

**THE SPECIES OF ANTROPORA NORMAN, 1903 (BRYOZOA :
CHEILOSTOMATIDA), WITH THE DESCRIPTION OF A NEW GENUS IN
THE CALLOPOROIDEA**

KEVIN J. TILBROOK

Summary

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TILBROOK, K. J. 1998. The species of *Antropora* Norman, 1903 (Bryozoa: Cheilostomatida), with the description of a new genus in the Calloporoidea. *Records of the South Australian Museum* 31(1): 25–49.

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The cheilostomate bryozoan genus *Antropora* was introduced by Norman (1903b) for *Membranipora granulifera* Hincks, 1880a, described originally from Madeira. Norman (1903b) was clearly familiar with Hincks' species, noting that it was commonly dredged from shell gravel off Madeira, at depths of 70–100 fathoms. *Antropora granulifera* forms encrusting unilaminar sheets; autozooids display a simple morphology, with negligible gymnocyst, moderate cryptocyst and lack spines. Small interzooidal avicularia are present; embryos are brooded in endozooidal ovicells and interzooidal communication is achieved through basal pore chambers.

Harmer (1926) was the first modern authority to make use of *Antropora* Norman, describing *A. granulifera* from material collected in the Indo-Malaysian region by the 'Siboga' Expedition (1899–1900). Harmer reviewed published records of *Membranipora granulifera* Hincks, and showed its distribution to range from Madeira and the Cape Verde Islands (Calvet 1907), to the Red Sea (Waters 1898), Sri Lanka and southern India (Thornely 1905; 1912). *Membranipora marginella* Hincks, 1884, from the Mergui Archipelago, west Thailand and also recorded subsequently from the Red Sea (Waters 1898),

was also assigned to *Antropora* by Harmer (1926). Canu and Bassler (1929) published a generic diagnosis of *Antropora* based on the work of Hincks (1880a), Norman (1903b), and Harmer (1926) and reproduced their figures of the type species but did not list further records of it. Hastings (1930) reported both *A. granulifera* and *A. marginella* from various localities in the Panama Canal area.

Subsequent to Hastings (1930) *Antropora* and its type species have been ascribed an almost pantropical distribution and the taxonomic identity of both have become blurred. Additional confusion has been promoted by the introduction and usage of two similar genera, *Dacryonella* Canu and Bassler, 1917 and *Membrendoecium* Canu and Bassler, 1917. *Dacryonella* was introduced for the Eocene fossil *D. octonaria* Canu and Bassler, 1917, but Recent *D. typica* Canu and Bassler, 1928a, was later described from the Gulf of Mexico. In the same work Canu and Bassler (1928a) also described a new species, *Antropora pustulata*, which they stated differed from *A. granulifera* in the presence of an extensive gymnocyst, six distal spines, sporadic kenozooids and hyperstomial ovicells, all characters which demonstrate that this species clearly does not belong in *Antropora*. Later Canu and Bassler

(1929) described from the Philippines and assigned to the genus *D. minor* (Hincks, 1880b), *D. ogivalina* sp. nov., *D. trapezoides* sp. nov. and *D. subvespertilio* sp. nov. *Membrendoecium* was introduced for *Amphiblestrum papillatum* Busk, 1884, by Canu and Bassler (1917) who later (Canu and Bassler 1929) assigned to the genus *M. savarti* (MacGillivray, 1890), *M. ovatum* sp. nov., *M. lagunculum* sp. nov. and *M. japonicum* sp. nov. from the Philippines and *M. claustracrassum* from the Galapagos Islands (Canu and Bassler, 1930). Neither genus has won acceptance by subsequent authors although Marcus (1937) described *Membrendoecium leucocypha* sp. nov. from Curaçao. Silén (1941) placed *Membrendoecium* in the synonymy of *Antropora* and Osburn (1950) was unable to distinguish between *Antropora*, *Dacryonella* and *Membrendoecium*.

Cook (1968a) provided a diagnosis of *Antropora* and discussed the constitution of the genus and the work of the previous authors. She rejected *Membranipora nigrans* Hincks, 1882 and *Membranipora marginella* Hincks, 1884, both assigned to *Antropora* by Harmer (1926) and re-examined specimens attributed to both *A. granulifera* and *A. marginella* by Harmer, questioning the determinations of several of them. Cook (1968a) also noted the similarity between *Amphiblestrum papillatum* Busk, 1884, and *Membranipora trifolium* var. *minor* Hincks, 1880b, suggesting that they were congeneric.

The need for a review of the genus *Antropora* became apparent during the course of a current study of reef-associated bryozoans recently collected from Vanuatu, from Fiji and from several localities on the Great Barrier Reef. Specimens of a species attributed to *Antropora granulifera* by Ryland and Hayward (1992) were seen to be quite distinct from those figured by Ristedt and Hillmer (1985) as the same species and from those described by Cook (1968a) and Mawatari and Mawatari (1981). This paper redescribes *Antropora granulifera* (Hincks, 1880a) and stabilises the taxon through the selection of a neotype specimen. Type and original published material of all of the other species redescribed herein have been re-examined. Six species of *Antropora* are described and figured, including *Antropora erectirostra* new species. The new genus *Parantropora*, type species *Parantropora penelope* new species, is distinguished from *Antropora* by the lack of discernible dietellae, the presence of lateral-wall septula and the occurrence of very large spatulate

vicarious avicularia. The systematic status of the two genera is discussed in relation to several other speciose and taxonomically difficult calloporoidean families.

All material examined is listed; holding institutions are indicated by the following abbreviations: NHM – Zoology Department, The Natural History Museum, London; USNM – Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC.

SYSTEMATICS

The taxonomic order is based on that adopted by Hayward and Ryland (1995) as advocated by Gordon (1984; 1986; 1989). Generic and specific taxonomic diagnoses are given; the descriptions and measurements are based on the examined specimens. The synonymies for each taxon and lists of examined material are deliberately extensive due to the review nature of the paper.

Class Gymnolaemata Allman, 1856

Order Cheilostomatida Busk, 1852

Suborder Neocheilostomatina d'Hondt, 1985

Superfamily Calloporoidea Norman, 1903a

Genus *Antropora* Norman

Antropora Norman, 1903b: 87.

Antropora: Harmer, 1926: 232; Canu and Bassler, 1929: 93; Marcus, 1937: 50; Silén, 1941: 43; Osburn, 1950: 51; Cook, 1968a: 137; Mawatari and Mawatari, 1981: 25; Gordon, 1986: 37; Ryland and Hayward, 1992: 229.

Membrendoecium Canu and Bassler, 1917: 17.

Membrendoecium: Canu and Bassler, 1929: 28; Marcus, 1937: 124.

Dacryonella Canu and Bassler, 1917: 28.

Dacryonella: Canu and Bassler, 1928a: 56; Canu and Bassler, 1929: 130.

Generic diagnosis

Colony encrusting, unilaminar or multilaminar. Autozooidal cryptocyst moderately developed around the opesia, gymnocyst negligible or absent. Spines absent. Small interzooidal avicularia present. Large autozooidal-sized vicarious avicularia may be present. Ovicells endozooidal,

presence generally indicated by a slight cap-like thickening at the distal end of the autozoid. Basal pore-chambers (diatellae) present.

The vicarious avicularia are similar in size to autozooids; rostrum broadly triangular, narrowing distally, its lateral walls raised, projecting medially. Opesia of avicularium continuous, almost circular proximally, surrounded by a narrow granular cryptocyst, the junction with the distal part indicated by small proximally pointing condyles; distal part of opesia extending almost the entire length of the rostrum, a slight oral shelf is apparent distally; mandible wide, slightly pointed distally.

Type species

Membranipora granulifera Hincks, 1880a.

Remarks

Much of the confusion surrounding the identity of the type species, *Membranipora granulifera* Hincks, seems to stem from Harmer's (1926) account, which was clearly based on several different species. Neither Hincks (1880a) nor Norman (1903b) described colony form in *Antropora granulifera* and both considered that it was morphologically variable, but there is no doubt that they described the same species. Canu and Bassler (1929) reproduced Hincks's (1880a) original figure, as well as those of Norman (1903b) and Harmer (1926), adding a magnification to that of Hincks, but there is no indication that they examined any of the material described by these authors. The lack of any acceptable type material of *M. granulifera* certainly contributed to the confusion surrounding its taxonomic identity and selection of a neotype (see below) to stabilise the taxon will finally resolve the problem.

The interzooidal avicularia of *A. granulifera* are the most distinctive feature of the species and the most distinctive of any species of *Antropora*. Both Hincks (1880a) and Norman (1903b) gave unambiguous descriptions, noting that their position at the distal corners of the autozooids, with rostra directed medially and almost touching at their distal tips, was constant in all the specimens they examined. Of recent authors, only Ristedt and Hillmer (1985) have noted this feature and correctly identified their material. Harmer (1926) based his description on a suite of specimens from the 'Siboga' expedition, around the Philippines and Indonesia, and on specimens from Ceylon and Japan in the collections from the Zoology Museum, Cambridge. He noted that

'adventitious' avicularia were directed distally or transversely and although he stated that three of the specimens he examined (NHM 1928.3.6.47., Mindanao; NHM 1928.3.6.48., Kei Islands; NHM 1936.12.30.5., Ceylon) agreed with Hincks's original description of *A. granulifera*, and are clearly the same species, he included other specimens which are not actually attributable to *A. granulifera*. Harmer (1926) described these latter specimens with vicarious avicularia, including those from Japan (NHM 1928.9.13.16,17.) as 'young type' colonies, which in fact are attributable to *A. typica*.

Although Mawatari and Mawatari (1981) describe and figure vicarious avicularia in *Antropora granulifera*, no evidence of these structures can be seen in either the Neotype specimen or other specimens of *A. granulifera sensu stricto*. Despite *A. granulifera* itself not producing vicarious avicularia, several other species of *Antropora* do and the generic diagnosis has been amended to take account of this fact.

Gordon (1986) amended the generic description of *Antropora* to include *Antropora pacifera* sp. nov. from New Zealand. However, this species appears to be a member of the genus *Alderina* and so the generic amendment should not be accepted.

Several Recent species allegedly attributable to *Antropora* Norman have not been covered in this paper, mainly due to the lack of type material available for examination; these are as follows:

Dacryonella levigata Canu and Bassler, 1927: 6, pl. 2, figs 7,8.

Membrendoecium compressum Osburn, 1927: 124, figs 1,2; Osburn, 1940: 358 (as *Canua* (*Membrendoecium*) *compressum*).

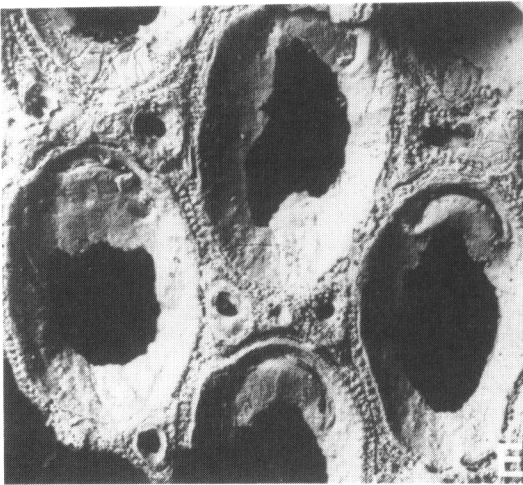
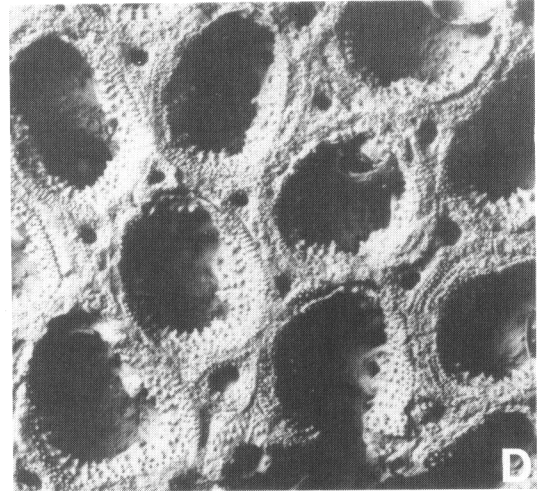
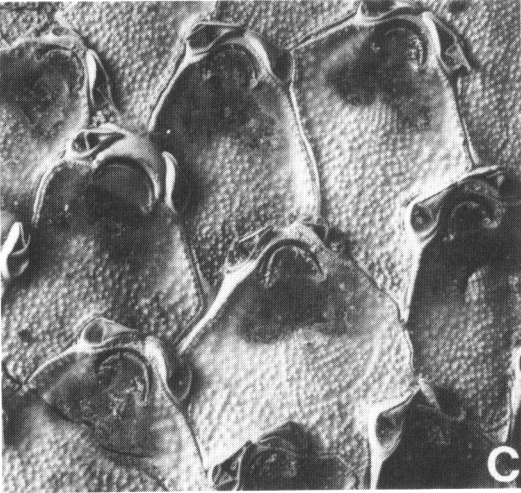
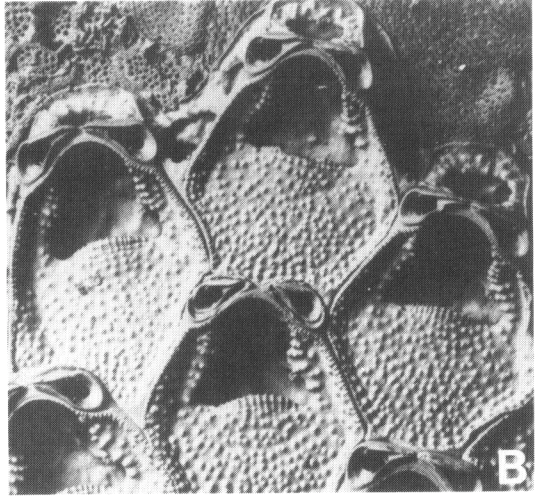
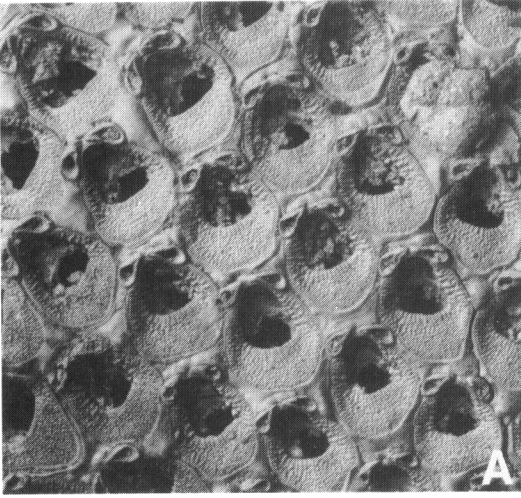
Membrendoecium parvum Canu and Bassler, 1928b: 4, 61, pl. 1, figs 1,2.

Crassimarginatella leucocypha Marcus, 1937: 46, pl. 8, fig. 20 A; pl. 9, figs 20 B,C; Rucker, 1967: 819, fig. 12c (as *Antropora leucocypha*); Mawatari and Mawatari, 1981: 29, fig. 3 (as *Antropora leucocypha*).

Antropora erecta Silén, 1941: 44, figs 56, 57; Mawatari and Mawatari, 1981: 27, fig. 1.

Antropora granulifera (Hincks, 1880a)
(Fig. 1A)

Membranipora granulifera Hincks, 1880a: 72, pl. 9, fig. 4.



Membranipora granulifera: Waters, 1898: 659, 668; Thornely, 1912: 143.

Amphiblestrum granulifera Thornely, 1905: 110.

Antropora granulifera Norman, 1903b: 87, pl. 8, fig. 4.

Antropora granulifera: Harmer, 1926: 232 (in part), pl. 14, figs 11–14; Hastings, 1930: 714; Osburn, 1940: 358; Osburn, 1950: 52, pl. 9; Cook, 1968a: 138, fig. 9; Cook, 1968b: 149; Mawatari and Mawatari, 1981: 28 (in part), fig. 2; Ristedt and Hillmer, 1985: pl. 1, fig. 3; Cuffey, 1987: 506, fig. 168.

not *Antropora granulifera*: Ryland and Hayward, 1992: 229, fig. 2c.

Dacryonella trapezoides Canu and Bassler, 1929: 133, pl. 14, figs 2,3.

Material examined

Neotype, here chosen: NHM 1919.6.25.23., Madeira, Norman Coll.

Other material examined: NHM 1919.6.25.24., Madeira, Norman Coll.; NHM 1879.5.28.6., Madeira, Rev. R. B. Watson; NHM 1879.5.28.11., Madeira, Rev. R. B. Watson; NHM 1911.10.1.628., Madeira, 25–70 feet; NHM 1882.10.18.125–138., Darros Id, Amirante Is, 22 fathoms, HMS Alert; NHM 1903.1.29.10,11., Fuafatu, Funafuti, 60 fathoms; NHM 1928.3.6.47., Siboga Stn 133, Lirung, Talaut Is, S. of Mindanao. 0–36m; NHM 1928.3.6.48., Siboga Stn 257, Kei Is, 0–52m; NHM 1928.9.13.15., Ceylon (Sri Lanka); NHM 1929.4.26.81., Jicaron Islands, St George Coll.; NHM 1936.12.30.5., Ceylon (Sri Lanka), L. R.

Thornely; NHM 1970.8.4.23., Calypso Coll., Stn P.7, 6m; NHM 1997.10.6.4., Iririki Island, Vanuatu; USNM 7936., (Cotypes of *D. trapezoides*. 2 pieces) Alb. Sta. 5151, off Sirun Id, Tawi-tawi Is, Philippines. 24 fathoms; NHM 1931.12.30.43,44., (Topotype of *D. trapezoides*.) Alb. Sta. 5151, off Sirun Id, Tawi-tawi Is, Philippines. 24 fathoms. (exc. USNM).

Description

Colony forming flat, unilaminar sheets. Autozooids irregularly polygonal to hexagonal in fairly distinct alternating longitudinal rows, separated by discernible grooves. Frontal surface bordered by a crenulated mural rim, raised particularly to the distal end of the autozooid. Gymnocyst proximal, very reduced or negligible; cryptocyst occupying generally less than one half of total autozooid length, flat or very slightly convex, coarsely beaded. Opesia roughly triangular to slightly trifoliate, constricted at the proximal edge of the operculum opening. Distal to each autozooid a pair of medium-sized triangular, interzooidal avicularia. Rostra raised and acute to frontal plane, directed medially, often touching at the midline, or rarely very slightly disto-medially, particularly in ovicellate zooids; mandibles long and acutely triangular. Ovicell endozooidal, small, indistinct.

Mature dried colonies are chocolate brown in appearance, lighter and more translucent at the growing edge. The opercula are slightly darker than the rest of the frontal membrane. Cook (1968a) describes the opercula of fertile zooids as showing a slight dimorphism, i.e. wider and darker in colour than other autozooids.

FIGURE 1. A, *Antropora granulifera* (Hincks, 1880a), Neotype specimen NHM 1919.6.25.23., Madeira. Group of autozooids. x27. B, *Antropora subvespertilio* (Canu & Bassler, 1929), NHM 1912.12.22.12., Grapples Bank, Puerto Rico. Group of autozooids at the growing edge of the colony with paired distal avicularia and trifoliate opesia. x72. C, *Antropora subvespertilio* (Canu & Bassler, 1929), NHM 1912.12.22.12., Grapples Bank, Puerto Rico. Group of zooids with frontal membrane intact, note the wider operculum in the ovicellate zooids. x45. D, *Antropora tinctoria* (Hastings, 1930), Paratype specimen NHM 1929.4.26.72., Gorgona, Colombia. Group of autozooids, the interzooidal angles filled with either small rounded kenozooids or small interzooidal avicularia. x63. E, *Antropora tinctoria* (Hastings, 1930), Paratype specimen NHM 1929.4.26.72., Gorgona, Colombia. Group of autozooids, showing the size of the interzooidal kenozooids and avicularia and zooidal opercula. x108. F, *Antropora typica* (Canu & Bassler, 1928a), NHM 1928.9.13.16., Okinose, off Tokyo, Japan. Group of autozooids showing the position of the teardrop-shaped interzooidal avicularia and the extensive gymnocyst. x63.

Measurements (mm): mean±standard deviation

Specimen	n	Autozoid Length	Autozoid Width	Opesial Length	Opesial Width	Avic. Length
NHM 1919.6.25.23. Neotype.	25	0.56±0.06	0.41±0.03	0.28±0.05	0.23±0.06	0.16±0.05
Cook (1968a)	–	0.40–0.58	0.27–0.40	0.20–0.32	–	0.11–0.15
C and B (1929) (<i>D. trapezoides</i>)	–	0.55	0.45	0.20–0.22	0.20–0.25	–
NHM 1997.10.6.4.	25	0.60±0.08	0.52±0.06	0.30±0.02	0.26±0.06	0.14±0.02

Remarks

Antropora granulifera is especially characterised by the presence of two medially directed avicularia, often touching at the midline, at the distal end of every autozoid. *A. granulifera* has been reported from the warm-temperate eastern Atlantic, from the tropical eastern Pacific and from numerous localities in the Indo-West Pacific, but the taxonomic identity of the species has not been adequately reviewed.

Hincks's (1880a) description of this species is very accurate, but seems to have been overlooked by subsequent authors. Harmer's (1926) later account of *A. granulifera* seems to have caused confusion; many of the specimens he described clearly do not belong to this species, as noted by Powell (1967) and Cook (1968a). For the stabilisation of the taxon, and in the absence of the original holotype specimen, there is justification in selecting a neotype specimen, from Madeira, the type locality. No extant specimens are known from the collection of T. H. Hincks, but a Norman Collection specimen from Madeira, NHM 1919.6.25.23., is clearly the same species as that figured by Hincks (1880a) and is accordingly here selected as neotype.

Canu and Bassler (1917) erected a new genus *Dacryonella*, and later (Canu and Bassler 1929) described *D. trapezoides* sp. nov. from the Philippines; examination of type series material of *Dacryonella trapezoides* shows it to be indistinguishable from *Antropora granulifera*. (The USNM cotype specimens are heavily calcified and very abraded, but have very similar proportions to the neotype specimen of *A. granulifera*.)

Cook (1968a) examined *A. granulifera* specimens from the Canary Islands and several stations off West Africa and was confident that this material represented a single species, noting that in all characters other than size it was similar to material from the Indo-Pacific; material from the Indo-Pacific having larger zooids than that from Panama, Madeira and West Africa.

The account of *A. granulifera* by Mawatari and Mawatari (1981) and their fig. 2, leaves a certain doubt as to the true identity of the specimens they were describing. They described the presence of vicarious avicularia, illustrating a mandible, and the interzooidal avicularia are far smaller relative to the size of the autozoid, than in specimens of *A. granulifera* examined here. Two specimens from Japan (NHM 1928.9.13.16,17.) and one from Malaysia (NHM 1928.3.6.49.), in the Natural History Museum, London, formerly referred to *A. granulifera* are here regarded as belonging to *A. typica* (below). Two further specimens, from Aden (NHM 1966.1.2.3.) and Muscat (NHM 1981.2.6.1.) respectively, contain shell debris which shows no evidence of *A. granulifera*, but instead is encrusted by a mixture of *A. tincta* and *A. minor*. The species figured by Ryland and Hayward (1992) is not *A. granulifera*; however, as their specimen has not been available for examination, no specific designation can be given.

Norman (1903b) describes and figures three pairs of dietellae and several, usually four, 'lucid spots' in the basal wall, similar to those seen in *A. typica*.

Distribution

Madeira; Cape Verde Is; Indian Ocean; Ceylon (Sri Lanka); Malaysia; Philippines; Iririki Island, Vanuatu; Hawaii; Jicaron Id, Panama; Secas Is, Panama; Gulf of Panama; Petatlan Bay, Mexico; Puerto Rico; Bermuda.

This species is found in warm temperate and tropical waters globally. The record from Japan must be considered unsubstantiated.

Antropora subvespertilio (Canu and Bassler, 1929)
(Fig. 1B,C)

Dacryonella subvespertilio Canu and Bassler 1929: 134, pl. 14, fig. 1.

Measurements (mm): mean±standard deviation

Specimen	n	Autozoid Length	Autozoid Width	Opesia Length	Opesia Width	Avic. Length
C and B (1929)	–	0.35	0.40–0.45	0.19	0.11	–
<i>D. subvespertilio</i>						
NHM 1912.12.22.2.	30	0.53±0.06	0.43±0.04	0.22±0.02	0.18±0.01	0.15±0.01

Material examined

Holotype: USNM 7937, Alb. Sta. 5179, off Romblon Light, Romblon, Philippines, 37 fathoms.

Other material examined: NHM 1912.12.22.2. (as *Antropora granulifera*), Grapples Bank, SE corner of Puerto Rico, 124–142 fathoms.

Description

Colony unilaminar, encrusting. Autozooids distinct, broad, separated by shallow grooves. Frontal membrane bordered by thin, rounded mural rim. Gymnocyst negligible; cryptocyst, extensive, below mural rim, finely granular, somewhat convex. Opesia trifoliate, less than half frontal area, the proximal border convex with two lateral opesiular indentations, rather deep and rounded, with crenellate edges. Distal to each autozoid, two small, triangular interzooidal avicularia, directed medially, often touching, or slightly disto-medially, particularly in ovicellate zooids; rostrum slightly raised, acutely pointed distally, rounded proximally; two small articulatory condyles; mandibles acutely triangular, slightly recurved. Ovicells endozooidal, small, smooth, cap-like. Operculum of ovicellate zooids wider than autozooids, closing the ovicell.

Remarks

Antropora subvespertilio, originally described from the Philippines, is easily identified by the presence of the two medially directed avicularia distal to each autozoid and the possession of lateral, opesiular indentations of the cryptocyst, giving the characteristic trifoliate opesia.

Specimen NHM 1912.12.22.2., from Puerto Rico, originally assigned to *A. granulifera*, is undoubtedly the above species when compared with the type specimen from the Philippines. This mistaken attribution is understandable as in the dried specimen of *A. subvespertilio* the shape of the opesia is hidden by the opaque frontal membrane.

Distribution

Philippines and Puerto Rico.

Antropora tincta (Hastings, 1930)

(Fig. 1D,E)

Crassimarginatella tincta Hastings, 1930: 708, pl. 5, figs 16–19; pl. 17, fig. 120.

Antropora tincta Osburn, 1950: p. 54, pl. 4, fig. 7; pl. 29, figs 7,8.

Antropora tincta: Cook, 1968a: 140, fig. 11; Cook, 1968b: 150; Mawatari and Mawatari, 1981: 34, fig. 4; Hayward, 1988: 276, fig. 2f.

Material examined

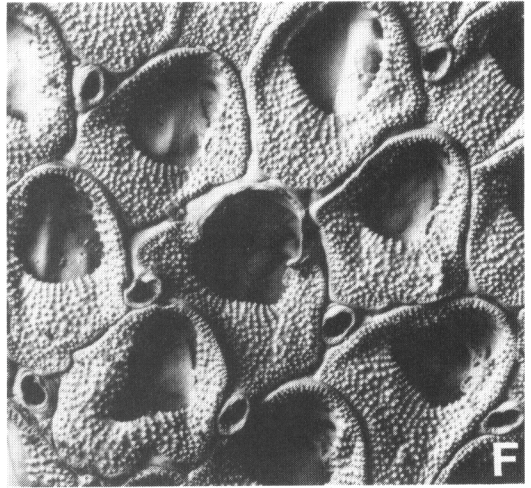
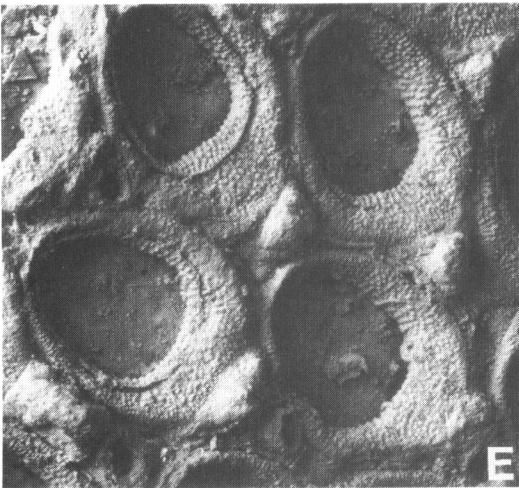
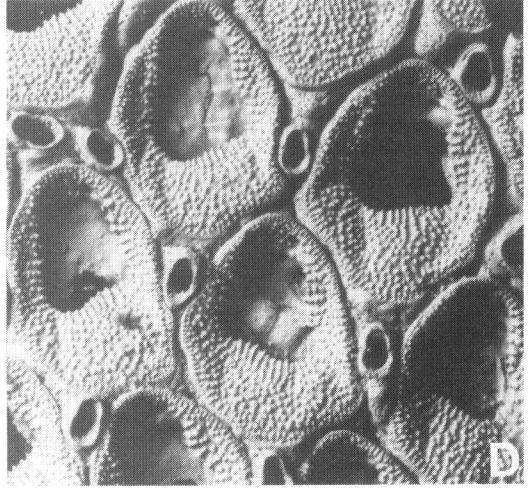
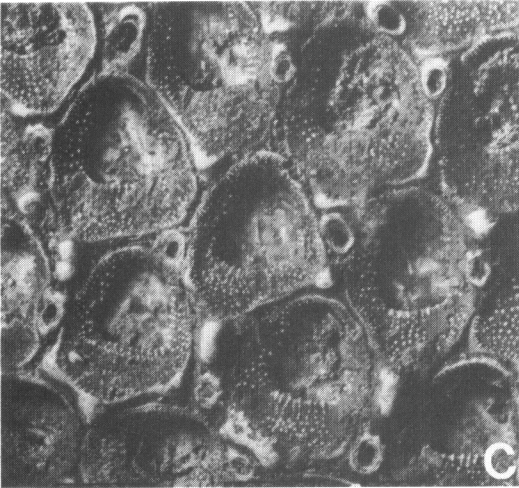
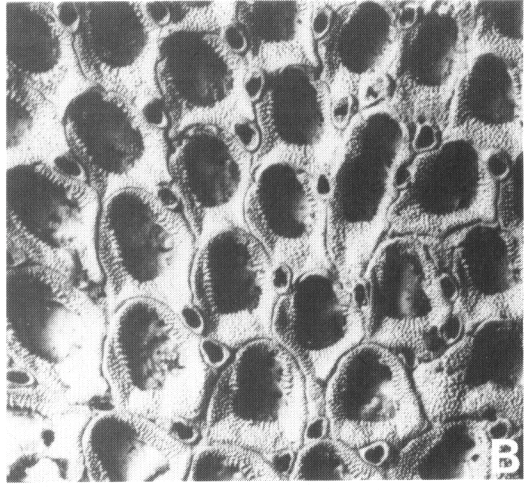
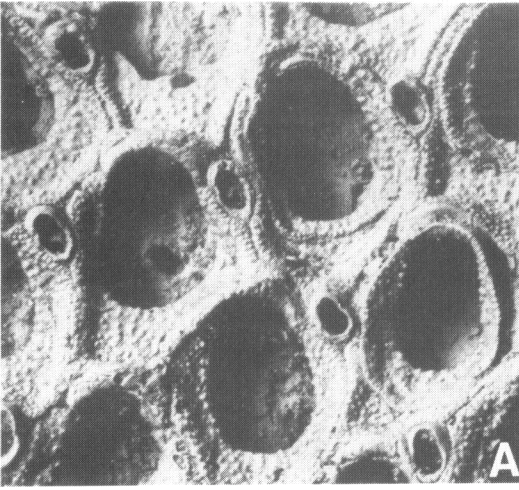
Paratype: NHM 1929.4.26.72. (part), Gorgona 3, St. George Coll. (Figured by Hastings 1930: fig. 120.)

(Holotype specimen NHM 1929.4.26.28. Galapagos Stn 9A, cited by Hastings (1930), cannot be located.)

Other material examined: NHM 1930.9.18.1., Puntas Arenas, Central America; NHM 1966.3.2.2., East of Angel de Guardia Id, Gulf of California, 40 fathoms; NHM 1966.9.2.6. (in part) (as *Antropora* sp.), Massawa Harbour, Red Sea coast of Ethiopia, N. A. Powell; NHM 1970.2.8.7., Teshie Rocks, E of Accra, 1–2m. Coll. W. Pople; NHM 1970.8.10.19., SE of Tema, Ghana. Coll. W. Pople; NHM 1975.9.10.7–9., South Seymour Id, Galapagos Islands; NHM 1992.1.23.17., Tamarin, Mauritius; NHM 1961.11.2.53. (as *Crassimarginatella leucocypha*), Campeche Bank, Gulf of Mexico, 24°4'N, 91°51'W, 26 fathoms. Coll. A. Cheetham.

Description

Colony encrusting, multilaminar. Autozooids distinct, irregularly oval, with thin mural rim. Gymnocyst vestigial; cryptocyst, narrow, granular, concave, thicker proximally, inner margin sometimes denticulate. Opesia almost filling entire frontal area. Interzooidal angles with either small rounded kenozooids or small interzooidal avicularia; mandible semi-circular to triangular with a rounded tip, no crossbar, but condyles are present. Endozooidal ovicells, forming rather shallow caps on autozooids, are described by Mawatari and Mawatari (1981). Colour, when alive or dried, ranging from white to light pink to pinkish-brown with increasing age and calcification.



Measurements (mm): mean±standard deviation

Specimen	n	Autozoid Length	Autozoid Width	Opesial Length	Opesial Width	Avic. Length
NHM 1929.4.26.72. Paratype.	30	0.37±0.07	0.28±0.03	0.28±0.03	0.17±0.02	—
Cook (1968a)	—	0.35–0.52	0.29–0.36	0.19–0.34	—	0.06–0.13
M and M (1981)	—	0.3–0.5	0.2–0.4	0.2–0.4	0.1–0.2	—

Remarks

The most characteristic features of this species are the presence of kenozooids, its often multilaminar nature and its pinkish coloration even when dried. Osburn (1950) noted that colonies may develop erect irregular branches (to 50mm high) particularly when in association with gastropods shells inhabited by pagurid crabs. The dry sectioned specimen (NHM 1966.3.2.2.) from the Gulf of California shows well the multilaminar form of *A. tincta*, as well as its pinkish coloration.

Marcus (1937) described *Crassimarginatella leucocypha* sp. nov. from Brazil, distinguishing it from *A. tincta* by the frequency of kenozooids, the size of the interzooidal avicularia and the shape of their mandibles. Hastings (1930) remarked that some colonies of *A. tincta* have no avicularia whilst in others they are very frequent, a feature noted in *Antropora leucocypha* by Winston (1982). The distinction between the two species has been maintained subsequently, although Cook (1968a) and Winston (1982) both noted the similarity between *A. leucocypha* and *A. tincta*, but there has been no recent redescription of Marcus' species and his type material has not been available for study. Winston's (1982) figures 36 and 37, appear to show two different species though she attributes them to smaller (younger?) and larger colonies, respectively. Specimen NHM 1961.11.2.53. from the Gulf of Mexico, was originally attributed to *Crassimarginatella leucocypha*, but is undoubtedly *A. tincta*. (NHM 1986.8.14.9. as *Antropora leucocypha*, from Fort Pierce, Florida, is a specimen of *Antropora*

minor.) *Crassimarginatella leucocypha* Marcus, 1937, may perhaps prove to be a junior synonym of *A. tincta* (or *A. minor*), but in the absence of accessible holotype material this question cannot be satisfactorily addressed. Rucker (1967) figured as *Antropora leucocypha* a species which looks like neither of the two London specimens mentioned above. Mawatari and Mawatari (1981) figured specimens attributed to *A. leucocypha* and *A. tincta* from Japan which appear to be indistinguishable both in shape and size, although they differentiated between the two species on the basis of the form, size and occurrence of avicularia. In their description of *A. leucocypha*, Mawatari and Mawatari (1981) noted vicarious avicularia as large as the autozooids; these were illustrated in their figure 3, but appear to be regenerated autozooids, showing two cryptocystal rims, rather than vicarious avicularia as described.

A. tincta has a morphology not unlike that of species of the genus *Akatopora* Davis, 1934, as discussed by Gordon (1986); future investigations of *Akatopora* species may remove *A. tincta* from the genus *Antropora* Norman.

Distribution

Galapagos Islands; Point Conception, California; Gulf of California; Peru; Mazatlan, Mexico; Jicaron Islands, Panama; Gorgona Islands, Colombia; Gulf of Mexico; Balboa, Brazil; Ghana, West Africa; Mauritius; Japan.

This species has been recorded from tropical and subtropical regions of the E. Pacific, W.

FIGURE 2. *Antropora minor* (Hincks, 1880b). A, Holotype specimen NHM 1899.5.1.654., Bahia, Brazil. Group of zooids, two ovicellate zooids to the left of frame. x108. B, NHM 1885.12.24.13., (Holotype specimen of *A. marginella* Hincks, 1884), Mergui Archipelago. Group of zooids (including ovicellate zooids) showing the coarsely granular cryptocyst and lack of gymnocyst. x54. C, NHM 1888.4.16.9., Fernando Noronha, Brazil. Group of autozooids showing the raised avicularia and kenozooidal papillae. x72. D, NHM 1887.12.9.327. (Type specimen of *A. papillatum* Busk, 1884), 'Challenger' Stn 208, the Philippines. Group of autozooids showing the granular cryptocyst, minimal gymnocyst and raised avicularia. x90. E, NHM 1931.12.30.17. (as *Membrendoecium ovatum* Canu & Bassler, 1929), off Sirun Island, Tawi-tawi Islands, Philippines. Group of autozooids showing kenozooidal papillae and evidence of regenerative growth. x72. F, NHM 1997.10.6.2., Suva Barrier Reef, Fiji. Group of autozooids showing the positioning of the small interzooidal avicularia, and shape and size of a large vicarious avicularium (centre). x63.

Atlantic, W. Africa and Japan but has not been reported from the SW Pacific.

The following species form a distinct group within the genus *Antropora* Norman, 1903b due to the presence of large vicarious avicularia as well as small interzooidal avicularia common to all members of the genus. The vicarious avicularia are extremely similar in form in all these species, however, their occurrence, and the regularity and form of the small interzooidal avicularia differ greatly.

Antropora minor (Hincks, 1880b)
(Fig. 2A–F)

Membranipora trifolium var. *minor* Hincks, 1880b: 87, pl. 11, fig. 6.

Membranipora trifolium var. *minor*: Hincks, 1885: 147, pl. 8, fig. 7; Robertson, 1921: 47; Waters, 1906: 14.

Dacryonella minor Canu and Bassler, 1929: 131, pl. 13, figs 9–12.

Membrendoecium minus Marcus, 1937: 50, pl. 9, fig. 22 A,B.

Antropora minus Cook, 1968a: 139, fig. 10; Mawatari and Mawatari, 1981: 34.

Amphiblestrum papillatum Busk, 1884: 66, pl. 3, fig. 1.

Membranipora papillata Waters, 1898: 668, 682.

Antropora papillatum Thornely, 1905: 110.

Membrendoecium ovatum Canu and Bassler, 1929: 95, pl. 6, figs 3–5.

Antropora ovata Cuffey and Cox, 1987: 86, fig. 2H.

Dacryonella ogivalina Canu and Bassler, 1929: 132, pl. 13, fig. 8.

Antropora ogivalina Scholz, 1991: 280, fig. 4.

Membrendoecium claustracrassum Canu and Bassler, 1930: 7, pl. 1, figs 3–7.

Antropora claustracrassa Osburn, 1950: 50, pl. 4, fig. 6.

Antropora claustracrassa: Cuffey and Cox, 1987: 86.

Membranipora marginella Hincks, 1884: 358, pl. 13, fig. 1; Hincks, 1893: 204; Waters, 1898: 658, 669.

not *Amphiblestrum marginella* Thornely, 1905: 110.

Antropora marginella Harmer, 1926 (in part): 234; Hastings, 1930: 714; Powell, 1967: 164, pl. 1, fig. 5.

Material examined

Holotype: NHM 1899.5.1.654., Bahia, Brazil. Hincks Coll.

Other material examined: NHM 1888.4.16.9., Fernando Noronha, Brazil; NHM 1931.12.30.41., Alb. Sta. 5151, off Sirun Island, Tawi-tawi Islands, Philippines. 24 fathoms. (exc. USNM); NHM 1992.1.23.17., Tamarin, Mauritius; NHM 1975.18.70. (as *Antropora* sp.), Tungku Beach, Dent Peninsula, NE Sabah; NHM 1975.18.71.72. (as *Antropora* sp.), East coast of Labuan Id, Sabah; NHM 1966.9.2.6. (in part) (as *Antropora* sp.), Massawa Harbour, Red Sea coast of Ethiopia, N. A. Powell; NHM 1887.12.9.327. (2 slides.) (Type of *Amphiblestrum papillatum*), 'Challenger' Stn 208, near the Philippines. 11°37'N., 123°31'E. 18 fathoms, blue mud; USNM 7935 (Type of *Dacryonella ogivalina*), Alb. Sta. 5147, off Sulade Id, Sulu Arch., Philippines. 21 fathoms; NHM 1931.12.30.42. (as *Dacryonella ogivalina*), Alb. Sta. D5217, Anima Sola Id, Ragay G., off N. Burias, Philippines. 13°20'N., 123°14'15"E. 105 fathoms. (exc. USNM); USNM 8472 (Cotype of *Membrendoecium claustracrassum*, 2 pieces), Alb. Sta. D2813. Galapagos Is 40 fathoms; NHM 1933.12.10.10. (as *Membrendoecium claustracrassum*), Alb. Sta. D2813. Galapagos Is 40 fathoms. (exc. USNM); USNM 7867 (Cotype of *Membrendoecium ovatum*, 2 pieces), Alb. Sta. 5137, Julo, Philippines. 20 fathoms; USNM 7868 (Cotype of *Membrendoecium ovatum*, 2 pieces), Alb. Sta. 5179, off Romblon Light, Romblon, Philippines. 37 fathoms; NHM 1931.12.30.16. (as *Membrendoecium ovatum*), Alb. Sta. 5179, off Romblon Light, Romblon, Philippines. 37 fathoms. (exc. USNM); NHM 1931.12.30.17. (as *Membrendoecium ovatum*), Alb. Sta. 5151, off Sirun Island, Tawi-tawi Islands, Philippines. 24 fathoms. (exc. USNM); NHM 1931.12.30.41. (as *Dacryonella minor*), Alb. Sta. 5151, off Sirun Island, Tawi-tawi Islands, Philippines. 24 fathoms. (exc. USNM); NHM 1885.12.29.13. (Syntype of *Antropora marginella*), Mergui Archipelago (off Thailand), Burma (Myanmar), India. Dr. Anderson Coll.; NHM 1899.5.1.602. (Syntype of *Antropora marginella*), Mergui Archipelago (off Thailand), Burma (Myanmar), India. Hincks Coll.; NHM 1997.10.6.2., Suva Barrier Reef, Fiji; NHM 1997.10.6.19., Suva Barrier Reef, Fiji. Reef Crest; NHM

1997.10.6.25., Tailevu Point, Viti Levu, Fiji; NHM 1997.10.6.26., Suva Barrier Reef, Fiji.

Description

Colony encrusting, multilaminar. Autozooids oval, bordered by a distinct, thin mural rim, separated by deep grooves, often wide. Gymnocyte generally minimal; cryptocyst coarsely granular, concave, deeper proximally than laterally, sloping basally. Opesia large, broadly oval or sub-triangular, narrowing distally, occupying over half of the frontal area. Single small interzooidal avicularia, elongate, rounded, mostly distally directed; mandible rounded or more acute, triangular, no crossbar; a cryptocystal rim around avicularium opesia; avicularium raised on small cystid (papillary eminences) seated in the angular interzooidal spaces. Small kenozooidal papillae are also often found at the proximal ends of autozooids in the interzooidal angles either in place of or in conjunction with the avicularia. Ovicells endozooidal, vestigial, indistinct, cap-like. The large autozooid-sized vicarious avicularia described above are often present, although they may be absent from large areas of some colonies; rostrum broadly triangular, its lateral walls raised.

Remarks

Antropora minor is characterised by the lack of a gymnocyte, the interzooidal avicularia on raised

cystids, papillae-like kenozooids found proximally to the autozooids, and the presence of large vicarious avicularia. However, the frequency and spacing of both the kenozooids and the vicarious avicularia vary greatly between colonies.

The presence of small kenozooids in *A. minor* is unusual in *Antropora* and is seen otherwise only in *A. tincta*. These two species are multilaminar, and kenozooids may reflect discontinuities in colony form associated with multilayered growth. Canu and Bassler (1929) in their discussion of *Membrendoecium ovatum*, state that while autozooidal regeneration is common in *Antropora* (*Membrendoecium*) species, it is extraordinarily frequent in this species (e.g. NHM 1931.12.30.17.); the presence of kenozooids may perhaps indicate or facilitate regenerative growth.

The synonymy of *Membranipora trifolium* var. *minor* Hincks and *Amphiblestrum papillatum* Busk was first proposed by Waters (1898; 1909) but rejected by Marcus (1937). Cook (1968a) commented on the similarity of *A. minor* with *A. papillatum*, but distinguished the two species on size, autozooids of *A. papillatum* being larger than those of *A. minor*.

Canu and Bassler (1929) remarked on the great resemblance of their new species, *Dacryonella ogivalina* to *Antropora minor* (Hincks, 1880b) but concluded that they were separate species due to the greater autozooidal dimensions of *D.*

Measurements (mm): mean±standard deviation

Specimen	n	Autozooid Length	Autozooid Width	Opesial Length	Opesial Width	Avic. Length
1899.5.1.654. Holotype.	30	0.32±0.03	0.24±0.02	0.19±0.01	0.14±0.01	0.08±0.01
C and B (1929) (<i>M. ovatum</i>)	—	0.50	0.35–0.40	0.30	0.22	—
C and B (1929) (<i>D. ogivalina</i>)	—	0.48–0.50	0.30	0.20–0.22	0.18–0.20	—
C and B (1929) (<i>D. minor</i>)	—	0.35–0.45	0.25–0.30	0.15–0.25	0.11–0.20	—
C and B (1930) (<i>M. claustracrassum</i>)	—	0.4–0.5	0.3	0.26–0.30	0.16–0.18	—
Cook (1968a) (<i>A. papillatum</i>)	—	0.30–0.42	0.15–0.23	0.12–0.15	—	0.05–0.09
Cook (1968a) (<i>A. minus</i>)	—	0.25–0.33	0.17–0.20	0.15–0.23	—	0.04–0.07
NHM 1899.5.1.602. (<i>A. marginella</i>)	30	0.32±0.04	0.22±0.02	0.19±0.03	0.13±0.02	0.09±0.01
NHM 1997.10.6.2.	20	0.35±0.04	0.28±0.03	0.19±0.03	0.15±0.02	0.08±0.01

ogivalina. A variation in autozooidal size in *D. ogivalina* was observed by Canu and Bassler (1929) leading them to present two sets of measurements, for small and large autozooids, from a single colony.

A comparison of specimens of *A. papillatum* from the Philippines, *D. ogivalina* from the Philippines, *M. ovatum* and *A. minor* from Brazil shows that despite the smaller average size of the autozooids of *A. minor* and the Philippine colonies of *A. papillatum* and *D. ogivalina* they are otherwise morphologically indistinguishable.

Canu and Bassler (1920) cite *Amphiblestrum papillatum* Busk, 1884 as the 'genotype' species of the genus *Membrendoecium* Canu and Bassler, 1917. With the synonymy of *A. minor* and *A. papillatum*, *Membrendoecium* Canu and Bassler, 1917 becomes a junior subjective synonym of *Antropora* Norman, 1903b.

Canu and Bassler (1930) noted that their *Membrendoecium claustracrassum* sp. nov. from the Galapagos Islands, could perhaps be the same species as *A. papillatum*, and comparison of cotype (USNM 8472) and topotype (NHM 1933.12.10.10.) material of *M. claustracrassum* with the specimens listed above, shows this indeed to be the case. The cotype material of *M. claustracrassum* also possesses several autozooid-sized vicarious avicularia which have not been noted previously.

Osburn (1950) noted that the ancestrula of *A. claustracrassa* was half the size of later zooids while autozooids originating secondary laminae were noticeably larger than other zooids; he also noted that occasionally the avicularia are replaced by small 'nodules' (kenozooids).

The presence of vicarious avicularia in *M. claustracrassum* suggests the synonymy of *A. minor* and *A. marginella*. Although neither the type specimen of *A. minor* (NHM 1899.5.1.654.) nor that of *A. marginella* (NHM 1899.5.1.602.) show vicarious avicularia, in all other respects the two specimens are identical and indistinguishable from *M. claustracrassum* which does possess vicarious avicularia.

Hincks (1884) did, however, describe vicarious avicularia in *Membranipora marginella* sp. nov., noting 'cells with a very large oral operculum of a dark horn-colour', concluding that they were either avicularia or a reproductive structure. Hincks (1893) later realised that they were in fact vicarious avicularia as noted by Waters (1898).

Thornely (1905) also noted the presence of vicarious avicularia, in her description of

Amphiblestrum marginella from Ceylon; she described the small interzooidal avicularia as more pointed than described by Hincks and 'directed upwards instead of downwards'; examination of her material (NHM 1936.12.30.6.) shows that she was describing a colony of the new species, *Antropora erectirostra*, which also has vicarious avicularia.

Harmer (1926) in his description of *A. marginella* was unsure about the presence of 'rosette-plates' (septula) but doubted that 'pore-chambers' (dietellae) were present. It is unsure to which specimens Harmer (1926) referred in his descriptions as material he examined has now been assigned to not only *A. minor*, but also *Parantropora laguncula* and *Retevirgula aggregata*.

A specimen from Fort Pierce, Florida (NHM 1986.8.14.9.), originally labelled *Antropora leucocypha* (Marcus, 1937), is undoubtedly *A. minor*. The taxonomic identity of Marcus' species, and any synonymy, is difficult without reference to the type material, in the absence of which no conclusion may be drawn.

Osburn (1927) in his original description of the multilaminar *Membrendoecium compressum* noted its similarity to *A. papillatum*, though it differed in its closely packed zooids and thicker colony. Marcus (1937) considered that *M. compressum* might be a synonym of *A. minor*. Osburn's type material has not been available for study.

The species described by Canu and Bassler (1929) as *Amphiblestrum papillatum* Busk (NHM 1931.12.30.25.), mentioned by Cook (1968a), differs from Busk's species in a number of ways: it has six to eight spines around the distal end of each autozooid, the opesial rim is greatly raised, it bears no avicularia, the gymnocyst is elongated, and finally it bears large globular hyperstomial ovicells. These features put this specimen within one of the genera akin to the genus *Crassimarginatella* Canu, 1900, rather than genus *Antropora* Norman.

Distribution

Bahia, and Fernando Noronha, Brazil; Guyamas, Mexico; La Libertad, Ecuador; Colombia; Panama Canal; Galapagos Islands; Tahiti; Enewetak Atoll; Chatham Islands; Fiji; Japan; Philippines; Singapore; Mergui Archipelago (off Thailand); Ceylon (Sri Lanka); Red Sea.

This species appears to have a circum-tropical distribution.

Antropora typica (Canu and Bassler, 1928a)
(Fig. 1F; Fig. 3A)

Antropora granulifera Harmer, 1926: 232 (in part), pl. 14, figs 12–14.

Antropora granulifera: Mawatari and Mawatari, 1981: 28 (in part), fig. 2.

Dacryonella typica Canu and Bassler, 1928a: 87, pl. 5, figs 4–8; pl. 32, figs 11, 12.

Dacryonella typica: Canu and Bassler, 1928b: 8, 65, pl. 1, fig. 10.

Antropora typica Rucker, 1967: 817, fig. 12b.

Antropora typica: Winston, 1986: 5, figs 1, 2.

Membrendoecium strictorostis Canu and Bassler, 1928a: 23, pl. 2, fig. 7.

Canua (*Membrendoecium*) *strictorostis* Osburn, 1940: 358.

Crassimarginatella cookae Hayward, 1988: 277, figs 2c–e.

Material examined

Holotype Series: USNM 7484 (2 pieces), Alb. Sta. 2319, North of Cuba. 23°10'37"N, 82°20'6"W, 143 fathoms; USNM 7485 (2 pieces), Alb. Sta. 2320, North of Cuba.

Other material examined: NHM 1932.3.7.51., North of Cuba. (exc. USNM); NHM 1899.7.1.988,989. (as *Antropora* sp.), John Adam's Bank, Brazil; NHM 1928.3.6.49. (as *Antropora granulifera*), Siboga Stn 310. E. Sumbawa, Malaysia; NHM 1928.9.13.16. (as *Antropora granulifera*), Okinose off Tokyo, Japan; NHM 1928.9.13.17. (as *Antropora granulifera*), Shikoku, Japan; USNM 7552 (Holotype of *Membrendoecium strictorostis*), Alb. Sta. 2319, North of Cuba. 23°10'37"N, 82°20'6"W, 143 fathoms; NHM 1934.10.8.9., Mauritius.

Description

Colony unilaminar, encrusting. Autozooids

distinct, oval, separated by indistinct grooves, may form longitudinal rows. Thin mural rim. Opesia two-thirds of total autozooid length, oval, with a narrow border of granular cryptocyst, broadest proximally, where it grades into smooth obvious gymnocystal calcification. A pair of small, distally directed, interzooidal avicularia at the distal end of most autozooids; mandible acutely triangular; rostrum narrow, acute, tear drop-shaped, distally directed, with a distinct granular cryptocyst proximally and elongate oval opesia; lacking a crossbar. Ovicell endozooidal, small, partly immersed beneath succeeding autozooid, but distinct in frontal view; hemispherical, imperforate, smooth, cap-like. Operculum of ovicellate zooids wider than autozooids, and closing the ovicell. Large vicarious avicularia occur sporadically, each with a semi-elliptical mandible equivalent to one-third total length, supported by a slightly raised, arched rostrum. One or, generally, two very thin areas of basal calcification, distally (see *A. granulifera* above). Canu and Bassler (1928a) describe living colonies as light rose in colour.

Remarks

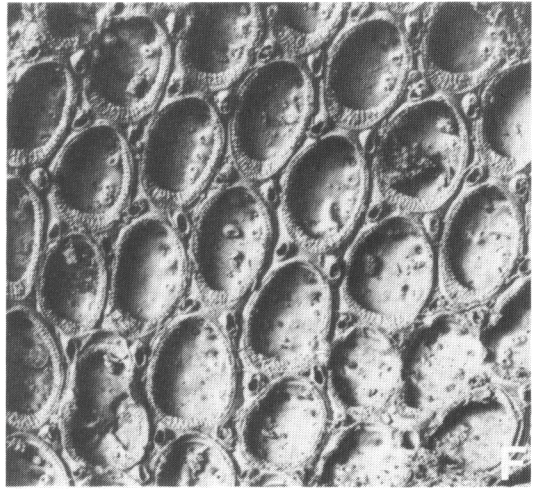
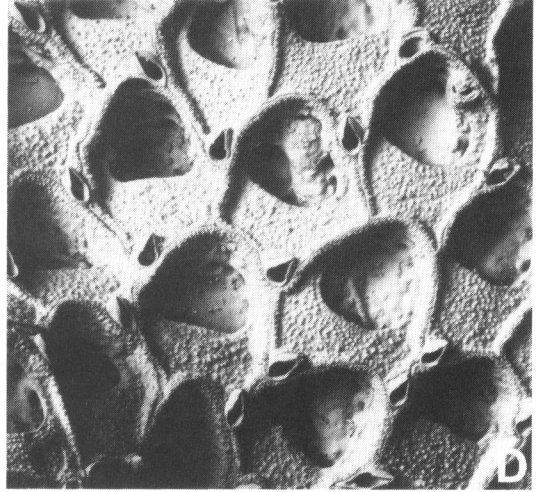
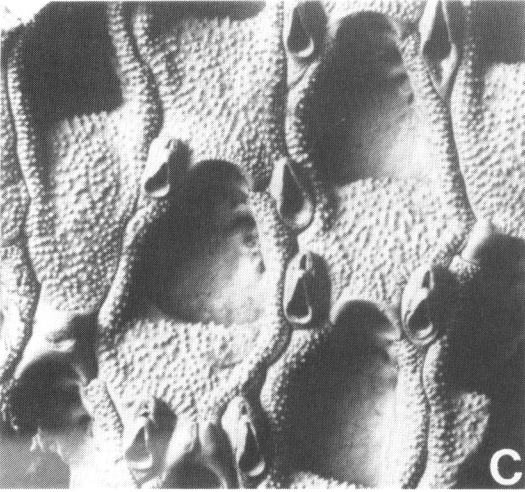
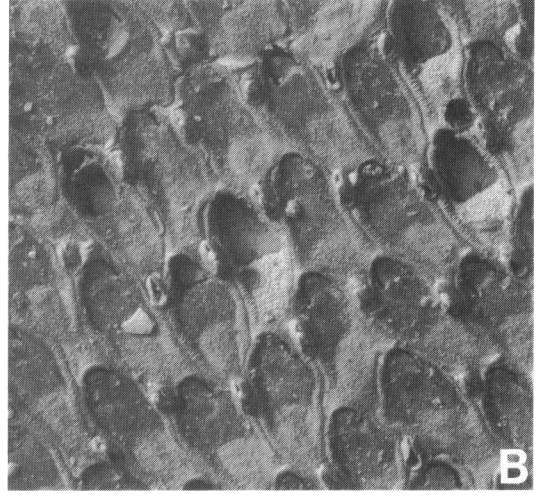
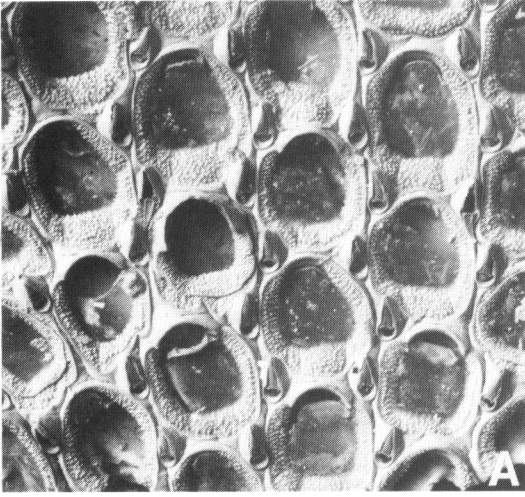
This species is characterised by the presence of frequent tear drop-shaped interzooidal avicularia, with acute distally pointing mandibles; the gymnocyst is obvious and the large vicarious avicularia are also often quite frequent.

The size of the autozooids varies greatly within colonies and between geographic localities, as noted by Canu and Bassler (1928a) in material from off Cuba, and has thus been mistakenly identified subsequently by several authors.

Harmer (1926) described material of *Antropora granulifera* from Malaysia (NHM 1928.3.6.49.) and Japan (NHM 1928.9.13.16, 17.) which are clearly referable to this species. Following Cook (1968a), Hayward (1988) recognised another Natural History Museum specimen (NHM 1934.10.8.9.), from Mauritius, assigned to *A.*

Measurements (mm): mean±standard deviation

Specimen	n	Autozooid Length	Autozooid Width	Opesial Length	Opesial Width	Avic. Length
USNM 7484 Holotype.	30	0.46±0.06	0.29±0.05	0.26±0.02	0.18±0.03	0.12±0.01
C and B (1928a)	–	0.45	0.30	0.20	0.15	0.10
C and B (1928b)	–	0.40–0.45	0.25–0.30	0.20–0.23	0.17–0.20	–
Hayward (1988) (<i>C. cookae</i>)	20	0.51±0.06	0.31±0.04	–	–	–



granulifera, as a different species, describing it as the new species, *Crassimarginatella cookae*. Comparison of the specimens cited by Harmer (1926) and Hayward (1988) with Canu and Bassler's (1928a) type series of *Dacryonella typica* (USNM 7484, 7485) shows them to be conspecific.

Canu and Bassler (1928a) described *Membrendoecium strictorostri* from Alb. Stn 2319, north of Cuba, the type locality of *Dacryonella typica*; comparison of the two sets of type material shows them to be the same species, though neither types show the vicarious avicularia seen in other material belonging to this species.

Canu and Bassler (1927) described *Dacryonella levigata* sp. nov. from Hawaii; the general description and appearance seem very similar to *C. typica*, although their measurements of *D. levigata* are smaller than those of the specimens listed above. In the absence of material of *D. levigata*, no firm conclusion as to its relation with *C. typica* can be voiced. Rucker's (1967) figured specimen is clearly recognisable as this species, as are those specimens figured by Winston (1986).

The fossil type series specimens from the Pliocene of Panama (USNM 70838), are not included in the above review as they differ from the Recent material in several respects, i.e. a more extensive cryptocyst, less frequent occurrence of the small interzooidal avicularia and absence of large vicarious avicularia, and cannot be synonymised with confidence.

Distribution

Cuba; Jamaica; John Adam's Bank off Brazil; Mauritius; Sumbawa, Malaysia; Japan.

Antropora erectirostra Tilbrook, new species (Fig. 3B,C)

Amphiblestrum marginella Thornely, 1905: 110.

Material examined

Holotype: NHM 1899.7.1.1086., Ceylon (Sri Lanka). Busk Coll.

Paratypes: NHM 1899.7.1.1084, 1085, 1087., Ceylon (Sri Lanka). Busk Coll.

Other material examined: NHM 1936.12.30.6. (as *Antropora marginella*), Gulf of Manaar, Ceylon. L. R. Thornely.

Etymology

erectus, L. upright; *rostrum*, L. beak. Named after its highly raised small interzooidal avicularia.

Description

Colony, encrusting, unilaminar. Autozooids about twice as long as wide, separated by deep grooves. Gymnocyst is minimal; cryptocyst granular, very deep proximally, sloping slightly basally, distal edge flat to somewhat convex. Opesia rounded, triangular, occupying half frontal area. On many autozooids one or two interzooidal avicularia are placed disto-laterally; mandible

Measurements (mm): mean±standard deviation

Specimen	n	Autozooid Length	Autozooid Width	Opesial Length	Opesial Width	Avic. Length
NHM 1899.7.1.1086. Holotype.	25	0.50±0.04	0.24±0.03	0.25±0.03	0.16±0.09	0.13±0.02

FIGURE 3. **A**, *Antropora typica* (Canu & Bassler, 1928a), NHM 1928.3.6.49., E Sumbawa, Malaysia. Group of zooids, showing several ovicellate zooids (note the wider opercula) and a large vicarious avicularium slightly left of centre. x36. **B**, *Antropora erectirostra* new species, Holotype specimen NHM 1988.7.1.1086., Ceylon (Sri Lanka). Group of autozooids showing the zooidal arrangement and highly raised interzooidal avicularia. x36. **C**, *Antropora erectirostra* new species, Paratype specimen NHM 1988.7.1.1085., Ceylon (Sri Lanka). Group of autozooids showing the granular cryptocyst and minimal gymnocyst; several of the interzooidal avicularia appear to have regenerated. x90. **D**, *Parantropora penelope*, new genus, new species, Holotype specimen NHM 1997.10.6.1., Magnetic Island, Townsville, Queensland, Australia. Group of autozooids. x45. **E**, *Parantropora penelope*, new genus, new species, Holotype specimen NHM 1997.10.6.1., Magnetic Island, Townsville, Queensland, Australia. Group of zooids including a very large vicarious avicularium at the centre top. x54. **F**, *Parantropora laguncula* (Canu & Bassler, 1929), NHM 1931.12.30.14., off Sirun Island, Tawi-tawi Islands, Philippines. Group of zooids including a very large vicarious avicularium. x36.

acutely triangular, arched, distally directed; rostrum distally pointed, raised. Rare vicarious avicularia, as large as autozooids; rostrum broadly triangular, narrowing distally, its lateral walls raised. Ovicells small, endozooidal. Kenozooids frequent in disturbed areas of a colony.

Remarks

The presence of the raised, distally directed interzooidal avicularia make this species easily distinguishable from others of the genus.

The autozooids form approximately parallel rows, becoming rather longer and slimmer with increasing colony size. The interzooidal avicularia are most acute and the rostrum most raised nearer the growing edge, the mandibles are more arched.

Thornely's specimen from Ceylon (NHM 1936.12.30.6. as *A. marginella*) is undoubtedly *A. erectirostra* (see *A. marginella* discussion above).

Silén's (1941) *Antropora erecta* sp. nov. is very similar to *Antropora erectirostra*, though he describes the colony as erect and branching, with the 'structure of a cylinder surrounding a cavity'; he makes no mention of the large vicarious avicularia, seen only rarely in *A. erectirostra*.

Distribution

This species is known only from Sri Lanka (Ceylon).

Parantropora Tilbrook, gen. nov.

Generic diagnosis

Colony encrusting. Autozooidal cryptocyst moderately developed around the opesia, gymnocyst negligible or absent. Spines absent. Small interzooidal avicularia present. Large spatulate vicarious avicularia present, much larger than autozooids. Ovicells endozooidal. Mural septula present.

Type species

Parantropora penelope Tilbrook, new species.

Etymology

The genus is named for its resemblance to *Antropora*.

Remarks

This genus is very similar to *Antropora*. However, the lack of dietellae, the presence of lateral-wall (mural) septula and the occurrence of very large spatulate vicarious avicularia, make species of this genus quite distinct. The presence

of 'special zooecia' was first noted by Canu and Bassler (1929) in *Membrendoecium lagunculum* sp. nov., though they failed to recognise them as avicularia. Whereas, the vicarious avicularia in species of *Antropora* are autozooid size and shape and so easily overlooked in a colony (Figs 2F and 3A), those of *Parantropora* are considerably larger than the surrounding autozooids; in *P. penelope* (Fig. 3E) they are one-third as long again, and in *P. laguncula* (Fig. 4A) almost half as long again, as the average autozooid.

Species of *Parantropora* generally have a more delicate structure to their side walls than do species of *Antropora*.

Parantropora penelope Tilbrook, new species (Fig. 3D,E)

?*Antropora granulifera* Ryland and Hayward, 1992: 229, fig. 2c.

Etymology

Named after my mother, Leah Penelope Tilbrook.

Material examined

Holotype: NHM 1997.10.6.1., Magnetic Island, Townsville, Queensland. Coll. J. S. Ryland.

Other material examined: NHM 1997.10.6.17., Erakor Id, Vanuatu; NHM 1997.10.6.18., Erakor Id, Vanuatu. Reef Flat; NHM 1997.10.6.15., Carter Reef, Great Barrier Reef, Australia; NHM 1997.10.6.16., Suva Barrier Reef, Fiji. Reef Flat; NHM 1997.10.6.23., Suva Barrier Reef, Fiji.

Description

Colony encrusting, unilaminar. Autozooids irregularly oval to hexagonal, separated by shallow grooves. Gymnocyst minimal; cryptocyst occupying slightly less than half total autozooid length, flat or slightly concave, coarsely beaded. Opesia subtriangular. At the distal end of each autozooid a pair (rarely one) of small, tear drop-shaped interzooidal avicularia. Rostrum acute to frontal plane, directed distally or disto-medially, with an acutely triangular mandible articulated on condyles. Large vicarious avicularia also present, generally larger than autozooids; rostrum raised distally, cryptocyst, narrow, coarsely granular, laterally constricted; opesia rounded; mandible spatulate, articulated on pointed, triangular condyles, angled slightly proximally, situated proximal to lateral rostral constriction. Ovicells endozooidal, small, granular, cap-like, derived from distal zooid. Ovicell not closed by

Measurements (mm): mean±standard deviation

Specimen	n	Autozoid Length	Autozoid Width	Opesia Length	Opesia Width	Avic. Length
NHM 1997.10.6.1. Holotype.	20	0.45±0.06	0.28±0.04	0.20±0.03	0.18±0.03	0.09±0.02
Specimen	n	Vic. Avic. Length	Vic. Avic. Width			
NHM 1997.10.6.1. Holotype.	6	0.6 ± 0.06	0.27 ± 0.02			

operculum. Mural septula present in the thin lateral walls, which may be strengthened by basolateral buttresses.

Remarks

Parantropora penelope looks superficially very similar to *A. typica*. However, it differs in its lack of a gymnocyst, its smaller opesia and in having large spatulate vicarious avicularia. *P. penelope* is distinguishable from *P. laguncula* by its smaller, more triangular opesia and more acutely pointed interzooidal avicularia.

The specimen figured by Ryland and Hayward (1992) as *Antropora granulifera* is certainly not Hincks's species; it is possible that *P. penelope* is the species figured, although its identity must remain uncertain until their material can be re-examined.

Distribution

Great Barrier Reef, Australia; Erakor Islands, Vanuatu; Suva Barrier Reef, Fiji.

This species appears to be limited to the tropical south west Pacific.

Parantropora laguncula (Canu and Bassler, 1929)
(Fig. 3F; 4A,B)

?*Biflustra savartii* Audouin, var. MacGillivray, 1891: 79, pl. 9, fig. 6.

?*Membranipora savarti*: MacGillivray, 1895: 38, pl. 5, figs 6,7.

Antropora marginella Harmer, 1926 (in part): 234, pl. 14, fig. 15.

Membrendoecium savarti Canu and Bassler, 1929: 94, pl. 6, figs 1–3.

Membrendoecium lagunculum Canu and Bassler, 1929: 96, pl. 6, figs 6–11.

Antropora lagunculum Mawatari and Mawatari, 1981: 33.

Material examined

Holotype Series: USNM 7869 (5 pieces), Alb. Sta. 5478, off Tacbuc Point, E Leyte, Philippines. 57 fathoms.

Other material examined: NHM 1997.10.6.5–7., Tideway Reef, Great Barrier Reef. 10m; NHM 1997.10.6.24., ?Mourilyan Harbour, Coll. Bob Pearson; NHM 1931.12.30.19. (as *Membrendoecium lagunculum*), Alb. Sta. 5478, off Tacbuc Str., E Leyte, Philippines. 57 fathoms. (exc. USNM); NHM 1931.12.30.14. (as *Membrendoecium savarti*), Alb. Sta. 5151, off Sirun Id, Tawi-tawi Is, Philippines. 24 fathoms. (exc. USNM); NHM 1931.12.30.15. (as *Membrendoecium savarti* var. *minor*), Alb. Sta. 5151, off Sirun Id, Tawi-tawi Is, Philippines. 24 fathoms. (exc. USNM); NHM 1928.9.13.19. (as *Antropora marginella*), Torres Straits, Australia; NHM 1928.3.6.50. (as *Antropora marginella*), Siboga Station 81. Borneo Bank, Strait of Makassar, Malaysia. 0–34m; NHM 1928.3.6.51. (as *Antropora marginella*), Siboga Station 164. W. of N. end of New Guinea. 32m.

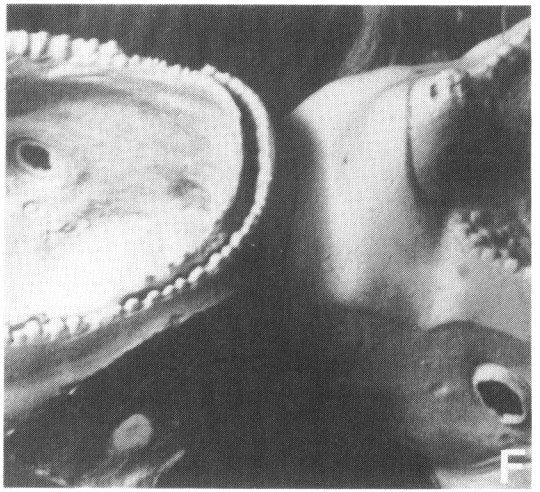
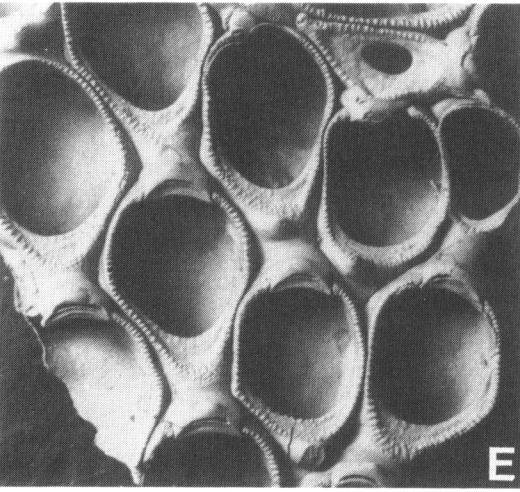
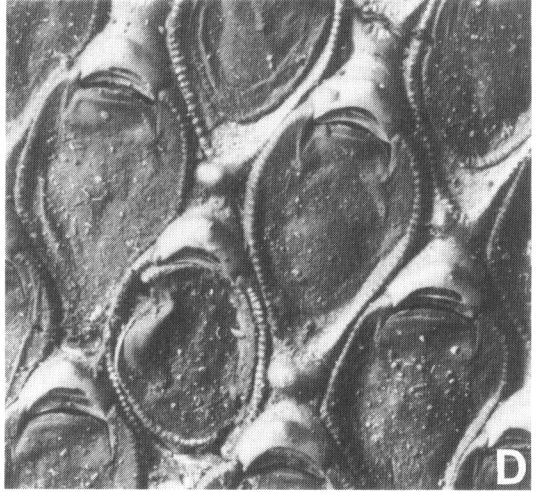
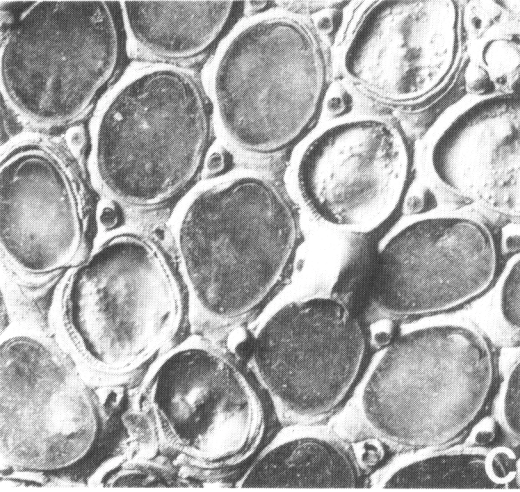
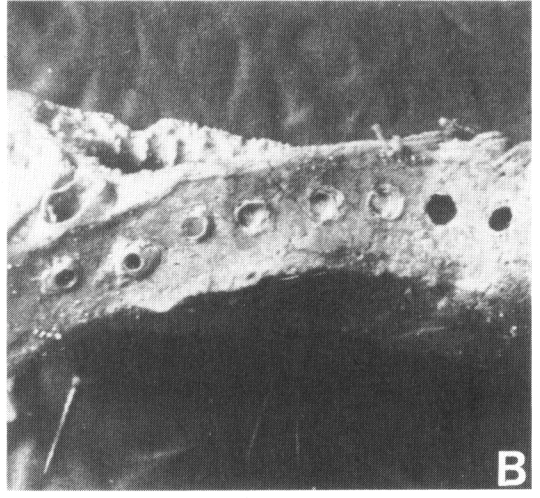
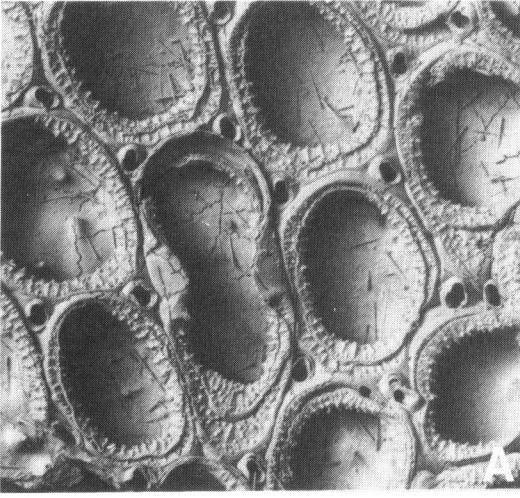
Description

Colony encrusting, unilaminar. Autozooids distinct, elongated or elliptical, separated by deep grooves. Gymnocyst reduced, surrounding zooids; cryptocyst coarsely granular, broadest proximally. Opesia elliptical or oval, occupying almost entire frontal area. Small, symmetrical, interzooidal avicularia are present at the interzooidal angles. Rostrum raised; mandible rounded-triangular, opesia with lateral constriction. Large vicarious avicularia frequent. Ovicells endozooidal, very small, smooth, raised cap-like.

Remarks

Parantropora laguncula is distinguished by its large oval opesia surrounded by a reduced gymnocyst.

According to Canu and Bassler (1929), MacGillivray (1891) recorded this species from



Measurements (mm): mean±standard deviation						
Specimen	n	Autozoid Length	Autozoid Width	Opesial Length	Opesial Width	Avic. Length
C and B (1929) (<i>M. savarti</i>)	–	0.40–0.42	0.30	0.24–0.29	0.16–0.20	–
NHM 1997.10.6.5.	25	0.39±0.08	0.33±0.04	–	–	0.07±0.01
Specimen	n	Vic. Avic. Length	Vic. Avic. Width			
NHM 1997.10.6.5.	8	0.62±0.08	0.32±0.06			

the Tertiary of Victoria and the Recent of Western Australia, attributing it to *Biflustra savarti* Audouin. However, the figure accompanying MacGillivray's (1891) description bears little resemblance to *Parantropora laguncula*, here described. Canu and Bassler (1929) reported *Membrendoecium savarti* from the Philippines, attributing the specific name to MacGillivray whilst changing the generic attribution. In the same paper (Canu and Bassler 1929) they describe a new species, *Membrendoecium lagunculum*, which, following comparison of material of both species deposited in the Natural History Museum, London, proves to be identical to *B. savarti sensu* MacGillivray *non* Audouin. The combination *Parantropora laguncula* (Canu and Bassler, 1929) is consequently the correct name for this species.

Canu and Bassler (1929) noted that autozoid size in *Membrendoecium lagunculum* was variable and considered it to be dependent on substratum type, with autozooids at the margins generally largest, although they do not provide any measurements for this species. They did not describe large vicarious avicularia, seen in the type series of *Membrendoecium lagunculum*, despite their depiction in three of the figures (Canu and Bassler 1929: pl. 6, figs 6, 8 and 11); instead these were described as large aberrant zooids, with 'deformed' opesia, at the

start of new autozoid series; the mandibular articulatory condyles can be clearly seen in their fig.11.

Silén (1941) considered that *Membrendoecium lagunculum* and *Antropora marginella* might prove to be a single species, by reference to Canu and Bassler's (1929) plate 6, figs 6–11 and Harmer's (1926) plate 14, fig. 15. Re-examination of Harmer's material of *Antropora marginella* shows that three specimens could be attributed to *P. laguncula*, namely NHM 1928.9.13.19. Torres Straits, Australia, NHM 1928.3.6.50. from Malaysia and NHM 1928.3.6.51. from New Guinea.

Distribution

Leyte and Tawi-tawi Is, Philippines; Torres Straits, Australia; Strait of Makassar, Malay; New Guinea; Great Barrier Reef.

This species is known from the Indo-Malaysian region and Western Australia and perhaps occurs more widely in the Southwest Pacific.

Genus *Retevirgula* Brown

Retevirgula Brown, 1948: 109.

Generic diagnosis

Colony thinly encrusting. Zooids united by

FIGURE 4. A, *Parantropora laguncula* (Canu & Bassler, 1929), NHM 1997.10.6.5., Tideway Reef, Great Barrier Reef, Australia. Group of zooids with thin cryptocystal rim and reduced gymnocyst (large vicarious avicularium visible in the centre). x45. B, *Parantropora laguncula* (Canu & Bassler, 1929), NHM 1997.10.6.7., Tideway Reef, Great Barrier Reef, Australia. Lateral wall showing septula. x144. C, *Retevirgula aggregata* Gordon, 1984, NHM 1928.9.13.18., Torres Straits, Australia. Group of zooids showing the deep separating grooves, small raised interzooidal avicularia and large globular keeled ovicell. x45. D, *Crassimarginatella papulifera* (MacGillivray, 1892), NHM 1881.10.21.355–9., Torres Straits, Australia. Group of zooids including ovicellate zooids, in which the operculum does not close the unifenestrate ovicell. x63. E, *Crassimarginatella papulifera* (MacGillivray, 1892), NHM 1881.10.21.355–9., Torres Straits, Australia. Group of zooids; note the presence of kenozooids. x45. F, *Crassimarginatella papulifera* (MacGillivray, 1892), NHM 1881.10.21.355–9., Torres Straits, Australia. Lateral view of two autozooids showing the mural pores and proximal papillae. x162.

short connecting tubes absent in some species. Opesia extensive, gymnocyst and cryptocyst reduced. Interzooidal avicularia common, sometimes replaced by kenozooids. Ovicells recumbent, smooth-walled or with a fenestra, often surmounted by an avicularium. Basal pore-chambers wanting. (Gordon 1984).

Type species

Membranipora acuta Hincks, 1885: 249, pl. 7, fig. 6.

Retevirgula aggregata Gordon, 1984
(Fig. 4C)

Antropora marginella Harmer, 1926 (in part): 234, pl. 14, fig. 15.

Retevirgula aggregata Gordon, 1984: 27, pl. 2, fig. D.

Retevirgula aggregata: Gordon, 1986: 30.

Material examined

NHM 1928.9.13.18. (as *Antropora marginella*), Torres Straits, Australia.

Description

Colony encrusting, unilaminar. Autozooids oval or rounded, distinct, separated by deep grooves. Gymnocyst minimal; cryptocyst granular, forming a very narrow rim; opesia rounded, occupying almost entire frontal area. Small interzooidal avicularia often found in the interzooidal angles; rostrum raised, rounded; mandible semicircular, distally directed. Kenozooids also present. Ovicells hyperstomial, smooth, globular, with a median suture, no fenestra.

Specimen	n	Autozooid	
		Length	Width
Gordon (1984).	—	0.45–0.55	0.27–0.33
NHM 1928.9.13.18.	30	0.41±0.04	0.30±0.04

Remarks

In his account of *Antropora marginella*, Harmer (1926) described prominent, hyperstomial ovicells, with distinct median keels, in some specimens, referring in particular to specimen NHM 1928.9.13.18 from the Torres Straits. Such ovicells are not a feature of *Antropora* and re-examination of the specimen shows it to be attributable to the recently described *Retevirgula aggregata* Gordon, 1984.

Gordon (1984) distinguished his new species from other species of *Retevirgula* Brown, 1948, by the absence of connecting tubes and avicularian pivot bars (*R. aggregata* possesses condyles instead), both included in Brown's (1948) original generic diagnosis.

Distribution

Described by Gordon (1984) from Kermadec Ridge (type locality Curtis Is) and off Kahurangi Point, north-west South Island, New Zealand; this new record from Torres Straits, NE Australia suggests a considerable geographical range in the SW Pacific.

Genus ***Crassimarginatella*** Canu

Crassimarginatella Canu, 1900: 369.

Oochilina Norman, 1903a: 595.

Generic diagnosis

Colony encrusting, or erect from an encrusting base. Gymnocyst variable in extent, usually reduced. Opesia extensive, occupying the larger part of the frontal area; cryptocyst reduced, moderate or very narrow. Avicularia vicarious, lacking spines, with or without a pivot bar. Ovicells prominent, unifenestrate, or small and cap-like. Mural or basal pore-chambers present (cf. Harmelin 1973). (Gordon 1984).

Type species

Membranipora crassimarginata Hincks, 1880a: 71, pl. 9, fig. 1–1a.

Crassimarginatella papulifera (MacGillivray, 1882)
(Fig. 4D–F)

Membranipora papulifera MacGillivray, 1882: 116, fig. 9.

Membranipora papulifera: Waters, 1898: 658, 659, 660, 669.

Crassimarginatella papulifera Brown, 1952: 56, fig. 13.

Crassimarginatella (*Crassimarginatella*) *papulifera* Gordon, 1986: pl. 4F.

Material examined

NHM 1881.10.21.355–9., (as *Membranipora* sp.), Torres Straits, Australia, HMS Alert.

Description

Colony encrusting, unilaminar. Autozooids distinct, elongate, separated by deep grooves. Frontal membrane bordered by a thin crenellated mural rim. Gymnocyte minimal, sometimes papillate proximally; cryptocyst finely beaded, minimal, broader proximally than laterally, sloping basally. Opesia oval, very large, equivalent to 80–90% of frontal area. Ovicells, smooth, cap-like, slightly pointed, hyperstomial, unifenestrate, with at least some material being derived from the gymnocyte of distal autozooid. Operculum broad, does not cover ovicell orifice. Interzooidal communication by mural dietellae. No spines.

Specimen	n	Autozooid	
		Length	Width
Brown (1952)	–	0.51–0.55	0.33–0.38
NHM 1881.10.21.355–9.	30	0.60±0.05	0.33±0.03

Remarks

The most striking feature of this species is the form of the ovicell, from which the specimen described above was identified using the plate published by Gordon (1986) of paralectotype material.

Norman (1903a) referred *Membranipora papulifera* MacGillivray, 1882, to his new genus *Oochilina*. However, this genus shared the same 'genotype' species, *Membranipora crassimarginata* Hincks, 1880a, with *Crassimarginatella* Canu, 1900, which therefore takes precedence.

Gordon (1986), in his discussion of *Crassimarginatella* (*Crassimarginatella*) *fossa* Uttley, 1951, assigned *Crassimarginatella papulifera* (MacGillivray, 1882) to the subgenus *Crassimarginatella* but now (Gordon, pers. comm.) regards each of the subgenera of *Crassimarginatella* as deserving generic status. This species is thus correctly *Crassimarginatella papulifera* (MacGillivray, 1882). Waters (1898), Brown (1952) and Gordon (1986) all record the presence of vicarious avicularia, but these have not been seen in the specimen described above, although there appears to be evidence of autozooidal regrowth, i.e. multiple occupancy of a single autozooidal skeleton.

Distribution

Port Phillip Heads, Victoria; Torres Straits, Australia; New Zealand (fossil).

DISCUSSION

Several other species that have formerly been assigned to *Antropora* Norman, 1903b have also been examined and found to have been wrongly attributed. Harmer (1926) attributed *Membranipora nigrans* Hincks, 1882 to *Antropora*, but examination of material of this boreal species (Holotype: NHM 1886.3.6.9., Queen Charlotte Id, Canada; NHM 1911.10.1.610,611., Spitzbergen?; NHM 1919.6.25.40., Spitzbergen?; NHM 1938.11.30.25., off Del Monte, California; NHM 1955.10.3.63., Greenland), shows that Canu and Bassler (1929) and Cook (1968a) were correct in expressing doubts about the congeneric status of *Membranipora nigrans* and *A. granulifera* (see further discussion in Prenant and Bobin 1966).

Membrendoecium japonicum Canu and Bassler, 1929, automatically placed in *Antropora* by the synonymy of *Membrendoecium* Canu and Bassler and *Antropora* by Silén (1941), is not a species of *Antropora*. Examination of original material (NHM 1931.12.30.18., Cape Tsiuka, Japan) shows the regular form of kenozooids in the autozooidal framework, a feature more similar to species of *Menipea* Lamouroux, 1812 (a genus of erect species) than to *Antropora sensu stricto* (which are all encrusting, although see Silén's (1941) description of *A. erecta*) but this is not its true generic assignment either.

Gordon (1986) amended Norman's (1903b) generic diagnosis of *Antropora* when describing his new species *Antropora pacifera*. This species was also examined (Paratype: NHM 1985.1.22.2., NZOI Stn B488.); it completely lacks avicularia, and the ovicells are not endozooidal, but larger, separate structures, that have an obvious ectooecial rim around the granular endooecium, a distinct feature of the genus *Alderina* Norman, 1903a (Gordon, 1984).

It may transpire that several of the unexamined species listed above (see generic introduction) will be synonymised with one or more of the species described herein but until original material has been located the validity of these species cannot be tested.

The genus *Antropora* is presently placed within the Family Calloporidae Norman, 1903a; however, as Ryland and Hayward (1977) conclude 'this is a somewhat heterogeneous group'. The genera assigned to the family Calloporidae would thus benefit from a full systematic investigation. The familial diagnosis of Calloporidae emphasises the presence of prominent hyperstomial ovicells.

The genera *Antropora* and *Parantropora* gen. nov., have small endozooidal ovicells which would suggest that they belong to a family other than the Calloporidae.

Soule, Soule and Chaney (1995) discuss the Calloporidae, concluding that the Hincksinidae Canu and Bassler, 1927, should be reinstated for membraniporines with endozooidal ovicells and Alderinidae Canu and Bassler, 1927, for those with hyperstomial ovicells. However, the type genus of Hincksinidae, *Hincksina* Norman, 1903a is generally assigned to the Flustridae Fleming, 1828 (Ryland and Hayward 1977), and this proposal is thus unacceptable.

Vigneaux (1949) introduced the Antroporidae for *Antropora* Norman, 1903b, *Ogivalina* Canu and Bassler, 1917, *Ogivalia* Jullien, 1882 and *Rectonychocella* Canu and Bassler, 1917, splitting it into two subfamilies, with *Antropora* the only genus in the Antroporinae. The adoption of Vigneaux's (1949) scheme would ease the problem; *Crassimarginatella* would fall within the Alderinidae Canu and Bassler, 1927, as would *Retevirgula*, but the exact familial assignment of *Parantropora* is as yet unclear.

The genus *Antropora* has a global distribution predominantly in the tropics. However, the type species, *A. granulifera* occurs from the warm temperate waters of the Atlantic to the tropical seas of the Pacific. Several other species, *A. typica*, *A. minor* and *A. tincta*, are found globally occurring in both warm temperate and tropical seas. The remaining species have more narrow geographical ranges; *A. subvespertilio* has a disjunct range in the Gulf of Mexico and the Philippines, whereas *A. erectirostra* has only been found from Sri Lanka. The two species of the new genus *Parantropora* appear to be limited to the tropical south-west Pacific, from the Indo-Malaysian region to the Great Barrier Reef and Fiji.

List of Fossil Species not covered in this paper.

Antropora daishakaensis Kataoka, 1957

Antropora elongata Kataoka, 1957

Antropora hataii Kataoka, 1957

Dacryonella minor Canu and Bassler, 1920

Dacryonella octonaria Canu and Bassler, 1917

Dacryonella octonaria minor Canu and Bassler, 1920

Dacryonella (Homalostega) pavonia (Marsson, 1887)

Dacryonella (Reptescharinella) transversa (d'Orbigny, 1852)

Dacryonella (Homalostega) vespertilio (Marsson, 1887)

Membrendoecium duplex Canu and Bassler, 1920

Membrendoecium lowei Canu and Bassler, 1920

Membrendoecium pyriforme Canu and Bassler, 1917

Membrendoecium rectum Canu and Bassler, 1920

Membrendoecium transversum Canu and Bassler, 1920

ACKNOWLEDGMENTS

I would like to thank the following: Dr P. J. Hayward (University of Wales, Swansea) for the chance to study south-west Pacific bryozoans and for his time and patience reading previous versions of this manuscript; Dr Dennis Gordon (NIWA, New Zealand) for useful discussions on the subject; Mary Spencer Jones (Dept of Zoology, Natural History Museum, London) for her patience on my visits to the Museum's collections; The Collections Manager, Dept of Paleontology, National Museum of Natural History, Washington, for the loan of several Canu and Bassler type specimens; Leverhulme Trust, whose grant to the author and Dr P. J. Hayward made this work possible.

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