose acule tips probably did not fuse in life. Part, at least, of the proximal rim of the orificial sinus was defined by costal elements. Four cryptocystal areas, occasionally 5, representing pore-chambers, occur frontally. The largest, with up to 7 septular pores evident, occurs on the axial side of the orifice and costal field. In 1 or 2 zooids in a segment this pore-chamber is shortened by the occurrence of an avicularium beside the orifice. More typically, avicularia are restricted to the zooidal margin, where 1 occurs facing laterally; it has a semicircular opesia, complete cross-bar, and triangular rostrum with no palate. Distal to this avicularium is a second pore-chamber (with ~2-3 pores) which curves obliquely round and down the dorsal surface. Immediately proximal to the avicularium, and partly overhung by it, is a third pore-chamber (with ~5 pores), which also curves round onto the dorsal surface. Near the proximolateral margin is a fourth frontal pore-chamber (with ~5 pores), of which the larger part curves obliquely upwards onto the dorsal surface towards the proximal end of the supraavicularian pore-chamber. Occasionally, a small rounded fifth pore-chamber (with 3 pores) is interpolated between the subavicularian and proximolateral chambers. Dorsally, the median boundary between zooids describes a series of curving zigzags along the segment. Of the 3 pore-chamber areas that occur on the dorsal side of each zooid, the downcurving supraavicularian one is notable for its superficial resemblance to a vibracular groove. Ovicell unknown.

TYPE. — *Holotype*: the segment illustrated in figure 4 a-d, from the Matanginui Limestone (Lower Eocene), Waipapa Creek, Chatham Island, type number BZ 161, in the collection of the Institute of Geological & Nuclear Sciences, Lower Hutt, New Zealand.

DISTRIBUTION. — Ypresian (Lower Eocene), Chatham Island, New Zealand.

ETYMOLOGY. — The specific name is a Latin adjective meaning wonderful, strange, singular.

REMARKS. — The Matanginui Limestone is a white, massive, bryozoan-echinoid-foraminiferan-bivalve packstone (WOOD *et al.* 1989). On Chatham Island it is up to 25 m thick and commonly soft. The occurrence of the foraminiferan *Asterocyclina* in the lower part of the limestone on Chatham Island indicates deposition in a shallow warm sea within the photic zone. The scarcity of shallow-water foraminifers in the middle and upper parts of the limestone indicate middle- to outer-shelf depths, the likely provenance of *C. miranda*. The bryozoan diversity in this limestone is extraordinarily rich, with abundant representation of erect branching, bilamellar, articulated, and rod-like forms, indicative of relatively fast, nutrient-rich currents.

FIG. 4 a-d. — *Caberoides miranda* sp. nov.: a-c, SEMs of best-preserved specimen, showing disposition of frontal pore-chambers, gymnocystal, and costal field in relation to the orifice and distolateral avicularium (x 114; x 285; x 211); d, same, dorsal view (x 120). (Holotype specimen, in collection of NZGS, Lower Hutt, from the Matanginui Limestone, Chatham Island, New Zealand, Lower Eocene.)

FIG. 4 e. — *Caberoides rockallensis* sp. nov., SEM of uncoated specimen (x 106). USNM specimen 172444 from Deep Sea Drilling Site 117A, Rockall Plateau, North Atlantic.



It is obvious from the light-micrograph illustrations of the frontal and dorsal sides of the late Paleocene "Vitaticellid [*sic*], n. gen." of CHEETHAM and HÅKANSSON (1972) that this species is very similar to *C. miranda*. Their two specimens, one comprising two zooids (illustrated in dorsal view) and the other comprising four zooids (illustrated in frontal view) have many features in common - namely the small costal field flanked by pore-chambers, a laterally facing avicularium, a proximolateral pore-chamber curving round dorsally, and an identical disposition of pore-chambers dorsally including the vibraculum-like chamber that originates distal to the avicularium. Their species differs only in details, including the proportionately larger avicularium and wider rims of the pore-chambers. We hereby name the species represented by their specimens *Caberooides rockallensis* sp. nov. We designate the larger of the two specimens (USNM slide 172444) (fig. 4, e) as *holotype*, the smaller (slide 172445) as *paratype*. Both specimens are held in the collection of the Smithsonian Institution (National Museum of Natural History), Washington, D.C.

Caberooides rockallensis was taken at Deep Sea Drilling Site 117A on the Rockall Plateau (57°20.17' N, 15°23.97' W, 1038 m) in the North Atlantic Ocean. On the basis of certain other taxa in the assemblage, CHEETHAM and HÅKANSSON estimated that the depth, in life, of the assemblage was not more than 60 m.

Genus *DITAXIPORA* MacGillivray, 1895

DIAGNOSTS. — Multizoidial, biseriate. Frontal shield lacking any trace of costae; comprising a T-shaped median gymnocrystal ridge flanked on either side by a wide pore-chamber with conspicuous septular pores in a single longitudinal series. An additional, small, pore-chamber occurs distal to the avicularium; a similar pore-chamber on the opposite side of the orifice may be confluent with the lateral pore-chamber. Avicularia single in autozooids, 1-2 in ovicelled zooids. Ovicell large, with an extensive area of endooecium exposed frontally. Dorsal surface with a single large pore-chamber per zooid.

RANGE. — Lutetian (lower Middle Eocene) to ?Messinian (uppermost Miocene).

TYPE SPECIES. — *Catenicella internodia* Waters, 1881.

CONGENERIC SPECIES. — Three other species may be included in this genus. These are :

Bactridium labiatum Canu, 1910, Bartonian, Biarritz, southwest France.

Ditaxipora lutecciana Canu, 1913, Lutetian, near Bordeaux, Southwest France.

Ditaxipora pannonicensis Braga in Antolini *et al.*, 1980, Priabonian, northeast Italy.

Ditaxipora internodia (Waters, 1881)

Fig. 5 a-c

Catenicella internodia Waters, 1881 : 318, pt. 18, figs 78-79. — WATERS, 1883 : 430.

Ditaxipora internodia - MACGILLIVRAY, 1895 : 22, pl. 2, fig. 31, 3ta. — MAPLESTONE, 1898 : 21; 1904 : 19t. — STACH, 1935a : 394; 1935b : 40, figs 2-3. — BASSLER, 1953 : G222, fig. 167, 6 a-b. — BROWN, 1958 : 82. — WASS, 1973 : 9.

Strophipora (Ditaxipora) internodia - CANU & BASSLER, 1929 : 452, fig. 185 F-G.

MATERIAL EXAMINED. — Australia. Royat Melbourne Institute of Technology : specimens of *Ditaxipora internodia* from Princetown (#507) and Fyansford (#514), Miocene, Victoria, collected by P.E. BOCK.

DESCRIPTION. — Segments up to 2.34 mm long and 0.47 mm wide, comprising up to 10 regularly alternating zooids; this alternation tends to be maintained even in the most proximal zooids of a segment. Paired joint-holes at the distal end of a segment imply branch bifurcations. Zooids 0.47-0.55 x 0.22-0.28 mm, near-rectangular with parallel sides or evenly tapering somewhat towards the proximal end. Orifice a little longer than wide, with a pair of condyles which separate the broad rounded poster from the anter. Frontal shield with 2 large cryptocystal areas

(pore-chambers), each with a linear row of septular pores along its length, separated by a T-shaped median gymnocystal ridge. This ridge is composed of 2 longitudinal components with a median suture-line between that runs into the cross-piece of the T. The lateral pore-chambers may curve narrowly round to the distal side of the orifice or, more usually, they terminate adjacent to the orifice, especially at the avicularium, leaving the small distal chambers isolated. A single avicularium per zooid, always on the outer (marginal) side of the orifice, with a semicircular opesia, complete cross-bar, and acute triangular rostrum. Ovicell large, similar to that in *Bryosutor subtilis*, with a granular endooecium bordered by smooth ectooecium, two 'flaps' of which encroach toward the centre of the granular area. Dorsal surface with a sinuous median interzooidal groove and a single large pore-chamber per zooid, each with linear septular pores.

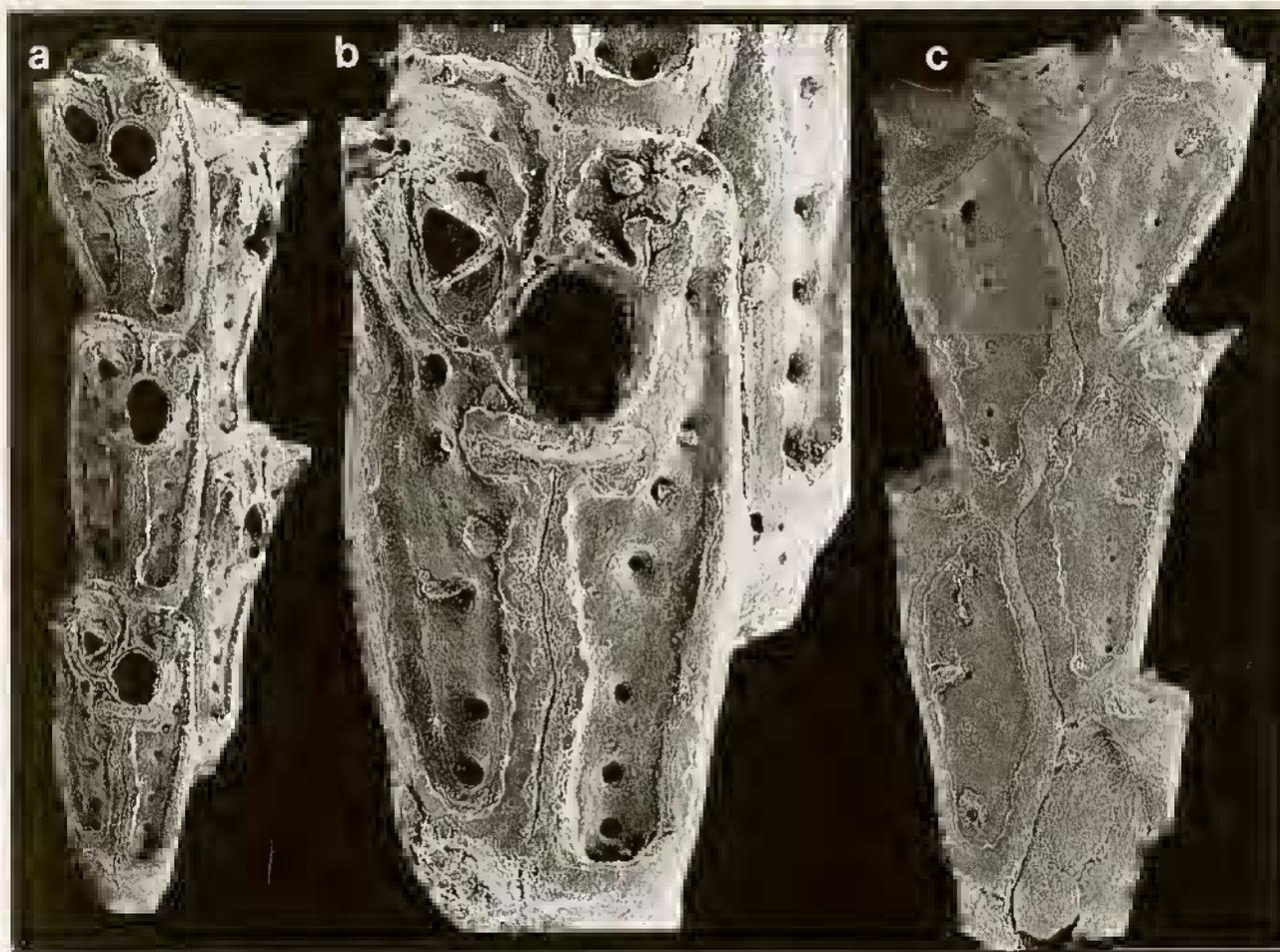


FIG. 5 a-c. — *Ditaxipora internodia* (Waters) : a-b, frontal views of zooids (x 65 ; x 185) ; c, dorsal surface of segment showing large pore-chambers (x 104). (From Princetown, Victoria, Miocene ; Bock Collection, Royal Melbourne Institute of Technology.)

DISTRIBUTION. — Victoria, Australia. Early Oligocene to Late Miocene.

REMARKS. — On the basis of the localities cited for this species by WATERS (1881, 1883), MACGILLIVRAY (1895), MAPLESTONE (1904), STACH (1935b), and BROWN (1958), and the stratigraphic work of COCKBAIN (1971), WASS (1973) gave the range of *Ditaxipora internodia* as Early Oligocene (Rupelian) to Late Miocene (?Tortonian/Messinian).

Both WATERS (1881) and MAPLESTONE (1898) noted the occurrence of a foramen in the middle of the gymnocystal ridge and depicted the cross-piece of the T as more oval, features not apparent in the material

described by MACGILLIVRAY (1895). MAPLESTONE (1898) and STACH (1935b) concluded that this variation is intraspecific. One of the segments in the material kindly donated to us by Phil BOCK (Royal Melbourne Institute of Technology) does have the median foramen in several zooids. These foramina are predator boreholes. *Catenicella internodia* var. *angustata* Waters, 1883 merely represents older internodes of this species according to STACH (1935b).

Ditaxipora pannonensis Braga in Antolini *et al.*, 1980 (fig. 6 a-c) from the Priabonian (Upper Eocene) of northern Italy is clearly related. It has a similar T-shaped gymnocystal ridge frontally and large dorsal pore-chambers dorsally. The ovicell is also similar, with proportionately larger proximal ectooecial 'flaps'. *Ditaxipora labiata* (Canu, 1910) from the Bartonian of France is likewise congeneric - the characteristic frontal gymnocystal ridge and large dorsal pore-chambers are typical of *Ditaxipora*, not *Ditaxiporina*, as LABRACHERIE (1968) correctly pointed out.

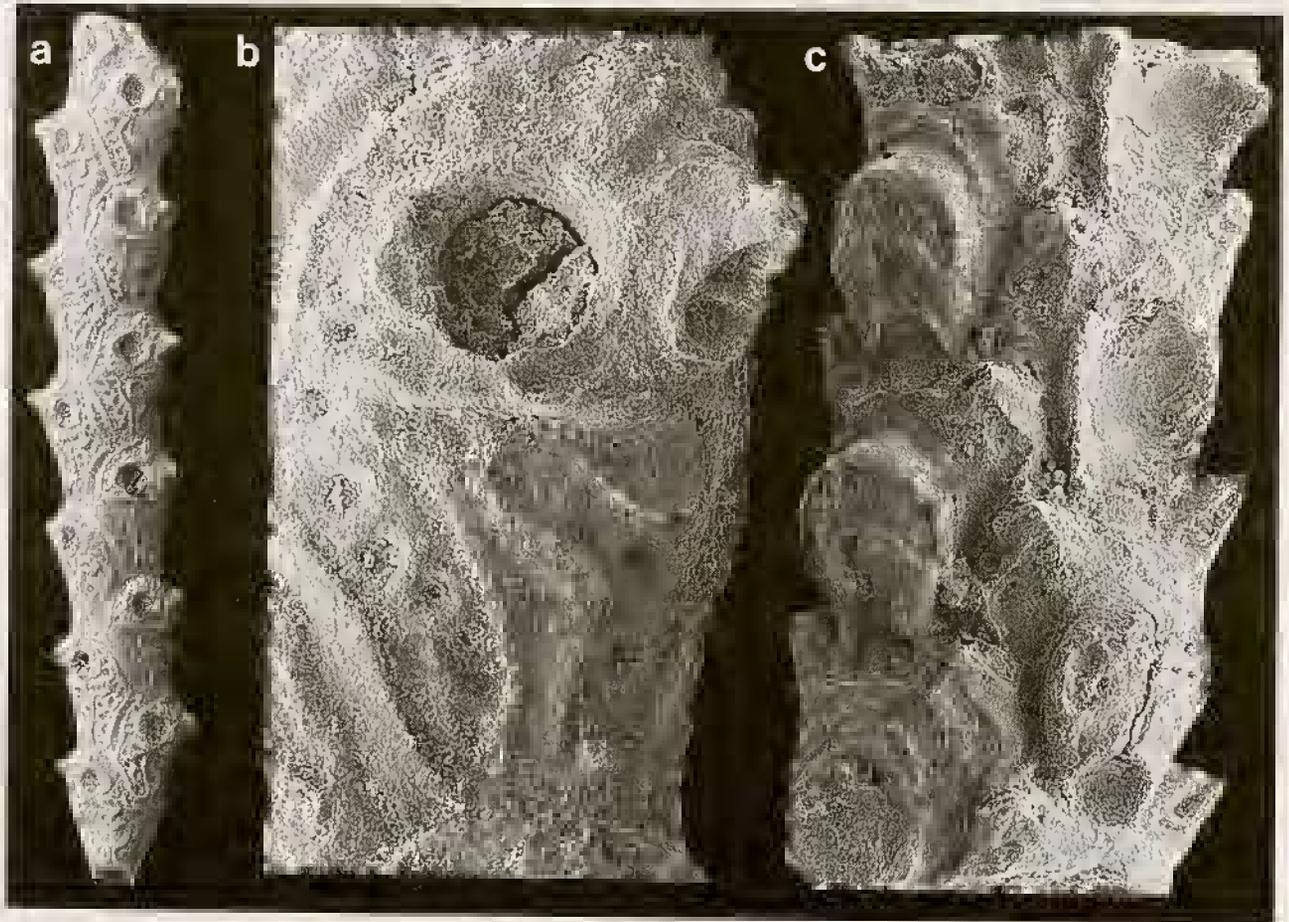


FIG. 6 a-c. — *Ditaxipora pannonensis* Braga in Antolini *et al.*: a, sterile segment (x 35); b, part of fig. a (x 216); c, ovicelled zooids (x 96). (From Pannone, late Eocene, Braga Collection, Dipartimento di Geologia, Paleontologia e Geofisica dell'Università di Padova.)

Genus *PLAGIOPORA* MacGillivray, 1895

DIAGNOSIS. — Multizoooidal, biseriate. Zooidal orifice slightly asymmetrical and at an angle to the segmental axis. Frontal shield lacking costae; comprising an obliquely set narrow gymnocystal band suborally that separates several broad, shallow, pore-chambers (cryptocystal fields) tiny sparse septular pores; the gymnocystal band with

or without foramina and a suture. An additional 1-2 smaller pore-chambers distolateral to the orifice. Avicularia paired or single. Ovicell unknown. Dorsal surface with broad pore-chambers confluent with the laterofrontal chambers.

RANGE. — Priabonian (Upper Eocene) to present day.

TYPE SPECIES. — *Plagiopora disticha* MacGillivray, 1895.

CONGENERIC SPECIES. — Two other species may be included in the genus. These are :

Plagiopora recens Gordon, 1989a, Holocene, near Norfolk Island, southwest Pacific.

Plagiopora alma sp. nov., Priabonian, Alma, near Oamaru, New Zealand.

Plagiopora disticha MacGillivray, 1895

Fig. 7 a-c

Plagiopora disticha MacGillivray, 1895 : 79, pl. 13, fig. 14 a-c. — MAPLESTONE, 1904 : 206. — BASSLER, 1953 : G212, fig. 160, 3 a-b. — GORDON 1989a : 1330.

MATERIAL EXAMINED. — Australia. Museum of Victoria : holotype slide P27769, from Muddy Creek, Victoria, Middle Miocene (single internode on slide subsequently inadvertently lost by DPG). Royal Melbourne Institute of Technology : slides of specimens from Princetown and Balcombe Bay, Victoria, Middle Miocene, collected by P.E. BOCK.

DESCRIPTION. — Segments up to 2.70 mm long and 0.47-0.72 mm wide (depending on avicularian projections) with up to 10 zooids per segment. Zooids 0.43-0.49 mm long and 0.37-0.45 mm wide (again, varying according to avicularian length), alternating along the segment with a zigzag interzooidal boundary axially. Frontal shield comprising large shallow cryptocystal areas (pore-chambers) separated by thin gymnocystal strips. The pore-chambers are arranged such that, when seen in frontal view, each zooid has 2 (supraavicularian and lateral-oral) on its inner, axial side (only 1 if there is no avicularium separating them), and 3 (supraavicularian, lateral-oral, proximolateral) on its outer, marginal side. The 2 inner ones have a single septular pore; the 3 outer ones have 2 to several pores clustered on or near the zooidal margin. The thin gymnocystal ridges separating, and surrounding, the pore-chambers are continuous. The ridge between the inner lateral-oral and outer proximolateral pore-chambers is widest and somewhat Y-shaped, with 6-7 small foramina distributed along the arms and tail of the Y; the longer arm that courses obliquely from the orifice to the branch axis has a longitudinal suture flanked by apparent vestigial costal elements, but the extent of their development varies considerably from zooid to zooid. Orifice longer than wide, orientated obliquely on the zooid. Avicularia usually paired, occasionally single, with complete cross-bar and acute triangular rostrum; facing laterally, the avicularian process short or considerably projecting. Ovicell unknown. Dorsal surface comprising a pair of large pore-chambers per zooid which are continuous with the outer lateral-oral and proximolateral ones on the frontal side; a few tiny septular pores occur near the lateral margin in each chamber. Axial interzooidal boundary sinuous dorsally, not zigzag.

DISTRIBUTION. — Victoria, Australia, Early Oligocene to Middle Miocene (Rupelian to ?Langhian/Serravallian),

REMARKS. — This species has been little reported on. According to the localities given by MAPLESTONE (1904) and COCKBAIN's (1971) corrected ages given by WASS (1973), this species is distributed from Early Oligocene to Middle Miocene. The range of the genus in time, however, was extended to the present day when GORDON (1989a) discovered in N.Z. Oceanographic Institute samples a new species, *P. recens* (fig. 8 a-c), at 831 m depth on the western flank of the Norfolk Ridge north of Norfolk Island. Although this was the first living ditaxiporine species to be discovered, only isolated segments (still with membranes intact) were found, so it was of some interest to discover several mature and attached colonies of a second living ditaxiporine (*Bryosutor utilis* sp. nov.) in MUSORSTOM samples from the far northern part of the Norfolk Ridge. This biogeographic connection

between the Norfolk Ridge and the Tertiary of Victoria is paralleled by other catenicelloidean Bryozoa, viz, species of *Petalostegus* and *Chelidozoum* (GORDON & d'HONDT, 1991). Subsequently, an Upper Eocene species (*P. alma* sp. nov., see below) was discovered at Alma, South Island, New Zealand.

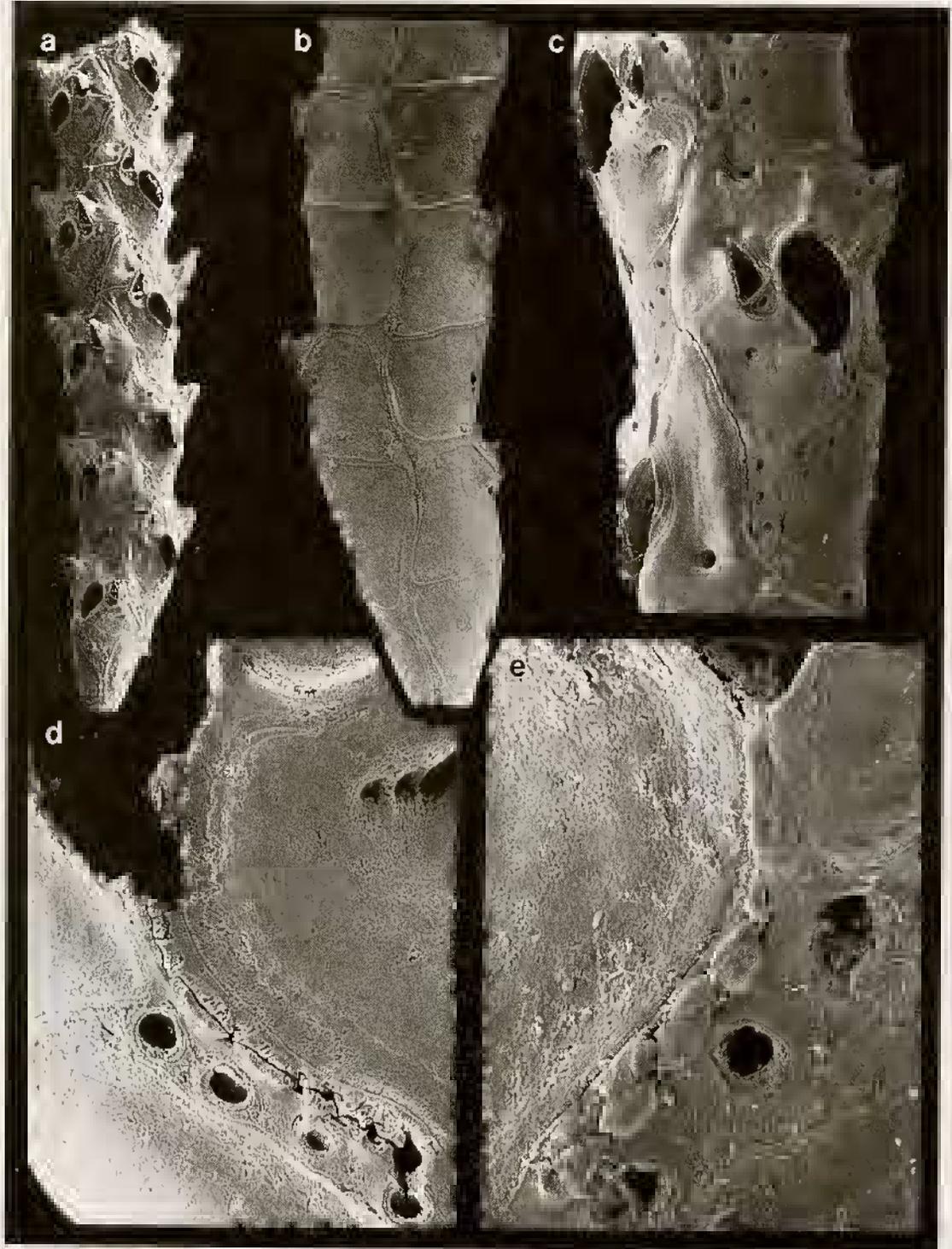


FIG. 7 a-e. — *Plagiopora disticha* MacGillivray : a, c, frontal views of segment and zooids (x 37 ; x 122) ; b, dorsal view of proximal end of a segment (x 65) ; d, e, magnified views of the median gymnocystal ridge and vestigial costal elements (x 388 ; x 683). (From Princetown, Victoria ; BOCK Collection, Royal Melbourne Institute of Technology.)

The finding of a suture and apparent vestigial costae in the median gymnocystal ridge in *Plagiopora disticha* (made possible by the remarkable preservation) is significant, for it indicates that *Plagiopora* was derived from a form with a costal field, a larger area of gymnocystal with extracostal windows, and smaller pore-chambers. *Plagiopora recens* is even more derived but may nevertheless be included in the genus in spite of no trace of vestigial costae. One significant difference in this species, however, is the occurrence of transverse gymnocystal ridges on the dorsal surface. *Plagiopora alma* also lacks any trace of costae or gymnocystal windows, although it is the earliest species of the genus. In frontal view, it more closely resembles *P. recens* than *P. disticha*. Dorsally, it is closer in appearance to *P. disticha* in lacking transverse gymnocystal ridges.

Plagiopora alma sp. nov.

Fig. 8 d-g

MATERIAL EXAMINED. — New Zealand, At Alma, north Otago, New Zealand, from the fine fraction in a calcareous conglomeratic tuff, Waiareka Volcanic Formation, Runangan age (= Priabonian, Upper Eocene); N.Z. Fossil Record File No. J41/f88, grid reference J41/453639, collected by D.P. GORDON, March 1993.

DESCRIPTION. — Unique segment 0.98 mm long and 0.32 mm wide, comprising 4 zooids. Zooids small, 0.39–0.45 mm long and ~ 0.16 mm wide, widest in the distal half, tapering narrowly in the proximal half if at the proximal end of the segment. Zooidal orifice somewhat pyriform and asymmetrical, slightly oblique, with the distal end a little closer to the segmental axis; proximal end with a sinus-like narrowing, with 1 or 2 condyles evident at the corners of the sinus. Frontal shield comprising shallow cryptocystal sectors (essentially broad flattened pore-chambers) separated by narrow gymnocystal ridges; these sectors include 1 on each side subjacent to the orifice and proximal to each lateral-oral avicularium (if there are 2), and a single large area over the proximal half of the zooid. There are 2 additional sectors distolateral to the orifice above each avicularium. Thus there are 3 such areas along every outer zooidal margin, each of which continues around the margin to the dorsal side. Septular pores are not evident in the cryptocystal sectors. Avicularia evidently generally paired, either side of the orifice, each with a complete cross-bar, the inner one facing frontally and directed obliquely towards the orifice, the outer one facing laterally and directed distally. Where the inner avicularium is lacking, as on the proximal zooid of a segment, the cryptocystal sectors adjacent to the orifice merge as one. Ovicell unknown. Dorsal side of segment with a sinuous median groove longitudinally paralleled by the gymnocystal margins adjacent to the cryptocystal sectors.

TYPE. — *Holotype*: the unique segment illustrated in figure 8 d-g, from the Waiareka Volcanic Formation, Alma, north Otago, New Zealand, type number BZ 162, Institute of Geological & Nuclear Sciences, Lower Hutt, New Zealand.

DISTRIBUTION. — Runangan (= Priabonian, Upper Eocene), Oamaru, South Island, New Zealand.

ETYMOLOGY. — The specific name is that of the type locality.

REMARKS. — The road cutting through the Waiareka Volcanic Formation has exposed a calcareous tuff packed with small stones, frequently encrusted by bryozoans, tubicolous polychaetes, and coralline algae. The fine fraction includes isolated segments of buguloidean and cellarioidean bryozoans, rare catenicellid fragments and, at one end of the exposure, the warm-water foraminiferan *Asterocyclina*. The overall setting appears to have been the shallow subtidal in well-oxygenated water of oceanic or near-oceanic salinity.

In its overall morphology, *Plagiopora alma* is somewhat intermediate between *P. disticha* and *P. recens*. Gymnocystal foramina are lacking in *P. alma*, as are vestigial costae, except that the proximal rim of the orificial sinus gives the appearance of being derived from a suboral pair. While the frontal side of the segment closely resembles that of *P. recens*, the dorsal side lacks transverse gymnocystal ridges. Although occurring earlier, *P. alma* is less derived in frontal-shield morphology than *P. disticha*.



Genus *AHCHEETHAMIA* nov.

DIAGNOSIS. — Multizoidal, biseriate. Frontal shield a porous gymnocyst. Proximal rim of orifice composed of a pair of vestigial costae. Avicularia single, borne laterally, ? or paired. Ovicell evenly porous like the frontal shield. Dorsal surface with numerous pores.

RANGE. — Bartonian (Middle Eocene).

ETYMOLOGY. — The genus is named after the author of the species, Dr Alan H. CHEETHAM (Smithsonian Institution) in recognition of his outstanding contributions to bryozoology.

TYPE SPECIES. — *Caberoides corniculatus* Cheelham, 1966.

Ahcheethamia corniculata (Cheelham, 1966)

Fig. 9 a-f

Caberoides corniculatus Cheelham, 1966 : 82, figs 60-61.

MATERIAL EXAMINED. — England. The Natural History Museum, London: Holotype specimen D48746, from the Upper Bracklesham Beds, Fisher Bed 21, Selsey, Sussex, England (National Grid Reference SZ 836936), collected by D. CURRY and presented November 1961; paratypes D48751, D48756, D48766, D48767, from same locality as holotype. Smithsonian Institution: 4 non-type specimens, from same locality as holotype.

DESCRIPTION. — Segments up to ~2.20 mm long and 0.68 mm wide, with up to 12 zooids per segment. Zooids 0.32-0.37 mm long and 0.26-0.37 mm wide, the gymnocystal frontal shield coarsely perforated by numerous pores. Orifice with a pair of small condyles; the concave proximal rim composed of a pair of broad vestigial costae. On the axial side of each orifice is an umbo, perforated like the frontal shield. On the outer, lateral, side of the orifice is a frontolaterally facing avicularium, the opesia semicircular, the cross-bar complete, the rostrum triangular; a process behind the rostrum may project beyond the avicularium. Ovicell recumbent, set obliquely to the segmental axis, perforated like the frontal shield. Dorsal surface of segment with a median zigzag suture line, the zooidal basal walls evenly perforated like the frontal shield.

DISTRIBUTION. — Lower Bartonian (Middle Eocene), Sussex, England.

REMARKS. — Our description of the species is based on SEM observations of uncoated specimens (most of which were generously provided by Dr Paul D. TAYLOR, The Natural History Museum, London). The perforations in the dorsal surface of each zooid are very curious. They do not appear to represent septular pores (no pore-chamber boundary is evident on the lateral margin); rather, they appear to be the same as the frontal gymnocystal pores, which is somewhat unusual.

Although *Ahcheethamia corniculata* segments resemble those of *Caberoides* in their general form, the species differs from the type and other species of *Caberoides* in having a porous frontal gymnocyst, only a suboral pair of vestigial costae, no frontal pore-chambers, and a perforated ovicell. The porous gymnocyst, in fact, invites comparison with that of *Ditaxiporina*.

The genus is at present monotypic.

FIG. 8 a-c. — *Plagiopora recens* Gordon : a, frontal view of a segment with seven zooids (x 39) ; b, dorsal view of a segment with six zooids (x 42) ; c, orifices and avicularia of two zooids (x 167). (From NZOI Stn G4, western flank of Norfolk Ridge north of Norfolk Island, 831 m depth).

FIG. 8 d-g. — *Plagiopora alma* sp. nov. : d, frontal view of the holotype segment (x 100) ; e, zooidal orifice (x 411) ; f, dorsal view of the holotype segment (x 100) ; g, close-up of frontal shield (x 217). (From Alma, North Otago, New Zealand, Priabonian, Institute of Geological & Nuclear Sciences, Lower Hut.)



FIG. 9 a-f. — *Ahcheethamia corniculata* (Cheetham) : a, fertile segment with three ovicelled zooids ($\times 43$) ; b, same, showing the three ovicells ($\times 95$) ; c, another segment, showing the distolateral avicularia ($\times 95$) ; d, e, dorsal surface ($\times 54$; $\times 152$) ; f, close-up of left-hand ovicelled orifice in fig. b ($\times 190$). (Figs a-c, f, uncoated holotype D48746, BMNH, London ; d-e, uncoated paratype D48756, BMNH ; from the Upper Bracklesham Beds, Sussex.)

Genus *DITAXIPORINA* Stach, 1935a

DIAGNOSTS. — Mullizoidal, biserial. Frontal shield an evenly porous gymnocyst. Proximal rim of orifice composed of a vestigial pair of costae, each with a lumen pore (pelma). Between each costa and the paired distolateral avicularia is a tiny pore-chamber. Ovicell smooth, imperforate or with a pair of ectoocelial fenestrae. Dorsal surface of zooids smooth; a tiny pore-chamber may occur subjacent to each avicularium.

RANGE. — Lutetian (lower Middle Eocene) to Rupelian (Lower Oligocene).

TYPE SPECIES. — *Catenicella septentrionalis* Waters, 1891.

Ditaxiporina septentrionalis (Waters, 1891)

Fig. 10 a-d, tt c-d

Catenicella septentrionalis Waters, 1891 : 5, pt. 1, figs 1-8. — BRAGA, 1963 : 41.

Ditaxiporina septentrionalis - STACH, 1935a : 395; 1935b : 46. — CHEETHAM, 1963 : 485. — BRAGA in ANTOLINI *et al.*, 1980 : 61, fig. 44. — BRAGA & BARBIN, 1988 : 528.

MATERIAL EXAMINED. — Italy. The Manchester Museum, U.K. : slides #7488/t40, #7490/140 of *Catenicella septentrionalis*, Waters Collection, from Montecchio Maggiore, Upper Eocene. Dipartimento di Geologia dell'Università di Padova : specimens from Pannone P1 and Toara, Collezione micropaleontologica, Upper Eocene.

DESCRIPTION. — Segments up to 4.22 mm long and 0.51-0.56 mm wide, with up to 8 zooids per segment. Zooids alternating, 0.48-0.74 mm long and ~0.30 mm wide, relatively slender, the most proximal zooid of a segment more or less claviform and proximally tapered. The axial furrow between the zooids zigzagging along the segment. Frontal shield a gymnocyst, almost evenly perforated (fewer centrally) by numerous pores. Orifice with a broad U-shaped sinusoidal poster, the proximal rim defined by a raised pair of short broad costae, with a thin suture-line between them and each with a proximal pore. Adjacent to the orifice is a pair of avicularia, the axial one possibly sometimes aborted, otherwise facing obliquely frontally, the marginal one facing laterally; each somewhat projecting, each with a semicircular opesia, complete cross-bar, and short triangular rostrum; a tiny pore-chamber occurs frontally between each avicularium and the adjacent costa. Ovicell subglobular, evidently smooth, covering approximately half the frontal shield of the distal zooid. Dorsal surface of segment smooth-surfaced, the basal wall of each zooid somewhat convex, with only a single tiny pore-chamber behind the lateral avicularium. The interzooidal furrow traces a sinuous course along the segment between the zooids.

DISTRIBUTION. — Northeast Italy, Upper Eocene.

CONGENERIC SPECIES. — Three other species may possibly be included in this genus. These are :

[?]*Catenicella granulosa* Canu, 1908, Lutetian, near Paris, France.

Catenicella subseptentrionalis Canu & Bassler, 1917, Rupelian, southwest Arkansas, USA.

Ditaxiporina bifenestrata Cheetham, 1963, Rupelian, southwest Arkansas, USA.

REMARKS. — The genus *Ditaxiporina* was discussed quite thoroughly by CHEETHAM (1963), who described a new species, *D. bifenestrata*, with bifenestratae ovicells. In all other respects this species closely resembles the type species. Although it is not impossible that the ovicell was truly bifenestratae, the possibility that the fenestrae represent eroded predator bore-holes cannot be ignored - selective predation of ovicells has been noted by GORDON & D'HONDT (1991) in the calenicelloidean genus *Petalostegus*. Apart from the type species, the ovicell has not been discovered in any of the other species ascribed to *Ditaxiporina*, which may be distinguished on the basis of zooidal characters, such as details of size, distribution of frontal pores, and placement and orientation of the avicularia.

The exact status of *Catenicella granulosa* is uncertain. It was described as lacking avicularia and, indeed, the unique (holotype) specimen (fig. 9 e) appears to lack them, but the preservation is so poor that it is impossible to be certain. The dorsal surface [now inaccessible, since it was glued to the slide after CANU (1908) illustrated it] was described as smooth and convex. Thanks to the courtesy of Dr Agnès RAGE (Institut de Paléontologie, Muséum national d'Histoire naturelle, Paris) and Dr Paul TAYLOR (Department of Palaeontology, The Natural History Museum, London) it was possible to borrow and scan (uncoated) the holotype specimen. Because of the poor state of preservation it is impossible to be certain if it belongs to *Ditaxiporina*, though the description of a smooth dorsal surface would support this.

The occurrence of uni-, bi-, tri-, and multizoooidal segments in the fossil samples (see WATERS, 1891) suggests the manner in which the segments grew. More significantly, the unizoooidal segments are nearly identical to those of the present-day species *Vasignyella otophora* (Kirkpatrick, 1890), which has only unizoooidal segments. In fact, the similarity is so great (GORDON & D'HONDT, 1991) that it is inconceivable that *Vasignyella* is unrelated to *Ditaxiporina*. For this reason, *Vasignyella* is here separated from the Savignyellidae and included in the Catenicellidae.

Subfamily VASIGNYELLINAE subfam. nov.

DIAGNOSIS. — As for the sole included genus.

Genus VASIGNYELLA Gordon 1989b

DIAGNOSIS. — All segments unizoooidal. Zoooidal frontal shield an evenly perforated gymnocyst. Proximal rim of orifice composed of a vestigial pair of costae, lacking lumen pores (pelmata). Between each costula and the distolateral pair of avicularia is a tiny pore-chamber. A row of small round uniporous pore-chambers occurs along each margin. Ovicell unknown. Dorsal surface smooth, with only a small pore-chamber behind each avicularium.

RANGE. — Holocene.

TYPE SPECIES. — *Catenaria otophora* Kirkpatrick, 1890.

Vasignyella otophora (Kirkpatrick, 1890)

Fig. 11 a-b

Catenaria otophora Kirkpatrick, 1890 : 17, pl. 5, figs 1-1c. — PHILIPPS, 1900 : 441. — THORNELY, 1912 : 139. — GRAVELY, 1927 : 89, pl. 11, fig. 6.

Savignyella otophora - HARMER, 1957 : 763, pl. 51, figs 19-21. — DUMONT, 1981 : 636. — WINSTON, 1986 : 27.

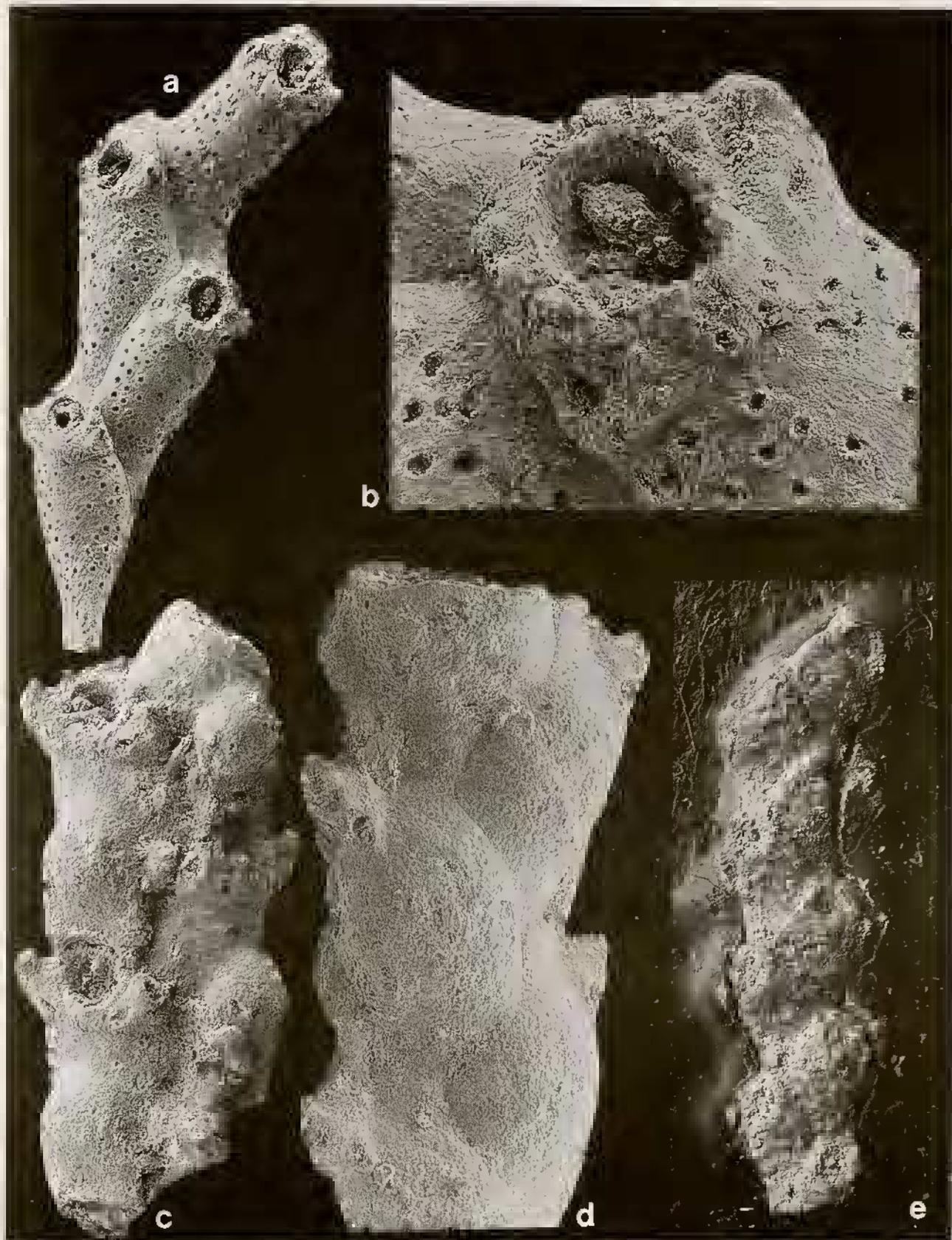
Vasignyella otophora - GORDON, 1989b : 453, figs 13-15. — RYLAND & HAYWARD, 1992 : 247, fig. 14a.

MATERIAL EXAMINED. — Western Samoa. N.Z. Oceanographic Institute : sparse material from Sa'aga, Upolu Island, collected by J.E. MORTON (University of Auckland).

DESCRIPTION. — Colony erect, comprising branching uniserial chains of unizoooidal segments. Zooids claviform, bent somewhat forward, 0.79–1.30 mm long and 0.24–0.25 mm wide. Frontal shield a porous

FIG. 10 a-d. — *Ditaxiporina septentrionalis* (Waters) : a, segment of four autozooids (x 79) ; b, close-up of the right-hand proximal zooid in fig. a - note the lumen pores in the suboral costae (x 317) ; c, ovicelled zooids (x 88) ; d, dorsal surface of zooids (x 108). (Figs a-b, Pannone, Italy, Upper Eocene ; Waters Collection, Manchester Museum. Figs c-d, same locality, Braga Collection, Dipartimento di Geologia, Paleontologia e Geofisica dell'Università di Padova.)

FIG. 10 e. — *Ditaxiporina granulosa* (Canu), uncoated unique holotype segment affixed to slide (x 56). (From Orglandes, near Paris, Middle Eocene ; slide R53352, Institut de Paléontologie, Muséum national d'Histoire naturelle, CANU Collection.)



gymnocyclus. Orifice with a pair of small condyles delimiting the anter from the broadly V-shaped poster. Proximal rim of orifice delimited by a pair of short broad costae with a median suture. Lateral-oral avicularia with triangular rostrum, the cross-bar lacking, facing frontolaterally. Ovicell unknown. A row of ~5 small circular pore-chambers occurs along each lateral margin, the septulum uniporous. An additional small pore-chamber occurs on each side between the avicularium and the adjacent costa, and behind the avicularian rostrum. Dorsal surface smooth.

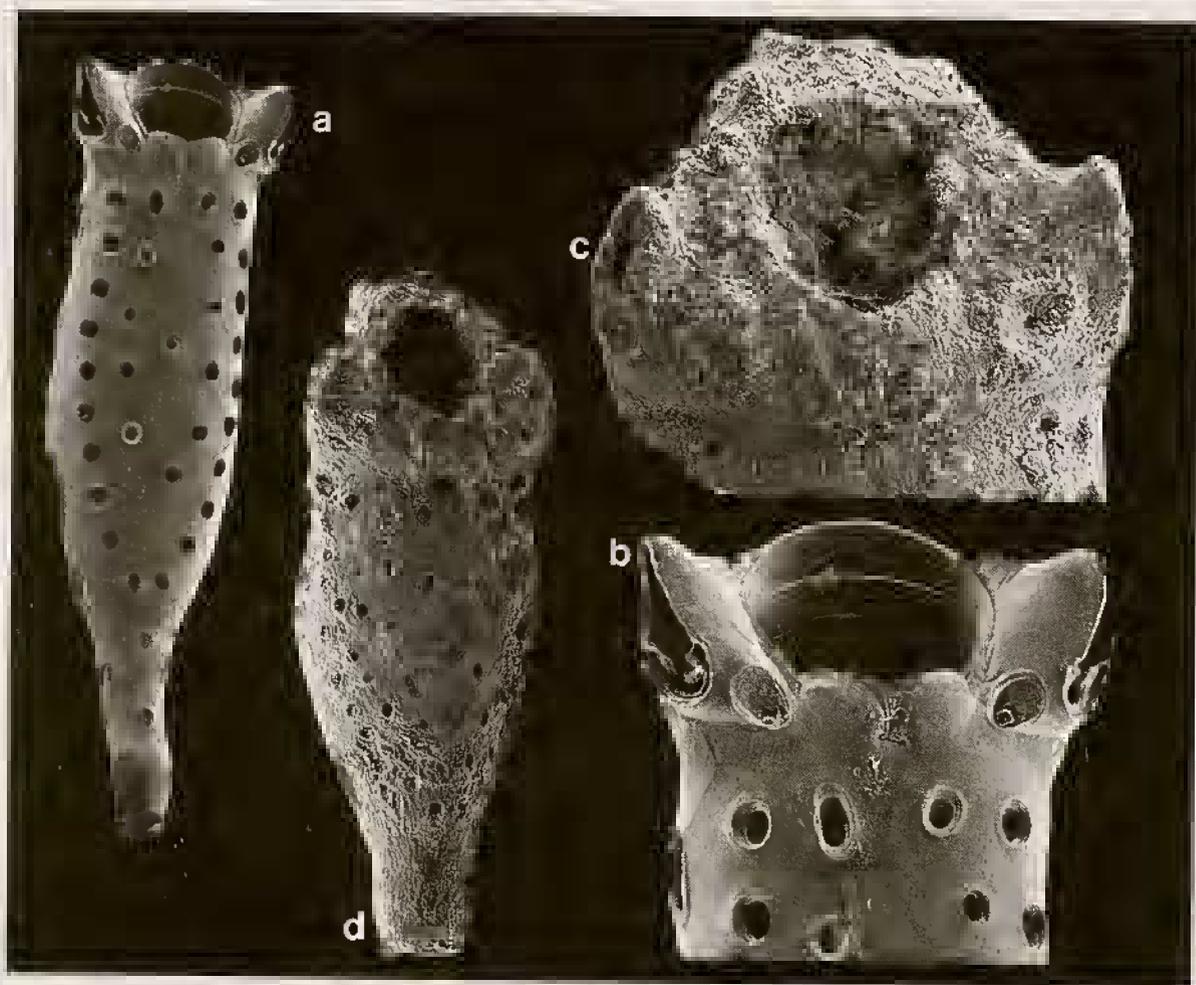


FIG. 11 a-b. — *Vasignyella otophora* (Kirkpatrick) : a, autozooid (x 103) ; b, same, close-up of orificial region -note the small pore-chambers between the avicularia and suboral costae, and the lack of lumen pores in the latter (x 205). (From Sa'aga, Upolu Island, Western Samoa.)

FIG. 11 c-d. — *Ditaxiporina septentrionalis* (Waters) : c, orificial region of another unizoidal segment ; cf. plate 10, b - note the lumen pores in the suboral costae (x 299) ; d, young unizoidal segment prior to budding of the additional zooids (x 149). (From Pannone, Italy, Upper Eocene ; Waters Collection, Manchester Museum.)

DISTRIBUTION. — Sudanese Red Sea, Indian Ocean, China Sea, Philippines, New Guinea, Great Barrier Reef, Fiji, Western Samoa, intertidal to 49 m.

REMARKS. — Although the unizoidal segments of *Ditaxiporina septentrionalis* appear to lack the small lateral pore-chambers found in *Vasignyella*, the arrangement of elements in the orificial region is extraordinarily similar, including the presence of small pore-chambers between the avicularia and costae and behind the avicularia. The costae of *Vasignyella otophora* lack lumen pores, however, and individual zooids are somewhat larger than those of *D. septentrionalis*. There is one other difference, which may be significant in view of its otherwise apparent universality among ditaxiporines - viz. the lack of an avicularian cross-bar in *Vasignyella*.

At present, *Vasignyella* is monotypic and has no known fossil record. The absence of small lateral pore-chambers in *Ditaxiporina* may indicate that *Vasignyella* was not derived directly from it but from a common predecessor. Significantly, ovicells have never been found in *Vasignyella*, possibly indicating internal brooding. Because of this, we propose a separate subfamily, Vasignyellinae, additionally characterised by only unizoooidal segments and the lack of an avicularian cross-bar. In our opinion, *Vasignyella* has no direct relationship with *Savignyella* Levinsen and *Halystis* Norman, although we suspect that the Savignyellidae may nevertheless be derived from an early catenicelloidean stock. We intend to discuss the genera of the Savignyellidae in a future paper.

SYSTEMATIC AFFINITIES

On the basis of the mixture of shared and derived characters among the genera discussed in this paper, we conclude that, with the exception of *Vasignyella*, all the other genera may be allied in the one subfamily, Ditaxiporinae Stach, 1935a, in which the family Ditaxiporinidae Cheetham, 1963 may be subsumed.

Diversification of the family Catenicellidae (Maastrichtian to present day) from the Cribrilinidae *sensu lato* presumably occurred during the Senonian, though the details are unknown. Although some cribrilinids evidently had articulated colonies, the segments were stick-like, not oligozoooidal. Segments of one or a few zooids, and relatively large ovicells, are shared with another catenicelloidean family, the Petalostegidae, which may be regarded as a sister group. These characters are thus synapomorphics for these two families. In the subfamily Ditaxiporinae, ancestral characters (plesiomorphies) include multiple costal elements, small or linear pore-chambers, and lateral-oral avicularia. Derived characters (apomorphies) include vestigial suboral costae or no costae, enlarged pore-chambers (especially dorsally), and gymnocystal ridges. The assignment of morphological polarities is based on evident trends in other catenicelloideans as well as in hippothooideans (separately derived from cribrilinids), viz. a reduction in the size of the costal shield and/or the number of costal elements with a concomitant increase in the area of either gymnocyst or cryptocystal elements (e.g., extracostal windows and/or pore-chambers), with accompanying specialisations (see BANTA & WASS, 1979; GORDON & D'HONDT, 1991). An autapomorphy found only among the Ditaxiporinae is biseriate multizoooidal segments of non-reproductive zooids (in contradistinction to the occasional fertile multizoooidal segments in some species of *Catenicella*). Although known only from the Holocene, *Bryosartor* is in many respects the least-derived ditaxiporine genus. In fact, there are significant similarities to *Costaticella* (Scuticellinae) in the multicostate spinocyst and the extracostal foramina. *Bryosartor* may be a much older genus than is indicated by its lack of a fossil record, a possibility supported by its occurrence on the northern Norfolk Ridge where a high proportion of archaic taxa occur (RICHER DE FORGES, 1987, 1990). Alternatively, *Bryosartor* may be a more recently derived genus which has retained ancestral features, but whose immediate predecessors are unknown.

There are several parallels between scuticelline/catenicellinae and ditaxiporine genera. For example, the earliest-occurring genera of both subfamilies have costal shields, and there are similar trends in the diversification of frontal-shield morphologies. *Strophipora* resembles *Ditaxipora* in the possession of a median gymnocystal band flanked by broad shallow pore-chambers that effectively make the frontal shield largely cryptocystal. For this reason, CANU and BASSLER (1929) proposed that the latter genus should be a subgenus of the former, a suggestion that STACH (1934) rightly rejected. *Cribricellina*, with its perforated gymnocystal shield, parallels *Ahcheethamia* and *Ditaxiporina*.

BIOGEOGRAPHY

The distributions in time and space of the genera of Ditaxiporinae and Vasignyellinae are shown in figures 12 and 13. Apart from the occurrence of two species of *Ditaxiporina* in southwest Alabama, the combined distribution of all the taxa is notably Tethyan. For the Ditaxiporinae, there are two main distributional clusters - amphiatlantic/European, and Australasian. *Ditaxiporina* is the only American (and amphiatlantic) genus. Interestingly,

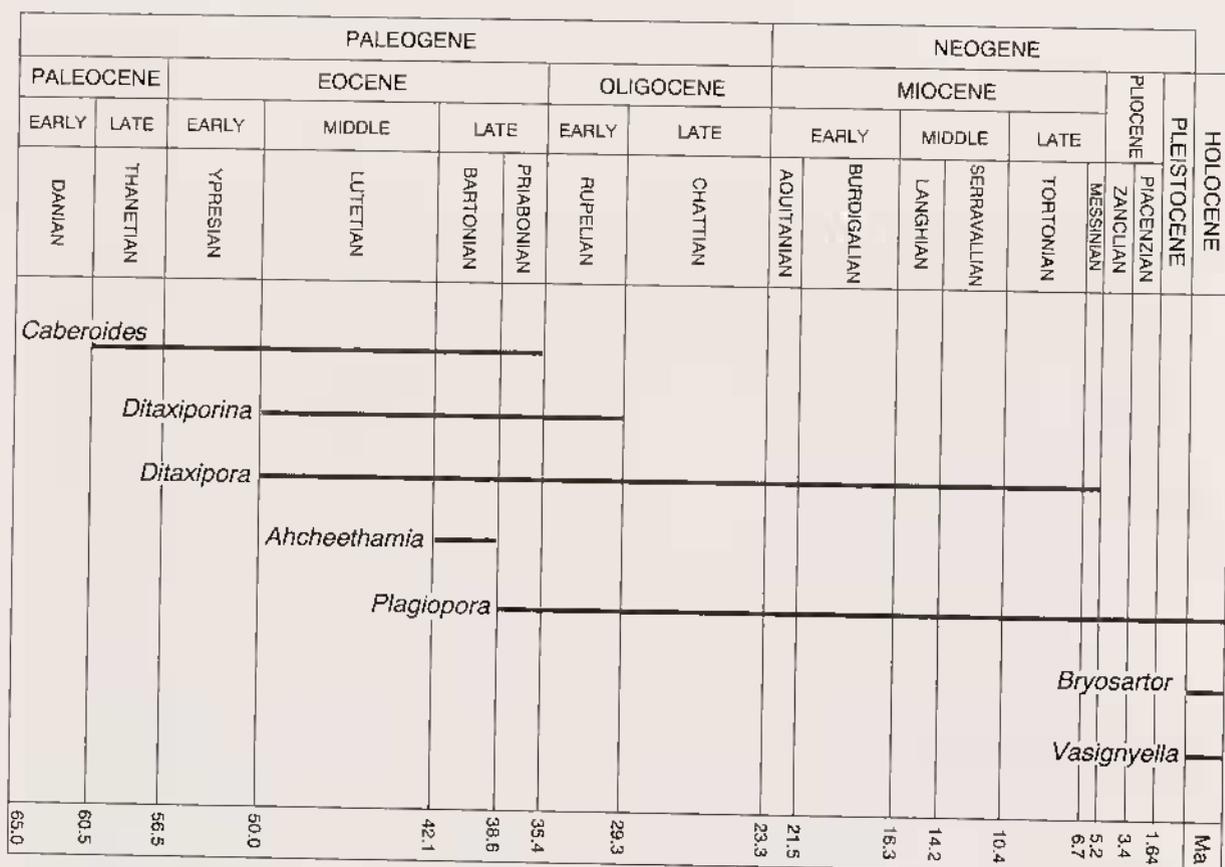


FIG. 12. — Stratigraphic distribution of the genera of the catenicellid subfamilies Ditaxiporinae and Vasignyellinae throughout the Cenozoic [chronometric scale based on HARLAND *et al.* (1990)].

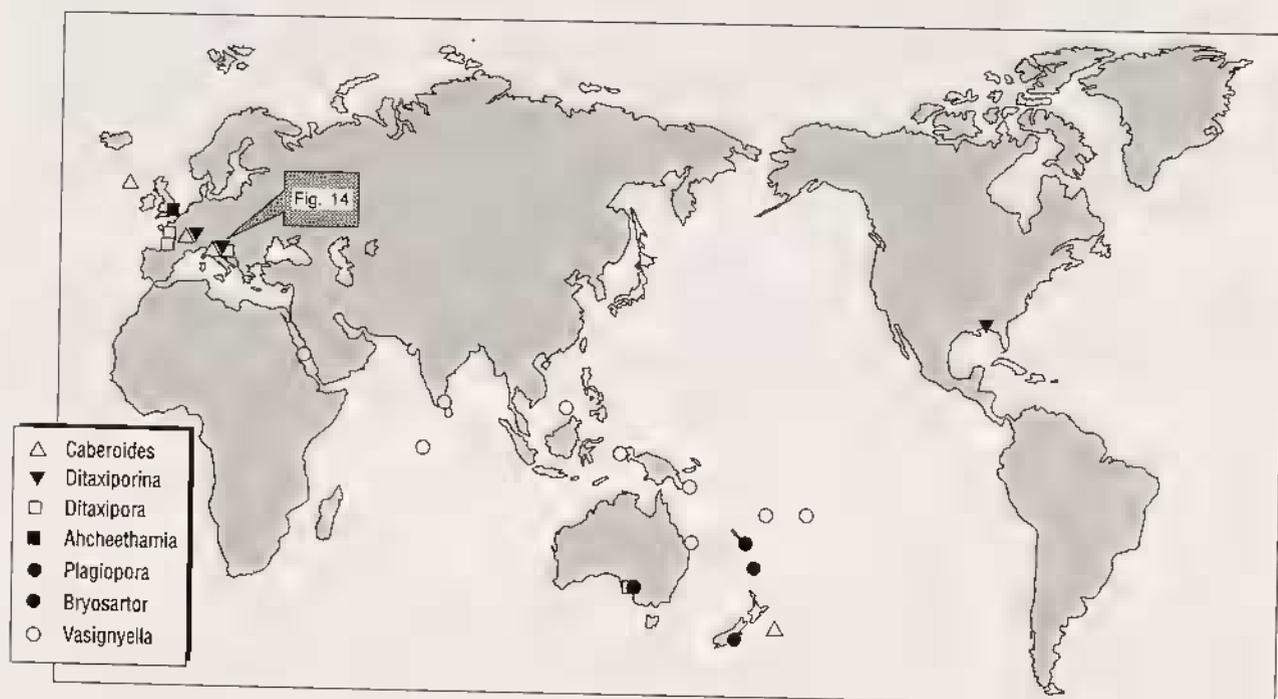


FIG. 13. — Biogeographic distribution of the genera of the catenicellid subfamilies Ditaxiporinae and Vasignyellinae.

the earliest-known genus, *Caberoides*, achieved a potentially Tethyan-wide distribution by the Ypresian, ranging from the Northeast Atlantic to Chatham Island, New Zealand within 10-Ma. Clearly, the earliest ditaxiporines must be sought in the Danian or Maastrichtian. Like *Caberoides*, *Ditaxipora* is found at either end of the Tethyan corridor. It is significant that the oldest species of both of these genera are European, indicating that the Australasian taxa are derivative. LAGAIJ and COOK (1973) and BRAGA (1987) have documented similar distributions in other cheilostomes, from which BRAGA concluded that faunal migration was eastwards from the Mediterranean to the Indo-Pacific. The information presented here supports that scenario for the amphiTethyan ditaxiporine genera.

The Ditaxiporinae of the western area of Tethys, belonging to the Paleogene of Venetia, occur in levels that are sometimes thick and continuous. Reported in the literature as 'Bryozoa marls' or 'Brendola marls', they are a key bed in studying the Upper Eocene sequences and are very rich in bryozoans. They outcrop over a wide area, including the Southern Trentino, the Lessini Mountains, the Berici Mountains, the piedmont area of the Asiago plateau, and the western Treviso Hills. This area, here called the Venetia shelf, was a structural high (fig. 14) where shallow-water marly calcareous deposits (nummulitic limestones, fossiliferous marls) were laid down. It corresponds largely to the resurrected Trento platform, an important Liassic structure drowned and successively overlain by Upper Jurassic pelagic limestones of the Ammonitico Rosso Formation (BOSELLINI, 1989).

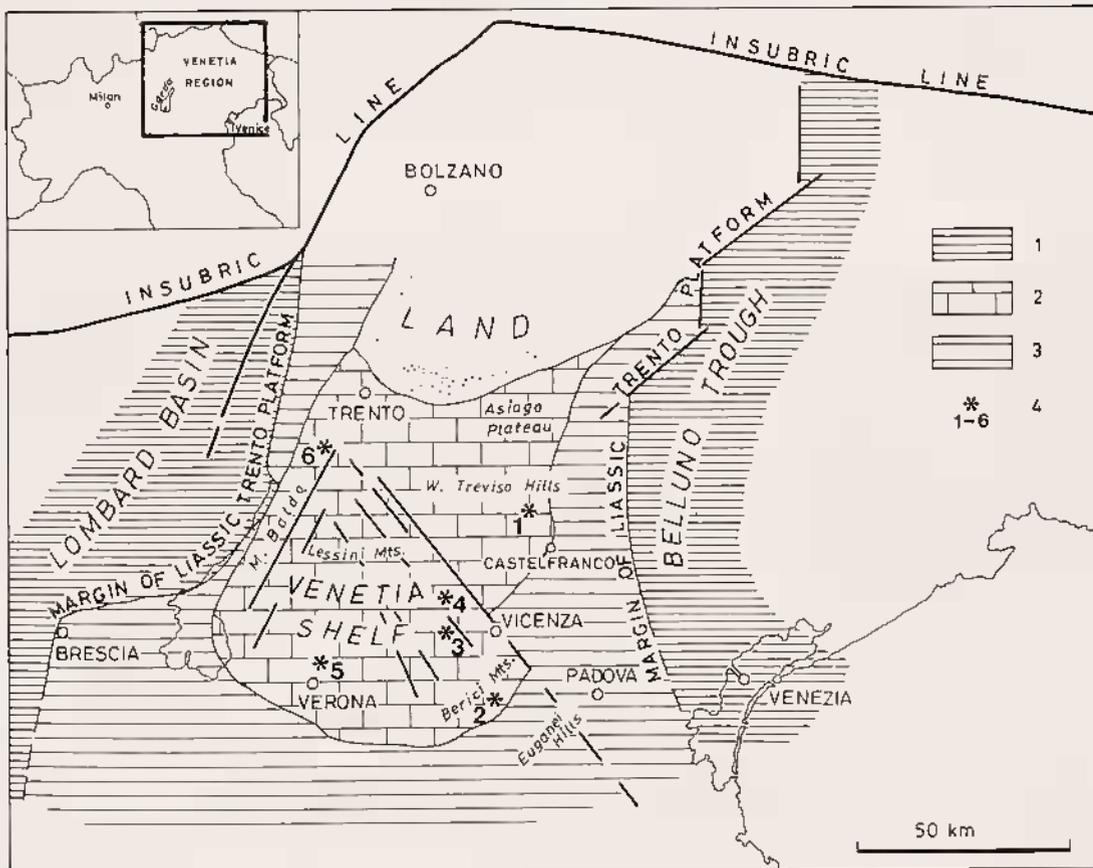


FIG. 14. — Location of the Upper Eocene bryozoan outcrops in the Venetia shelf, an important paleogeographic structure in the western Tethyan basin (modified from Bosellini 1989). Explanation of symbols:

- 1 : westward - marly limestones (Scaglia cinerea Formation); eastward - marls and sandy and calcareous shales (flysch facies)
- 2 : shallow water deposits (shelf facies)
- 3 : hemipelagic deposits
- 4 : main Upper Eocene bryozoan outcrops of Venetia (NE Italy), marked by asterisks (*): 1, Possagno; 2, Brendola-Toara, Montecchio di Costozza; 3, Val di Lonte; 4, Priabona; 5, Verona; 6, Pannone.

Paleoecologically, the Venetia shelf was marginally characterised by patch reefs, lagoons, and coastal embayments, with coralline-algal meadows and sublittoral bryozoan associations. The Bryozoa marls show an extremely rich diversity, with abundant representation of rigid-erect branching growth forms, indicative of relatively fast water flows well supplied with particulate food, especially microalgae. There were also articulated, rod-like, and vagrant colonial morphologies. Thus, in addition to cateniceid, there were also stratigraphically and paleoecologically significant species like *Lacrimula perfecta* (Accordi), typically associated with soft seafloor sediments of carbonate mud or more or less muddy sands.

A significant diversity occurs among the petrofacies of the different marginal deposits of the Venetia shelf. For example, the residue of the Pannone washed samples (western area) shows extrabasinal clasts (quartz, potassium feldspar, mica), presumably coming from a source area containing granitic and metamorphic rocks of the neighbouring northern land. In the eastern area (Possagno), silty clayey or clastic distal sediments prevail, originating from the eastern platforms or the above-mentioned area. In the centre of the shelf, east of Lake Garda (fig. 14, inset), the Bryozoa levels are fairly rich in carbonates and contain numerous nummulites, bivalves, algae, and coral fragments. The bryofaunas are, however, quite uniform and would not seem to have been limited by environmental factors.

According to sedimentological characteristics, faunal content, growth-form parameters, and inferences concerning the species in life, the depth range of the shelf would have been within the photic zone of the inner-outer interval, not more than 100 m. The sea was warm-temperate or subtropical, with well-oxygenated water of normal salinity, judging from the high species diversity of the Bryozoa. In summary, we can hypothesize that the modern, predominantly Australasian, distribution of cateniceid (including the Ditaxiporinae and Vasignyllinae) may be derived from a wider circumtropical Paleogene distribution (cf. LAGAN & COOK, 1973; BRAGA, 1987).

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