Review of the fossil Stylasteridae (Cnidaria: Hydrozoa) from the New Zealand region

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Abstract The five previously reported fossil calcified hydroids from the New Zealand region are discussed, resulting in: a change of generic placement of two species (Stylaster sensu Jones, 1970 to Calyptopora; and Paraerrina sensu Squires, 1962 to Lepidopora), and a query of the identification of Sporadopora mortenseni sensu Squires, 1962. Several records of bryozoans reported as stylasterids are also rectified. Four additional fossil stylasterids are reported from the region: indeterminate species of Inferiolabiata and Conopora from the early Miocene (Otaian) of Pakaurangi Point; a species of Errina from the early to middle Eocene (Waipawan-Bortonian) of Chatham Island; and a new species, Stylaster gigas, from the early Pliocene (Opoitian) of Kaawa Beach, North Island. S. gigas has one of the most massive coralla of any known stylasterid. The nine fossil stylasterids now known from the New Zealand region range from the early Eocene to the late Pliocene and are found from both North and South Islands as well as Chatham and Pitt Islands.

Keywords Cnidaria; Hydrozoa; Stylasteridae; new taxon; *Stylaster gigas*; new records; Cenozoic; New Zealand; Chatham Islands

INTRODUCTION

Knowledge of fossil calcified hydroids (Stylasteridae and Axoporidae) from the New Zealand region (including the Chatham Islands) began with Tenison-Woods (1880), who described Sporadopora marginata from the late Pliocene of Pitt Island, Chatham Rise. Squires (1958) described Sporadopora cleithridium (=Axopora cleithridium, see Cairns 1983b) from the late Miocene (Kapitean) of Port Craig, South Island. Later, Squires (1962) reported three additional fossil stylasterids from the early Miocene to late Pliocene of North and South Islands: Paraerrina sp. (=Lepidopora sp.), Sporadopora mortenseni (= Sporadopora sp.), and Distichopora spp. The latter is here identified as a bryozoan, as is Pliobothrus grantmackiei Squires, 1965, from the Waitakian (basal Miocene) of Kakanui, South Island (see Cairns 1983a). Jones (1970) listed two stylasterids from the early Miocene (Otaian) of Pakaurangi Point: Stylaster sp. (= Calyptopora sp. cf. C. reticulata) and Distichopora sp. (= bryozoan). Hayward's (1977) report of Distichopora from the early Miocene (Otaian) Waitakere Ranges is also a bryozoan. Finally, Cairns (1991) figured the type of Sporadopora marginata and briefly discussed or listed the other New Zealand fossil species.

Thus, five fossil species were known from the region (Table 1), ranging from the early Miocene to late Pliocene. Four additional species are reported herein (Table 1), including one new species (*Stylaster gigas*) and another species from the early Eocene.

Twenty-five of the 262 stylasterid species are known from only the fossil record (Cairns 1983a, 1991)—the four reported in this paper brings the number to 29. The greatest diversity of fossil stylasterids is 14 species from the late Miocene of Carboneras, southeastern Spain (Barrier et al. 1991), followed by eight species from the Paleocene of Denmark (Nielsen 1919), and four from the Eocene of Tonga (Wells 1977). Thus, the nine species now known from New Zealand compares favorably with other regions of the world, even though their stratigraphic range encompasses the early Eocene to late Pliocene.

MATERIAL AND METHODS

Fossil stylasterids previously reported from New Zealand (Tenison-Woods 1880; Squires 1958, 1962, 1965; Jones 1970; Hayward 1977) and additional specimens from the AU, OU, NZGS, and NZOI collections were examined.

Grid references for fossil localities are given as 6-figure numbers within the appropriate map sheet (i.e., Sheet R13) of the national 1:50 000 New Zealand Mapping Series (NZMS 260). Fossil localities are recorded within the national archival Fossil Record File of the Geological Society of New Zealand, based on the same map series (e.g., R13/f...). Local stages and their correlation are taken from Hornibrook et al. (1989) and based on foraminiferal biostratigraphy.

Abbreviations used in the text are:

AU Geology Department, University of Auckland; prefix for collections held in that institution.

Co Prefix for specimens in the coelenterate type catalogue of the NZGS.

GS Prefix for collections held in NZGS.

H Prefix for specimens in the AU catalogue of coelenterates.

NZGS New Zealand Geological Survey (now Institute of Geological and Nuclear Sciences Ltd.), Lower Hutt.

NZOI New Zealand Oceanographic Institute, Wellington. OU Geology Department, Otago University, Dunedin.

USNM United States National Museum, Smithsonian Institution, Washington, D. C.

SYSTEMATICS

Class HYDROZOA
Subclass ATHECATAE
Order FILIFERA
Superfamily HYDRACTINIOIDEA
Family STYLASTERIDAE

Stylaster gigas sp. nov. Fig. 1-8

DESCRIPTION: Coralla massive, up to 16 cm high and 20 cm across (H1195), with a basal encrustation 7 cm in diameter and main branches up to 5 cm in diameter. Holotype branch segment—chosen for its superior preservation, not its size—only 26.6 mm long and 10.6 mm in diameter. Coralla sparsely branched in three dimensions; branches circular in cross-section and bluntly tipped. Coenosteal texture reticulate, the strips 40–50 μ m in width and separated by narrow slits 5–6 μ m wide (Fig. 4). Corallum texture friable.

Cyclosystems uniformly distributed over coenosteum (Fig. 1, 3), 0.75–0.95 mm in diameter, and flush with coenosteal surface. Cyclosystems distinguishable only on well-preserved coralla with an intact upper coenosteal layer, which is by far the less common condition of the available specimens. In poorly preserved specimens, cyclosystems are sometimes evident on the worn coenosteal surface or in cross-section at branch fractures as a central gastropore encircled by 5–8 much smaller dactylopores. Based on 50 cyclosystems, the range of dactylopores per cyclosystem was 5–8, average 7.24 (σ = 0.75), and mode 8.

Gastropores circular and about 0.5 mm in diameter, tapering to a diameter of about 0.35 mm at narrowest point of gastropore tube,

just above gastrostyle tip. Tube below gastropore ring constriction of variable length (1–6 mm), depending on branch radius. Gastrostyles needle shaped, bearing thin (1.0–1.2 μ m wide), spinose, longitudinal ridges (Fig. 7). Gastrostyle length also a function of branch radius, some as long as 5 mm, but invariably only 0.24–0.28 mm in diameter, resulting in a height:width ratio of up to 21. Elongate gastrostyles held in place by thin (about 1.2 μ m wide) transverse tabulae (Fig. 6). Gastrostyle spines small and pointed, only about 1 μ m in diameter. Dactylotomes 8–12 μ m wide; pseudosepta 1–2 times dactylotome width; diastemas rare, but when present up to 4 times dactylotome width. Dactylostyles present, but preservation does not allow a detailed description of their structure.

Ampullae internal and sexually dimorphic. Female ampullae ellipsoidal cavities 0.8–1.0 mm in diameter located just beneath coenosteal surface, occurring at approximately same frequency as cyclosystems. A small porous depression about 0.3 mm in diameter, the incipient efferent pore, overlays each maturing female ampulla. Spent or worn female ampullae result in a cratered surface of semicircular depressions, the bases of which are quite spongy in texture (Fig. 5). Male ampullae much smaller, only 0.35–0.40 mm in diameter, occurring just beneath coenosteal surface but in concentrated masses, one often directly adjacent to another and thus outnumbering the cyclosystems. Male efferent pores not observed.

DISCUSSION: Stylaster gigas belongs to Stylaster (Group A) as defined by Cairns (1983a), species of which were previously assigned to the genus Allopora. Stylaster (Group A) is characterised by having: uniformly distributed cyclosystems; relatively few dactylopores per cyclosystem; robust gastrostyles and dactylostyles; and a branching mode. Cairns (1983a) listed 24 species in this group, which is cosmopolitan in distribution (5-1400 m) and known from the Miocene to Recent (Cairns 1992). Only two species in that group have massive coralla resembling that of S. gigas: S. miniatus (Pourtalès, 1868) and S. californicus (Verrill, 1866). S. miniatus, known only from the western Atlantic at 146-530 m (Cairns 1986), also has a similar coenosteal texture; long, tabulae-stabilised gastrostyles; and a similar number of dactylopores per cyclosystem (range 5-11, av. = 8.62), but differs in having larger, superficial female ampullae; larger internal male ampullae; and more delicate terminal branches. Some colonies of S. californicus, which is known from the eastern Pacific off California and Baja California at 10-53 m (Ostarello 1973, 1976), are just as massive as those of S. gigas,

Table 1 List of fossil Stylasteridae and Axoporidae known from the New Zealand region, arranged from geologically oldest to youngest.

Specimen	Age	Locality
*Errina sp.	Early Eocene (Waipawan-Bortonian)	Chatham Island (Waipapa Creek)
*Inferiolabiata sp. cf. I. labiata	Early Miocene (Otaian)	North Island (Pakaurangi Point)
Calyptopora sp. cf. C. reticulata (Stylaster sp. sensu Jones, 1970)	Early Miocene (Otaian)	North Island (Pakaurangi Point)
*Conopora sp. cf. C. laevis	Early Miocene (Otaian)	North Island (Pakaurangi Point)
Lepidopora sp. (Paraerrina sensu Squires, 1962)	Basal Miocene (Waitakian-Otaian)	South Island (Kakanui)
Axopora cleithridium (Squires, 1958)	Late Miocene (Kapitean)	South Island (Port Craig)
*Stylaster gigas, sp. nov.	Early Pliocene (Opoitian)	North Island (Kaawa Beach)
Sporadopora? mortenseni sensu Squires, 1962	Early Pliocene (Opoitian–Mangapanian)	North Island (Ruahine Range)
Sporadopora marginata	Late Pliocene	Chatham Rise (Pitt Island)

^{*}New records.

Previous reports of fossil Distichopora and Pliobothrus grantmackiei are now considered to be bryozoans.

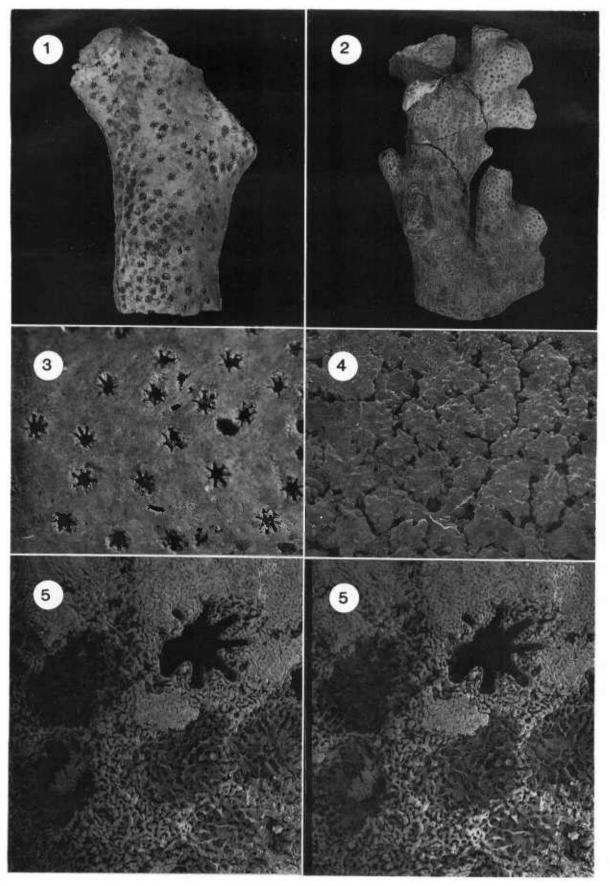


Fig. 1–5 Stylaster gigas. 1, Holotype (H1180), ×2.9 (branch height 26.6 mm). 2, Paratype (H1197), male colony, ×0.75 (colony height 105 mm). 3, Cyclosystems of holotype, ×7.5. 4, Reticulate coenosteal texture (paratype, USNM 91938), ×200. 5, Stereo view of a cyclosystem and several ruptured female ampullae (paratype, USNM 91938), ×27.

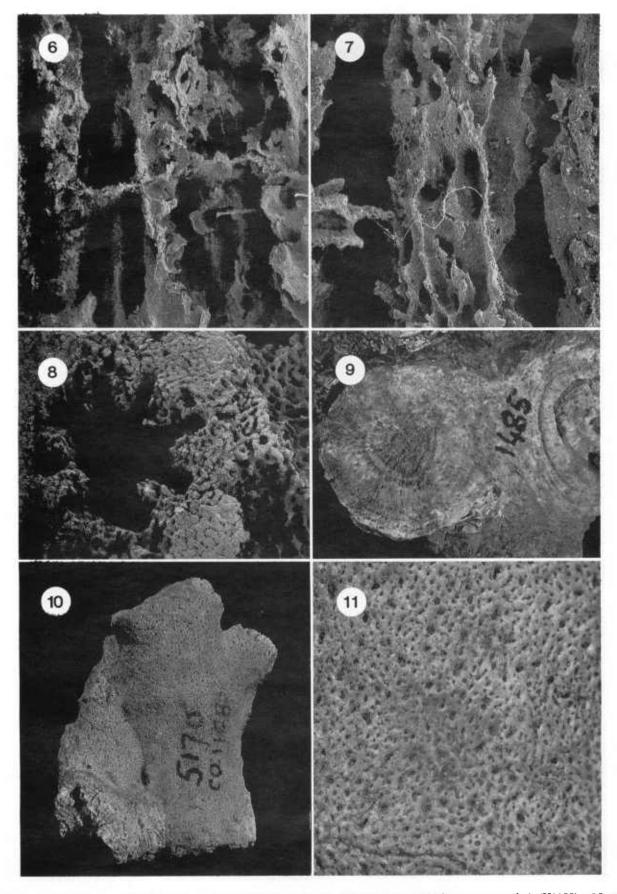


Fig. 6–8 Stylaster gigas. **6–7**, Mid-sections of elongate gastrostyles, Fig. 6 illustrating a stabilising transverse tabula (H1199), ×25, ×125, respectively. **8**, Cyclosystem (paratype, USNM 91938), ×50. **Fig. 9**, Sporadopora mortenseni of Squires (1962), Co 1327, ×1.9. **Fig. 10–11**, Axoporella cleithridium, holotype (Co 5170), colony (×2.3) and coenosteal texture (×7.5).

as well as having internal ampullae of the same size as those of *S. gigas. S. californicus* differs in having, on average, fewer dactylopores per cyclosystem (usually 4–6, rarely 8); a unique, papillose coenosteum; and rather short, squat gastrostyles.

MATERIAL EXAMINED: Holotype. 1 female branch fragment, H1180, from R13/f128 (S. Cairns, March 1991, AU12599). Paratypes. 16 branch fragments (6 female, 4 male, 6 indet.) from R13/f128 (S. Cairns, March 1991, USNM 91938); 14 branch fragments, H1181-H1194, 1199 from R13/ f128 (J. A. Grant-Mackie, March 1991, AU12599); 2 branch fragments, H614-H615, and 2 male colonies, H1197-H1198, from R13/f6027 (JAG-M, May 1962, AU8585); 1 colony and 1 branch fragment, H1195-H1196, from R13/f128 (JAG-M, May 1985, AU10304). Additional material seen but too poorly preserved to be included in type series: 37 branch fragments (JAG-M, May 1962, AU8585), and 1 branch fragment (JAG-M, May 1978, AU6925) from R13/f6027; 6 branch fragments (JAG-M, May 1985, AU10304), 1 large basal fragment (110× 110 × 85 mm, with pholad borings), 1 branch fragment (JAG-M, May 1987, AU10582), 32 branch fragments (JAG-M and N. Hudson, May 1988, AU11409, AU11411), and 3 branch fragments (JAG-M, May 1989, AU11950) from R13/f128.

TYPE FORMATION AND LOCALITIES: Kaawa Shellbed, Opoitian Stage, early Pliocene. R13/f128 (grid reference R13/646082), north end of Ngatutura Bay, Port Waikato area, North Island (type), and R13/f6027 (R13/647084), south end of Kaawa Beach, Port Waikato.

The two localities which yield this taxon are about 200 m apart. At both localities, the Kaawa Shellbed occurs in a cliff 10-15 m above the beach, and collections were made from fallen blocks. The first stylasterid specimens were collected from the more northerly location and their stratigraphic position within the 4 m thick shellbed was unknown, but in the mid 1980s, a large sliver of cliff fell, and in it the lower half of the shellbed retained its coherence and its relationship with the unconformably underlying lower Miocene strata. The basal pebbly, cobble-bearing shelly sandstone, about 20 cm thick, overlying a bored and cemented pavement cut on the Miocene rocks, was found to contain abundant stylasterids as well as a smaller, more delicate, arborescent scleractinian, Oculina virgosa Squires, and many other hard bottom organisms (e.g., barnacles, oysters, rock borers and nestlers, and brachiopods). Clearly, Stylaster gigas had been a prominent element in the basal Kaawa rocky bottom community for a brief period during the transgression that produced the Kaawa Formation. As transgression proceeded, this community migrated shoreward (eastward), and the area of the present coast became a sandy seafloor occupied by the rich molluscan fauna more typical of the Kaawa Shellbed.

DISTRIBUTION: Known only from the Kaawa-Ngatutura coast.

ETYMOLOGY: Latin gigas, giant; refers to its massive size.

Other fossil stylasterids known from the New Zealand region

Sporadopora marginata Tenison-Woods, 1880, from the late Pliocene of Pitt Island, Chatham Rise; and S. mortenseni Broch, 1942 (fide Squires 1962) (Fig. 9), from the Pliocene (Opoitian–Mangapanian) of the Rauhine Range, North Island, have growth forms similar to that of Stylaster gigas (thick,

bluntly tipped branches up to 2.8 cm in diameter) and also have internal ampullae, but can be differentiated by having uniformly arranged gastropores and dactylopores, not arranged in cyclosystems as in S. gigas. S. gigas also has dactylostyles; Sporadopora does not. The poor preservation of the type and subsequently collected specimens reported below, does not allow confident identification as S. mortenseni, originally described from the Recent of Three Kings Island at 119 m (syntypes deposited at Zoological Museum, Copenhagen). Additional specimens of North Island late Pliocene (Mangapanian) Sporadopora sp. are reported herein: five fragments (H909-H913) from strata of the Okiwa Group in a cutting on Parapara Road, Wanganui (\$22/f6537, AU1263, collected by J. A. Grant-Mackie and students, June 1963); and one colony fragment from the Komako Formation, on the south bank of Porewa Stream, Pohangina (T23/f6520, OU11051, collected by R. M. Carter, 1963).

Although technically not a stylasterid, Axopora cleithridium (Squires, 1958), the youngest representative of the calcified hydroid family Axoporidae, is known from four late Miocene (Kapitean) specimens from Port Craig, South Island. It also has a similar growth form to Stylaster gigas and Sporadopora: thick, bluntly tipped branches and long, slender gastrostyles. The holotype (Fig. 10) and three paratypes are deposited at the NZGS and USNM (see Cairns 1983b). A. cleithridium is distinguished from Sporadopora and Stylaster by lacking dactylopores (but does have unusually large coenosteal pores), by lacking ampullar cavities (its gonophores are assumed to have been superficial polyps), and by having a unique coenosteal texture composed of a reticulate maze of bifurcating and rejoining coenosteal strips separated by large coenosteal pores (Fig. 11).

The oldest stylasterid species to be reported (Squires 1962) from New Zealand was Paraerrina sp. from the Waitakian Gee Greensand (basal Miocene) at Kakanui. Cairns (1983a, p. 452) previously studied and commented on this unique specimen, expressing some doubt about its generic identification based on its lack of grooved dactylopores; it has, instead, a tendency for linearly arranged conical dactylopores (Fig. 13). Two Recent deep-water species have since been described from New Zealand that also have linearly arranged conical dactylopores: Lepidopora cryptocymas Cairns, 1985 and L. polystichopora Cairns, 1985. Examination of Paraerrina (OU6505) reported by Squires (1962) has convinced SDC that it is probably a species of Lepidopora not unlike the two recently described species. An additional South Island specimen is also reported (Fig. 12): one colony from the Waitakian-Otaian (early Miocene) Gee Greensand at All Day Bay (J42/f6937, OU9863, collected by J. D. Campbell and B. R. Patterson, October 1964).

An indeterminate species of *Distichopora* was reported by Squires (1962) from two middle–early Miocene localities; by Jones (1970) from numerous lower Miocene records at Pakaurangi Point, Kaipara, North Island; and by Hayward (1977) from Huia Stream, Waitakere Range, Auckland (lower Miocene). All of these specimens are bryozoans. The specimens of Squires (1962) are deposited at the NZGS; those of Jones (1970) and Hayward (1977) are at AU.

Another bryozoan misidentified as a stylasterid (see Cairns 1983a) was *Pliobothrus grantmackiei* Squires, 1965, from the Gee Greensand (Waitakian = basal Miocene), Kakanui, South Island. The holotype is AU H430, not the NZGS, as stated by Squires (1962). USNM 76870 contains topotypes. It is not without precedent to identify a bryozoan as

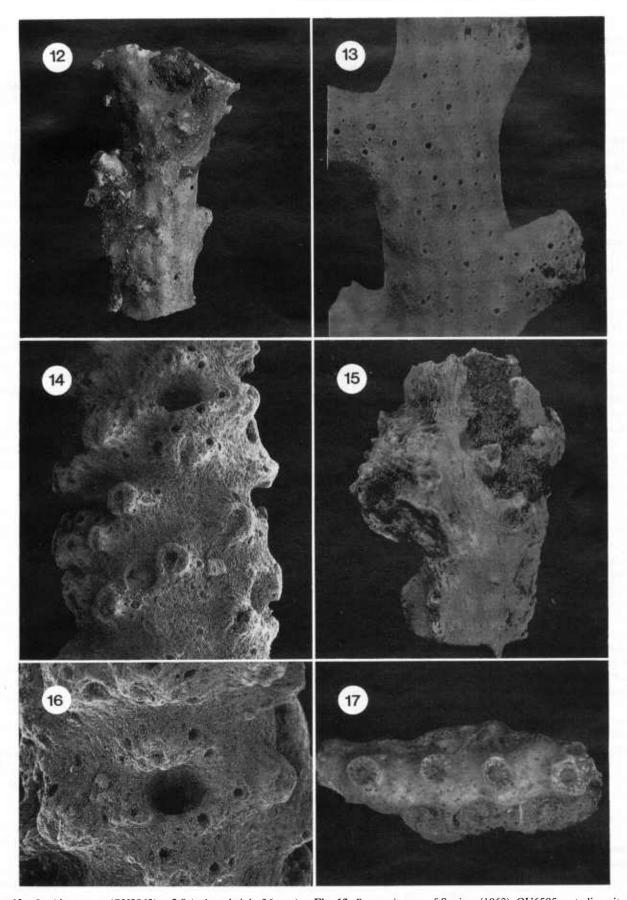


Fig. 12 *Lepidopora* sp. (OU9863), ×2.0 (colony height 36 mm). **Fig. 13**, *Paraerrina* sp. of Squires (1962), OU6505, note linearity of dactylopores, ×8.0. **Fig. 14**, **16**, *Errina* sp. (USNM 91940). **14**, Branch illustrating adcaulinc dactylopore spines and a gastropore, ×35. **16**, A gastropore surrounded by conical dactylopore spines, ×50. **Fig. 15**, *Inferiolabiata* sp. cf. *I. labiata* (H636), ×6.4 (colony height 12.5 mm). **Fig. 17**, *Conopora* sp. cf. *C. laevis* (USNM 91939), ×10.8 (branch length 6.9 mm).

a stylasterid, since these groups have many convergent structures. Another example is the stylasterid name *Leptobothrus spenceri* Hall, 1893, from the Miocene of Victoria, Australia, later correctly identified as the bryozoan *Porina gracilis* by Hall (1898). The reverse has also occurred: Zibrowius (1982) discussed four Recent stylasterids that were originally described as bryozoans.

Three fossil stylasterids are also reported from the early Miocene (Otaian) Pakaurangi Formation, Pakaurangi Point, Kaipara Harbour, North Island: Calyptopora sp. cf. C. reticulata Boschma, 1968; Conopora sp. cf. C. laevis (Studer, 1878); and Inferiolabiata sp. cf. I. labiata (Moseley, 1879). Calyptopora is represented by 18 small branch fragments in three collections. H632-H635 come from O08/f9847, a general collection made through the formation by J. A. Grant-Mackie and students, June 1963 (AU9180); H641-H642 (Q08/f9861) come from the Waiteroa Member, collected by B. G. Jones, 1966 (AU7019); and H643–H647 are from Q08/ f9872 in the Pakaurangi Member, collected by J. A. Grant-Mackie and students, June 1963 (AU7031). These specimens resemble C. reticulata in having a similar reticulate-granular coenosteal texture, cyclosystems of approximately the same diameter, and polychaete gall-tubes, which are invariably present on the Rccent species. The poor preservation of these specimens, however, does not allow a confirmation of the presence of cyclosystem lids or ampullar structures. Although not found at the University of Auckland, the four specimens listed by Jones (1970, p. 158) as Stylaster sp. and catalogued as AU H637-H640, are possibly the same species; they are also from the Waiteroa Member (Q08/f9860), collected by B. G. Jones, 1966 (AU7017). Recent C. reticulata is common on the Macquarie Ridge, Campbell and Bounty Plateaus, and Norfolk and Three Kings Ridges at depths of 216-2100 m (Cairns 1991).

Two small specimens of *Conopora*, one deposited at AU (H631, from Q08/f9847, in collection AU9180) and one at the USNM (91939), resemble *C. laevis*. Both specimens are small, the former having only three cyclosystems, the latter (Fig. 17) having four. Both specimens have sympodially arranged cyclosystems 0.7–0.8 mm in diameter; linearimbricate coenosteal texture including nematopores; and superficial female ampullae up to 1.1 mm in diameter. A longitudinal fracture of one cyclosystem revealed the characteristic double-chambered gastropore tube that lacks a gastrostyle. Whereas these specimens are most similar to *C. laevis*, their preservation and small size does not allow identification. *C. laevis* is common throughout the Indo-West Pacific at depths of 110–1035 m (Cairns 1991).

Inferiolabiata is represented by one small branch fragment (Fig. 15) 11.5 mm long (H636, from Q08/f9847, in collection AU9180, a general collection from the Pakaurangi Formation). It resembles *I. labiata* in having reticulate-imbricate coenosteal texture, several abcauline dactylopore spines, and a polychaete gall-tube. Dactylostyles and ampullar structure were not visible on this specimen, making identification uncertain.

Five small branch fragments of *Errina* sp.—the largest only 6.8 mm long and 1.25 mm in diameter—are reported from the Matanginui Limestone, Eocene (Waipawan–Bortonian: Ypresian–Wemmelian), 50 m north of the mouth of Waipapa Creek, Chatham Island (locality CH/f603, from collection GS14765, made by H. J. Campbell and P. A. Maxwell, March 1981) (Fig. 14, 16; USNM 91940). These specimens have gastropore diameters of 0.28–0.32 mm, some

of which appear to be bordered by a lower (abcauline) lip. Thick (0.25 mm wide), adcauline dactylopore spines and smaller (60 μ m diameter dactylopore) conical accessory spines occur uniformly over the coenosteum. One branch has superficial female ampullae 0.50 mm in diameter, with lateral efferent pores. Eleven Recent species of *Errina* are known from the New Zealand region (Cairns 1991), two of which are known from off Chatham Island: *E. cheilopora* Cairns, 1983, and *E. chathamensis* Cairns, 1991. The fragmentary Eocene specimens, although remarkably well preserved, do not allow for an accurate comparison or serve as a basis for a new species.

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