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Systematics and life history of *Antoniettella exigua*, a new genus and species of cribrimorph bryozoan from the Miocene of East Kalimantan (Indonesia)

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KEY WORDS - Bryozoa, Miocene, East Kalimantan, life history, Antoniettella exigua *gen. et sp. nov.*

ABSTRACT - A new genus and species of cheilostome bryozoan, Antoniettella exigua *gen. et sp. nov., is described from East Kalimantan (Indonesia) in rocks around the Burdigalian-Langhian boundary (Lower-Middle Miocene). Colonies encrust the undersides of platy scleractinian corals that formed patch reefs in turbid shallow waters. Included in the cribrimorph ascophorans, the monospecific genus* Antoniettella *differs from all existing cribrimorph genera and can be distinguished by a combination of its keyhole-shaped orifice and lack of pelmata, intercostal lacunae and ovicells. Colonies are always small in size, subcircular in outline, thick and usually multilayered, with new layers spreading outwards from the centre of the colony. Ecological categorization of* Antoniettella *as a 'spot colony' is discussed and its life history inferred. A survivorship curve suggests low initial rates of mortality followed by a constant rate of mortality. Colonies appear to have been well adapted to occupy and defend small patches of substrate space, possibly in a low-nutrient microenvironment.*

RIASSUNTO - [Sistematica e ciclo biologico di *Antoniettella exigua*, un nuovo genere di briozoo cribrimorfo del Miocene del Kalimantan Orientale (Indonesia)] - *Il presente lavoro descrive un nuovo genere e specie di briozoo cheilostoma,* Antoniettella exigua *gen. et sp. nov., in campioni provenienti da livelli carbonatici all'incirca al limite Burdigaliano-Langhiano (Miocene Inferiore-Medio) del Kalimantan Orientale (Indonesia). Le colonie di* Antoniettella exigua *incrostano le basi di coralli piatti che formano patch reef in acque torbide superficiali con elevato apporto di sedimenti terrigeni. Il genere* Antoniettella *appartiene al gruppo dei Cribrimorfi incluso nel subordine Aschophora ed è monospecifico. Il nuovo taxon differisce nettamente da tutti i generi finora descritti principalmente per la forma a buco di serratura dell'apertura e per l'assenza di pelmata, lacune intercostali e ovicelle. Le colonie sono sempre subcircolari e di piccola taglia ma spesse e di solito multilaminari con nuovi livelli di zooidi che si sviluppano a partire dal centro della colonia. Si discute la caratterizzazione ecologica di* Antoniettella *come 'spot colony' e si propongono ipotesi relative a strategie di colonizzazione e riproduzione. La curva di sopravvivenza mostra che il tasso di mortalità è inizialmente basso e successivamente si mantiene costante. Le colonie sembrano ben adattate a difendere la piccola area di substrato che incrostano, possibilmente in un microambiente con scarso apporto di nutrienti.*

INTRODUCTION

Bryozoans are common and diverse components of modern tropical reef environments (e.g., Cuffey, 1973; Winston, 1986; Kobluk et al., 1988). Nevertheless, they are poorly known in these settings, in part because they tend to be represented by inconspicuous small colonies encrusting the undersides of living corals and reef rubble. Knowledge of Cenozoic fossil bryozoans from tropical reefs is even more deficient. Encrusted surfaces of fossil corals and other substrates in fossil reefs are seldom favourably exposed, the combined effects of aragonite dissolution and cementation limiting opportunities for observing encrusting bryozoans in hand specimens. Thin sections occasionally reveal the presence of bryozoans but seldom provide adequate information on their external features to permit taxonomic identification. However, burial of reefs in some mixed carbonate-siliciclastic environments by muddy sediment may ameliorate the deleterious effects of carbonate diagenesis. If this mud is weathered away, or can be washed off, then surfaces with identifiable encrusting bryozoans may become visible. Just such a situation exists in the Miocene of the Kutai Basin, East Kalimantan. Here, moderately well-preserved bryozoans are found encrusting the undersides of platy corals, providing important insights into the composition of Miocene reef-associated bryozoan communities in the Indo-Pacific region, which is a major diversity hotspot at the present-day.

The aim of this paper is to describe a new cheilostome bryozoan genus and species - *Antoniettella exigua* - that encrusts corals from the Miocene of East Kalimantan. Unusually among cheilostomes found in these deposits, colonies are uniformly small and resemble the 'spot' category of encrusting bryozoans recognized by Bishop (1989). Spot colonies have been interpreted as adapted to the exploitation of temporal refuges, rapidly colonizing substrates that are ephemeral in duration or availability, reaching sexual maturity precociously, and dying while young and still small in size. Analysis of the size structure of populations of the new bryozoan is undertaken to allow aspects of its life history to be inferred and to test to what extent *A. exigua* matches the concept of a classical spot bryozoan.

GEOLOGICAL SETTING

The research area is located in the Kutai Basin, the largest sedimentary basin in Borneo, formed during the Middle to Late Eocene as consequence of tectonic extension across the Makassar Straits. The basin is characterised by rapid siliciclastic sedimentation related to high rates of uplift of the central ranges of Borneo

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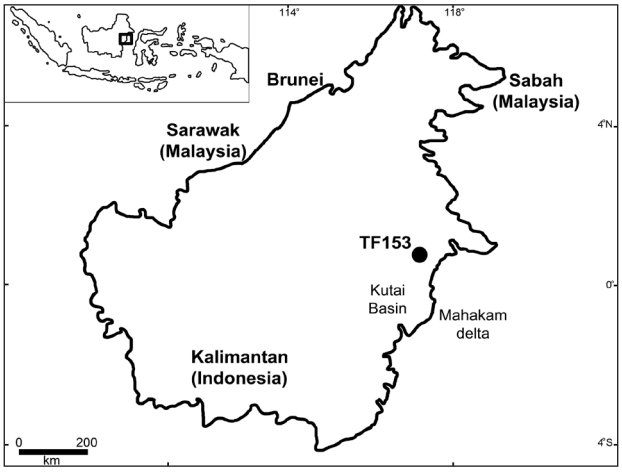

Fig. 1 - Position of the type locality of *Antoniettella exigua* gen. et sp. nov., TF153, the 'Rainy Section' in East Kalimantan, Indonesian Borneo.

towards the end of the Oligocene, the erosion of this landmass, and the development of deltaic and pro-delta environments (Wilson & Moss, 1999). Since the Early Miocene the Mahakam Delta has been actively prograding eastwards, contributing to the infilling of the Kutai Basin. Despite the rapid and constant siliciclastic input to the Mahakam Delta, shallow-water carbonate production occurred contemporaneously in the proximal delta-front environment. Carbonate outcrops of Miocene age have been interpreted as low-relief patch reefs that developed in turbid, shallow waters influenced by high levels of siliciclastic input (Wilson, 2005). These carbonates are considered as transitional shelf sediments deposited between deltaic and deep-marine facies (Allen & Chambers, 1998).

MATERIAL AND METHODS

Material examined comes from a site located near the village of Bontang (East Kalimantan, Indonesia). Specimens were collected in June 2011 during the second field season of the Throughflow Project from a muddy carbonate deposit exposed in a road cut, designated TF153 and known colloquially as the 'Rainy Section' (0.096440°N; 117.380370°E) (Fig. 1). Based on larger benthic foraminifera this section has been dated around the Burdigalian-Langhian boundary, within zones Tf1/2 following Renema (2007). Colonies of *Antoniettella exigua* gen. et sp. nov. encrust the bases of platy or, less often, the branches of ramose scleractinian corals. A total of 125 colonies were obtained from two different types of samples: (1) bulk samples, collected directly from the outcrop from a framestone with thin platy and branching corals in a clay matrix; and (2) float samples collected as hand specimens from a pile of platy corals lying adjacent to the outcrop. All of these specimens are catalogued and deposited in the Department of Palaeontology, Natural History Museum, London (abbreviated NHML).

Scanning electron microscopy (SEM) was carried out on several specimens, most of which were first soaked in a dilute solution of the detergent Quaternary-O to remove clay particles and were subsequently cleaned ultrasonically. SEM observations were made on uncoated specimens using a low-vacuum scanning electron microscope (LEO VP-1455) at the NHML. Measurements of the zooidal and colonial dimensions were made under the stereomicroscope at high magnification or alternatively from SEM images. Colony size (maximum and minimum diameter), number of zooids per colony, and number of layers of zooids were measured and counted for all 125 colonies. In damaged parts of the colonies in which the zooidal frontal shields had been lost, the number of zooids could be ascertained from the remaining vertical and basal walls. The various morphometric parameters of the zooids were measured in several colonies for up to 15-20 zooids whenever possible to evaluate intercolonial variability.

SYSTEMATIC PALAEONTOLOGY

Order Cheilostomata Busk, 1852
Suborder Ascophora Levinsen, 1909
Superfamily Cribrilinoidea Hincks, 1879
Family Cribrilinidae Hincks, 1879

Genus *Antoniettella* gen. nov.

Type species - *Antoniettella exigua* sp. nov.

Etymology - Named after Antonietta Rosso (Catania University) for her contributions to our knowledge of living and fossil bryozoans.

Diagnosis - Cribrilinidae with small, spot-like encrusting, often multilaminar colonies; autozooids thick, costae numbering 8 to 11, no intercostal pores, orifice with a sinus, oral spine bases numbering 3 to 8, ovicells not observed; small, subcircular polymorphs developed distolateral to some orifices.

Description - Colony encrusting, multiserial, unilaminar or multilaminar, thick but small in size. Autozooids angular and polygonal, enlarging through astogeny, with an increasing ratio of length to width. Frontal shield moderately convex, composed of 8 to 11 costae, closely-placed, some tightly fused along their entire length, some spaced at the margin of the costate shield. Intercostal lacunae and costal lumen pores (pelmata) absent or not evident because of relatively poor preservation and neomorphism of the skeleton. Primary orifice longer than wide, possessing a pair of small rounded shallow, downwardly directed condyles separating a horseshoe-shaped anter from a smaller U-shaped poster. Peristome sinusoidal, quite high. Oral spines present. One or two small oval or subcircular polymorphs sometimes present distolateral to the orifice are probably kenozooids but possibly adventitious avicularia. No ovicells. Ancestrular characters unclear, a single distal zooid seemingly budded from the ancestrula.

Remarks - This new genus differs from all existing genera of cribrimorphs in the unique combination of colony morphology (small in size yet multilayered), orifice shape, and absence of intercostal lacunae, pelmata and

ovicells. The keyhole shape of the orifice (Pl. 1, fig. 4), with a small sinus-like poster and larger anter, is found only in a minority of cribrimorphs; notably species of the Cretaceous genera *Andriopora*, *Lagynopora* and *Leptocheilopora* Lang, 1916 and the extant genera *Bellulopora* Lagaaij, 1963 and *Figularia* Jullien, 1886. However, *Andriopora*, *Lagynopora*, *Leptocheilopora* and *Bellulopora* all differ from *Antoniettella* in possessing costate ovicells (Ostrovsky & Taylor, 2005). Furthermore *Andriopora* develops uniserial colonies, and the apertural bar is strongly developed in *Lagynopora* and sharply bent proximally in *Leptocheilopora*. The Recent genera *Bellulopora* and *Figularia* have intercostal pores, not clearly present in *Antoniettella*.

The presence of the sinus was probably important in providing a passage for water to flow into the ascus when the lophophore was extended, a function fulfilled in most cribrimorphs by intercostal spaces which appear to be lacking in *A. exigua*. It is likely that the fissures apparent in some zooids are abrasional or diagenetic in origin. They contrast with colonies of *Puellina* spp. from the same locality which show unequivocal intercostal pores.

Antoniettella exigua sp. nov.
(Pl. 1, figs 1-7; Pl. 2, figs 1-8; Fig. 2)

Material - Holotype: Natural History Museum, London NHML BZ5842; Paratypes: NHML BZ5843 - BZ5844 - BZ5845 - BZ5846 - BZ5847. Miocene, Burdigalian-Langhian, Bontang, East Kalimantan, Indonesian Borneo.

Etymology - The specific name derives from the Latin *exiguus*, meaning small or spot, in reference to the characteristically small size of the colonies.

Diagnosis - See genus.

Description - Colony encrusting, multiserial, unilaminar or often multilaminar, with up to four layers of zooids, each layer thick; size typically small (Pl. 2, figs 1, 5), only a few mm in diameter with a minimum of four and a maximum of 68 zooids exposed (i.e. not overgrown), the majority of colonies with 20-30 exposed zooids, approximately circular in outline.

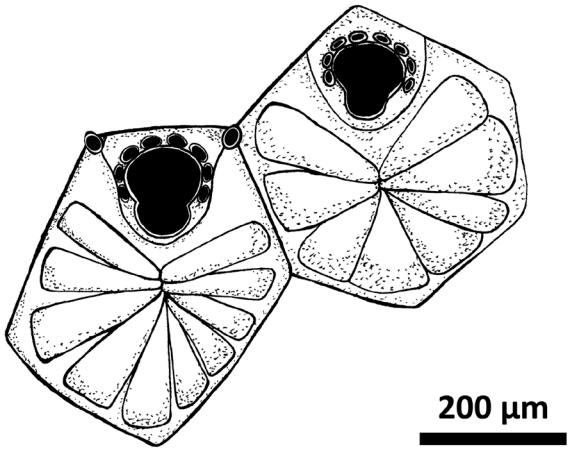

Fig. 2 - Interpretive drawing of two zooids of *Antoniettella exigua* gen. et sp. nov.

Astogenetic zone	Zooid size (mm)		Ratio L/W
	L	W	
Periancestrular 1st and 2nd generation (N=60)	0.25	0.18	1.39
Intermediate 3rd to 5th generation (N=150)	0.41	0.45	0.91
Edge 6th generation (N=100)	0.48	0.58	0.82

Tab. 1 - Morphometric data for *Antoniettella exigua* gen. et sp. nov. (10 colonies). Abbreviations: N = number of zooids measured for generation, L = mean length of the zooid, W = mean width of the zooid.

Autozooids angular in outline shape (Pl. 1, figs 2-3), pentagonal or hexagonal, enlarging progressively during astogeny from the periancestrular zone to the edge of the colony, with the ratio of length to width increasing. Quantitative characters of the various generations of zooids are given in Tab. 1. Frontal shield cribrimorph (Pl. 1, figs 2-3), slightly convex, usually composed of 8 to 10 prominent costae, rarely 11 costae; intercostal lacunae and costal lumen pores not visible. Two or three oval communication pore windows (mean L= 40 µm and mean W = 15 µm) along distolateral vertical walls, sometimes visible along the margins of zooids at the colony growing edge (Pl. 1, fig. 6). Primary orifice longer than wide (L= 0.15-0.17 mm, W= 0.10-0.14 mm), a pair of rounded shallow condyles directed downwards and separating a horseshoe-shaped anter from a smaller poster that has a broad U-shaped sinus with a nearly straight or slightly convex proximal edge (Pl. 1, fig. 4). Orifice surrounded by a low peristome, higher distally. Oral spines articulated, represented by spine bases only, diameter 20 µm, their number uncertain, some zooids showing only three or four, but as many as eight in others, arranged in an arc around the distal edge of the orifice (Pl. 1, figs 4-5, 7). One or two small oval or subcircular structures sometimes present distolateral to the orifice may be polymorphs, probably kenozooids but possibly adventitious avicularia (Pl. 1, figs 2, 4-5). Ancestrular characters unclear, a single distal zooid seemingly budded from the ancestrula. Periancestrular zone formed by 5 or 6 small zooids. Ovicells not observed in sample of 125 colonies, presumed to be lacking in the species.

Remarks - Colonies of *Antoniettella exigua* gen. et sp. nov. were found associated with scleractinian corals, both platy genera such as *Echinopora*, *Pachyseris* and *Fungophyllia*, and less often branching genera of Acroporidae. Found together with *A. exigua* are 26 other bryozoan species (4 cyclostomes and 22 cheilostomes), 20 of which are rare and represented by only one or two specimens. This bryozoan assemblage is dominated by *A. exigua* (54%), followed by *Reptadeonella* spp. (10%), *Disporella* spp. (8%), *Bryopesanser* sp. A (8%), *Cosciniopsis* sp. A (4%), Celleporidae spp. (4%)

and *Microporella* sp. A (2%). Colonies of all of these species tend to be rather small with the exception of *Reptadeonella* spp. Other groups of encrusters observed on the undersurface of the corals, including serpulids, molluscs and abundant thread-like foraminifera, often completely overgrow the bryozoans.

Distribution - Lower-Middle Miocene (Burdigalian-Langhian boundary) of East Kalimantan (Indonesia) (Fig. 1).

DISCUSSION

Antoniettella exigua gen. et sp. nov. colonies are typically small, spot-like, essentially subcircular to circular (Fig. 3d) and often multilayered (Fig. 3a; Pl. 2, fig. 5). Rarely colonies are more irregular in shape, elongated in one direction to form an equilateral triangle (minimum diameter corresponding to the base and maximum diameter corresponding to the height of the triangle), in general due to irregularities in the substrate or growth interference from other organisms such as cemented bivalves, foraminifera, serpulids and other species of bryozoans.

The ancestrula apparently budded a single zooid distally. Budding then proceeded in a spiral pattern for two generations of autozooids corresponding to the periancestrular zone, after which zooidal buds of increasing size were oriented radially in all the directions or only in one direction depending on the availability of substrate space. The ancestrula sometimes appears overgrown or obscured by secondary calcification or sediment (Pl. 2, fig. 4), giving the false impression that the oldest zooid is the smallest budded autozooid.

Colonies are characterised by thick margins (Pl. 2, fig. 2), which are 0.40 mm in height on average, and the production of up to four additional layers of zooids. These intracolony overgrowths always originate from the centre of the colony, directly above or near the ancestrula, partially or completely covering earlier layers of zooids (Pl. 2, fig. 5). The constancy in location of the overgrowth origins makes it extremely unlikely that they represent fouling of adult colonies by larvae of the same species (i.e., intracolonial overgrowths).

Analysis of colony size

Multilaminar colonies account for 60 (48%) of the 125 specimens studied (Fig. 3a). The majority (39%) of the multilaminar colonies have two zooidal layers, while 7% and 2% of the colonies have three and four layers respectively. The number of zooids forming the exposed frontal layer of the colony ranges from a minimum of 4 to a maximum of 68 (Fig. 3b). With respect to the number of exposed zooids, 7% of colonies have from 1 to 9 zooids, 27% from 10 to 19 zooids, 40% from 20 to 29 zooids, 19% from 30 to 39 zooids, 4% from 40 to 49 zooids, 1% from 50 to 59 zooids, and 2% from 60 to 69 zooids. The average diameter of colonies in about 80% of cases is in the range 1 to 3 mm, with only a few colonies (3%) less than 1 mm in diameter and a higher proportion (17%) more than 3 mm (Fig. 3c). There is no significant correlation between colony diameter and number of layers.

A survivorship curve (Fig. 4) has been constructed based on the pattern of size-frequency distribution of all 125 available colonies. The shape of such curves is primarily influenced by the change in mortality rate as colonies grow (McKinney & Taylor, 1997). The first portion of the curve, with the percentage of survivorship plotted on a logarithmic scale, is nearly horizontal up to an average colony diameter of 2 mm, indicating a very low initial mortality rate. Thereafter, the curve is a straight line, reflecting a constant probability of death.

Life history

The consistently small size and subcircular outline (Pl. 2, figs 1, 5) of the encrusting colonies of *Antoniettella exigua* gen. et sp. nov. invites comparison with so-called 'spot colonies' as defined by Bishop (1989). Classical examples of spot colonies among cribrimorph bryozoans, such as the Plio-Pleistocene species *Cribrilina puncturata* (Wood, 1844) from the Red Crag of England, are small in size (25-50 zooids with a colony diameter of 1.5-2 mm), approximately equidimensional in shape, and produce

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EXPLANATION OF PLATE 1

Antoniettella exigua gen. et sp. nov.

Fig. 1 - Holotype NHML BZ5842, group of zooids; scale bar = 500 μm.

Fig. 2 - Holotype NHML BZ5842, close-up of a hexagonal zooid; scale bar = 100 μm.

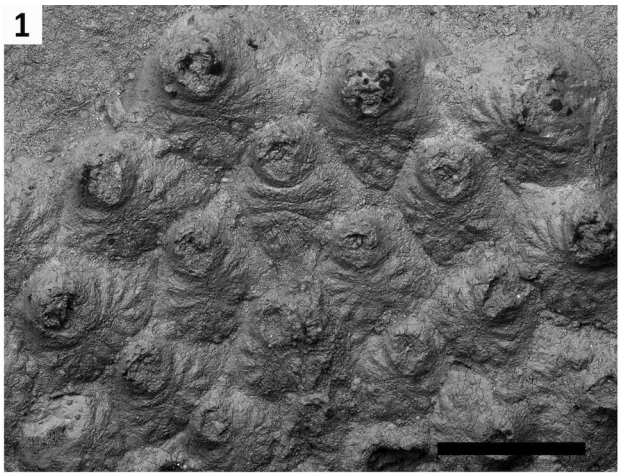
Fig. 3 - Paratype NHML BZ5843, close-up of a pentagonal zooid, note possible predator boring to the lower right of the orifice; scale bar = 100 μm.

Fig. 4 - Paratype NHML BZ5843, close-up of the orifice: showing two distolateral oval structures (kenozooids or adventitious avicularia); scale bar = 50 μm.

Fig. 5 - Paratype NHML BZ5843, close-up of an orifice showing four oral spine bases; scale bar = 100 μm.

Fig. 6 - Paratype NHML BZ5844, close-up of zooid located on the edge of the colony showing two lateral oval pore windows on the upper left margin; scale bar = 100 μm.

Fig. 7 - Paratype NHML BZ5844, close-up of an orifice showing eight oral spine bases; scale bar = 100 μm.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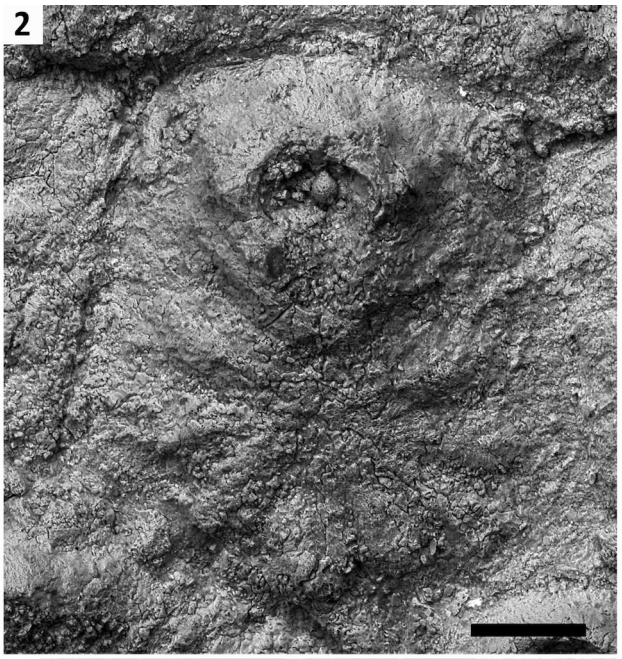
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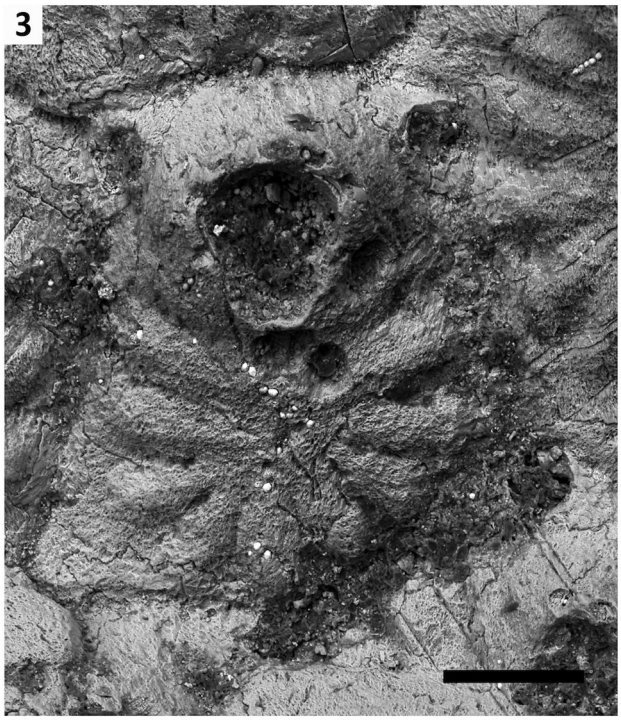
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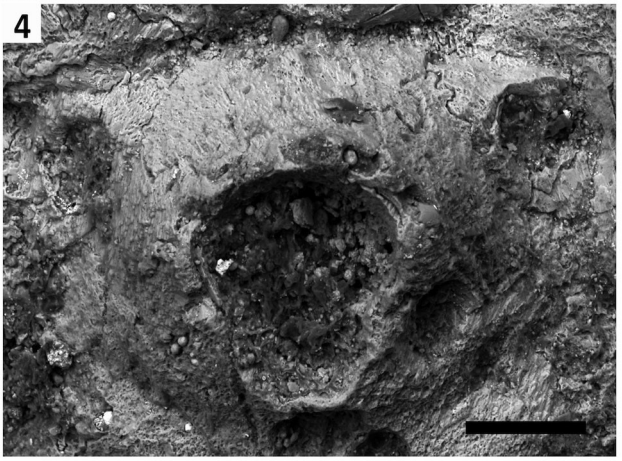
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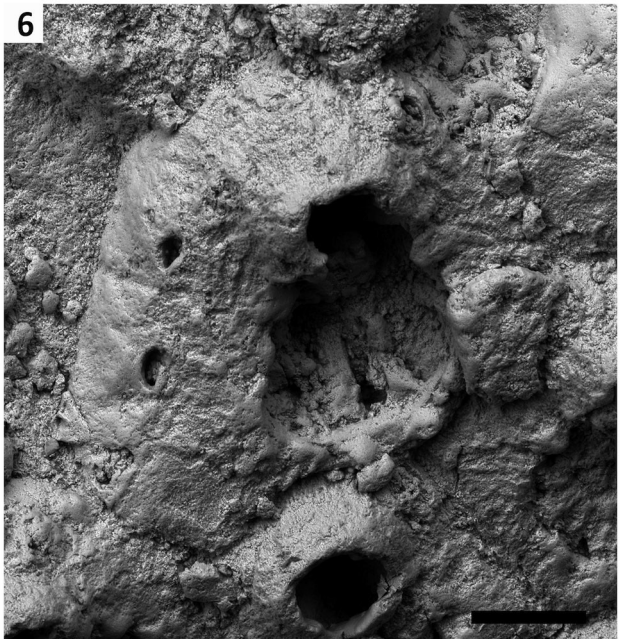
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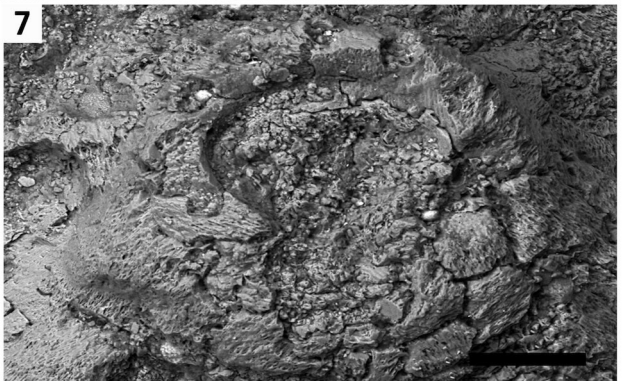
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ovicells as early as the three-zooid stage (Bishop, 1989). Colonies of *A. exigua* match this definition in size and shape, being approximately as broad as long and typically having only 20-30 exposed zooids with a colony diameter of 1-3 mm. However, none of the colonies observed have ovicells, an absence which is discussed below.

Spot colonies were interpreted by Bishop (1989) as being adapted for the colonization of temporal refuges provided by substrates that are available to be colonized only for a short period of time. In these circumstances it is imperative that colonies recruit speedily, grow quickly and produce larvae rapidly. Colonies of *Antoniettella exigua* usually grew on the undersides of platy scleractinian corals, except for a few specimens observed encrusting the branches of ramose corals. These substrates are likely to have been long-lasting, in contrast to substrates typically utilized by spot colonies, potentially offering a large surface area for the development of extensive two-dimensional colonies. However, it is possible that storms or rivers periodically introduced sediment into the system, causing the demise of these encrusting communities (cf. Berning et al., 2009), or that the undersides of the corals were normally buried and only occasionally available for encrustation over relatively short periods of time.

A further contrast between *Antoniettella exigua* and classical spot colonies is evident when survivorship curves are compared between this species and *Cribrilina puncturata*. The survivorship curve for *C. puncturata* shows a low initial mortality rate followed by an abruptly increasing rate. The rapidity of mortality increase correlates with the height of the concave surfaces of the bivalve shells encrusted by *C. puncturata*, with the most rapid rates in the smallest substrates which were usually the most ephemeral (Bishop, 1992). While the first portion of the *C. puncturata* curve has approximately the same trend as *A. exigua*, even though the mortality rate is lower, the second part contrasts with the straight-line relationship seen in *A. exigua* (Fig. 4) and indicating a constant mortality rate for each size class. Furthermore, there is no correlation between substrate and colony size in *A. exigua*.

Other examples of spot cribrimorphs have been reported in Maastrichtian thalassinoidean burrows by Voigt (1987), on *Lepidocyclina* tests from the early Chattian by Berning et al. (2009) and in Recent caves by Harmelin (1986). The dwarf Maastrichtian cribrimorphs were observed on the walls of mm-scale borings or cavities produced by sponges and bivalves that were too narrow for most other encrusting organisms. Abundant and well-preserved cribrilinid species form spot colonies on lepidocyclinids in a relatively turbid shallow-water setting. Minute forms of Recent *Cribrilaria minima* Harmelin, 1984 and *C. pedunculata* (Gautier, 1956) are quite abundant in obscure caves, which presumably acted as refuges. However, these occurrences of spot colonies may also be explained in terms of low food availability (Okamura et al., 2001), or as response to a potential frequent disturbance and abrasion due to suspended particles and high rates of sedimentation (Berning et al., 2009).

The small size of *Antoniettella exigua* colonies in the Miocene coral reef habitat of Kalimantan is comparable with two bryozoans common under foliaceous colonies in the Recent of Jamaica, the ascophoran *Drepanophora tuberculatum* and the cyclostome *Disporella fimbriata* (see McKinney & Jackson, 1989, pp. 110-112). Described as 'solitary' colonies, these species recruit very rapidly, release larvae within three months, and usually die within six months.

In the case of *Antoniettella exigua* the spot-like morphology is always coupled with thickened colony margins and quite often with multilaminar growth. In general, thick colonies present a greater barrier to overgrowth by competitors than thin colonies (Buss, 1980, 1981), while multilaminar growth potentially allows fouling organisms to be smothered. These attributes suggest that *A. exigua* may place more emphasis on resisting overgrowth (e.g., Pl. 2, fig. 8) and fouling than is typical for ephemeral spot colonies.

Large stable substrata in modern tropical reefs, such as corals and coral rubble, are encrusted predominantly by cheilostome species (e.g., *Parasmittina* sp., *Rhynchozoon* spp. and *Trematooecia aviculifera*) that produce large colonies with a prevalence of frontal budding and self-overgrowth that increase colony thickness as an adaptation to cope with continual interactions with highly

EXPLANATION OF PLATE 2

Antoniettella exigua gen. et sp. nov.

Fig. 1 - Holotype NHML BZ5842, view of entire colony; scale bar = 500 μm.

Fig. 2 - Paratype NHML BZ5845, view of the edge of a colony showing two thick layers; scale bar = 500 μm.

Fig. 3 - Holotype NHML BZ5847, ?tatiform ancestrula and periancestrular zone of a single-layered colony; scale bar = 200 μm.

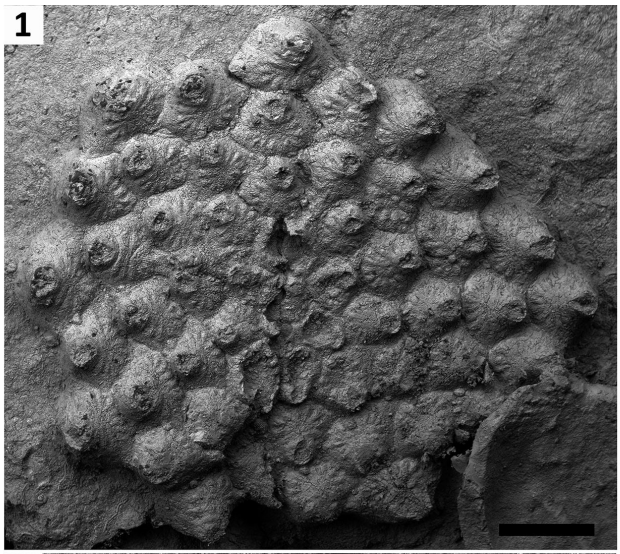
Fig. 4 - Holotype NHML BZ5847, close-up of the ?tatiform ancestrula; scale bar = 200 μm.

Fig. 5 - Paratype NHML BZ5844, view of a two-layered colony, the white line marking the outline of the second layer of zooids; scale bar = 500 μm.

Fig. 6 - Paratype NHML BZ5844, view of the pseudoancestrula appearing as a smaller autozooid; scale bar = 200 μm.

Fig. 7 - Paratype NHML BZ5845, view of pseudoancestrula; scale bar = 200 μm.

Fig. 8 - Paratype NHML BZ5846, example of overgrowth of a lichenoporid cyclostome (left) by *Antoniettella exigua*; scale bar = 500 μm.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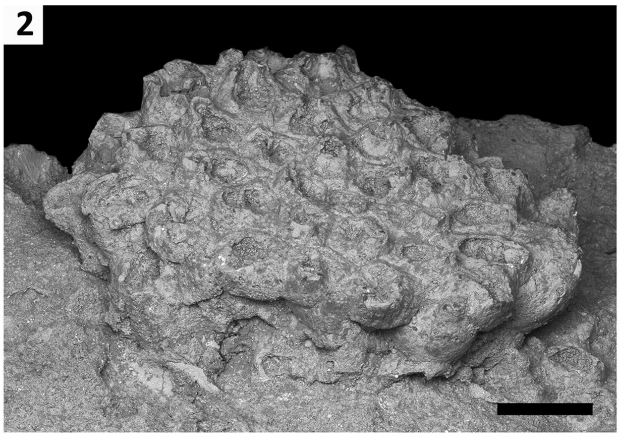
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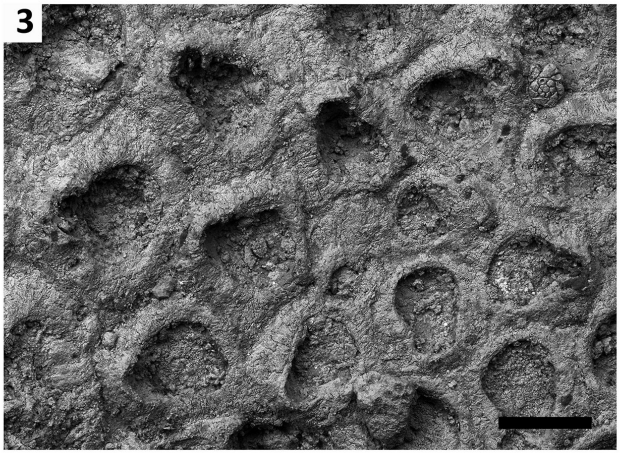
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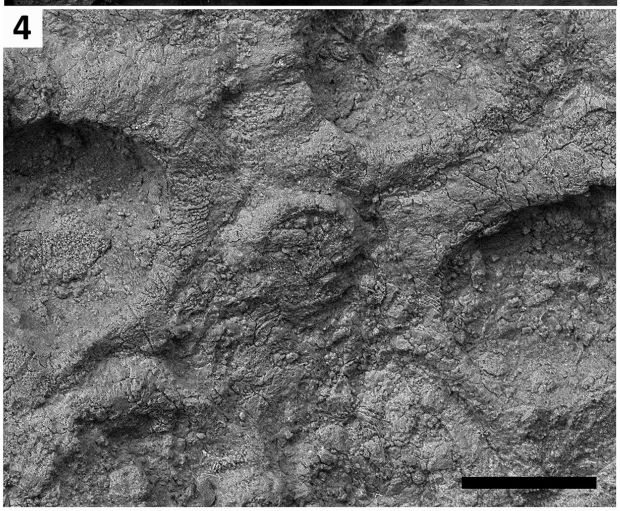
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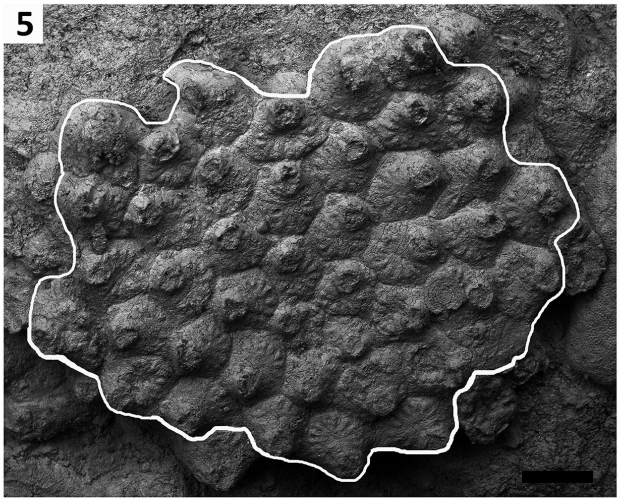
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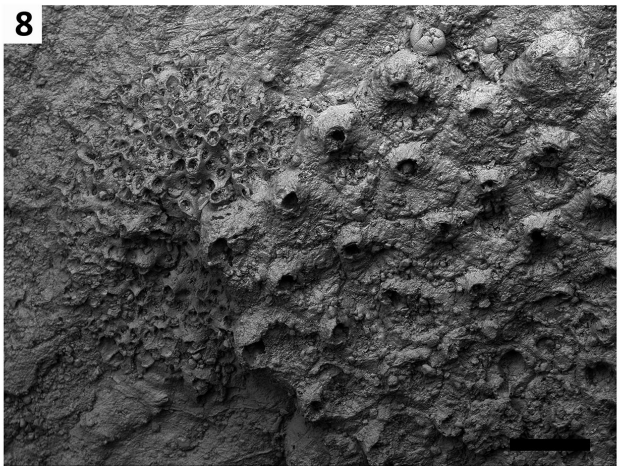
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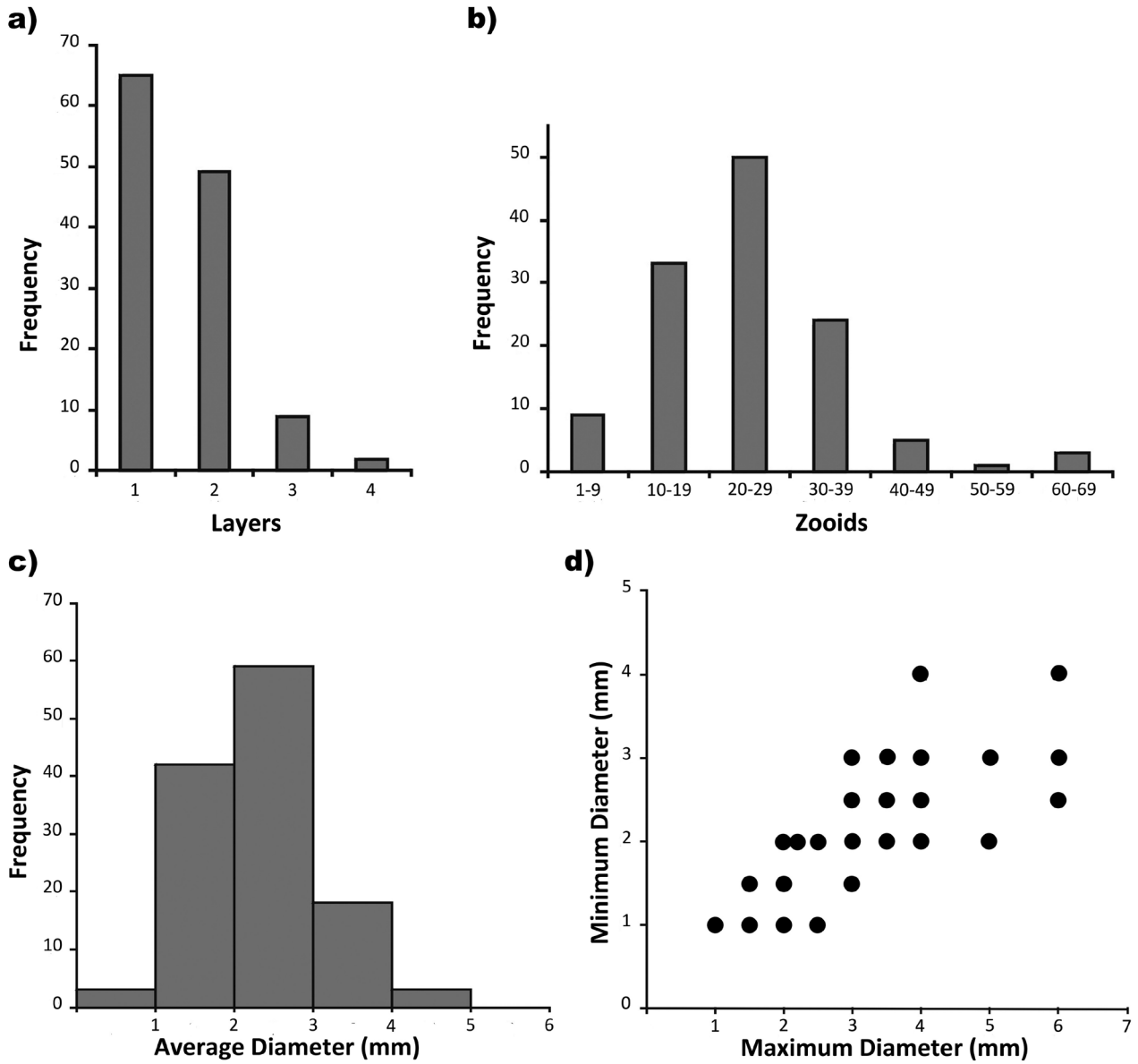

Fig. 3 - Graphs summarizing quantitative data for *Antoniettella exigua* gen. et sp. nov. a) Histogram of number of layers of zooids in each colony. b) Histogram of number of zooids per colony. c) Histogram of average diameters of colonies. d) Plot of minimum versus maximum colony diameters.

aggressive spatial competitors and predators (McKinney & Jackson, 1989, p. 162). The capacity for frontal budding in ascophoran cheilostomes is generally dependent on the presence of areolae and a hypostegal coelom (Lidgard, 1985), structures lacking in cribrimorphs such as *Antoniettella exigua*. Nonetheless, some ascophoran species without a hypostegal coelom and areolae, such as *Celleporella hyalina* (Linnaeus, 1767), are able to develop frontal buds from frontally directed pore chambers located near the proximolateral margins of the zooids. There is no evidence for comparable pore chambers in *A. exigua*. Different types of frontal budding *sensu-lato* may also occur among anascans and cribrimorphs. For example, the Recent anascan *Antropora tincta* (Hastings, 1930) is capable of producing multilaminar colonies through eruptive frontal budding, some zooids continuing to grow upwards to extend their vertical walls above the frontal surfaces of adjacent zooids and thence to bud laterally across the old colony surface (Lidgard, 1985). Frontal budding is unusual in cribrimorphs. However, the genus *Vicariopora* Zágoršek & Kázmér, 2001 from the Eocene of Hungary develops multilamellar, columnar colonies with concentric zooecial layers. In addition, this unusual growth form has been recorded as result of the expansion of cuticle and coelomic tissue derived from pelmatidia in *Corbulipora,* and through a special type of pore chamber in *Anaskopora* (Bock & Cook, 2001). Pelmatidia are lacking in *Antoniettella exigua* and though pore windows are visible at growing edges (Pl. 1, fig. 6) these are not exposed in mature zooids. Therefore, neither of the known modes of cribrimorph frontal budding appear to occur in *A. exigua* and, unfortunately, the imperfect preservation of all available specimens does not allow the origin of frontal budding to be ascertained in this bryozoan.

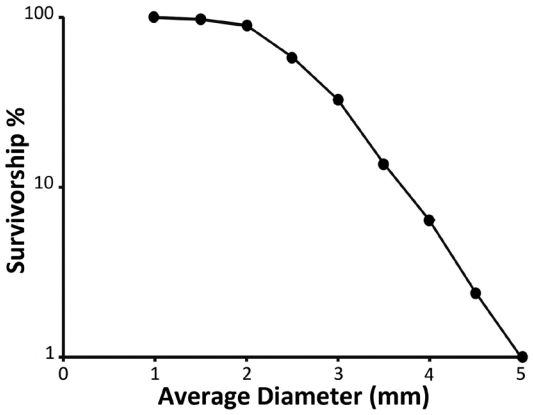

Fig. 4 - Survivorship curve based on the average diameter of 125 available colonies of *Antoniettella exigua* gen. et sp. nov.

Nevertheless it is clear that overgrowths start directly above or near the ancestrula more or less at the centre of the colony, as is frequently the case in ascophoran cheilostomes, particularly schizoporellids and celleporids (Ristedt, 1996). The likelihood is that frontal budding in *A. exigua* originates through upward growth of the ancestrula itself, producing a pseudoancestrula resembling a small autozooid in the new layer. This pseudoancestrula in turn may then have produced its own frontal bud to initiate a third layer of zooids, etc.

The lack of ovicells complicates the recognition of *Antoniettella exigua* as a classic spot colony which are sexually mature at a small colony size (Bishop, 1989). Two possible reasons for this absence can be suggested. First, it is possible that the population of *A. exigua* sampled was non-reproductive because it inhabited a marginal setting atypical for the species. If this is true, one would expect to find source populations of the species from more optimal environments in which ovicells are present. Such populations have not been found so far. Alternatively, *A. exigua* may have been an internal brooder. Internal brooding has been reported among numerous families of cheilostome bryozoans, including anascans belonging to Flustridae, Candidae, Steginoporellidae, Poricellariidae and Chlidoniidae, and ascophorans belonging to Adeonidae, Adeonellidae, Watersiporidae, Cryptosulidae and Euthyrisellidae (Ostrovsky et al., 2006). However, internal brooding is poorly documented among cribrimorphs, although it is perhaps present in two Recent species from South Africa, *Cribrilina simplex* O'Donoghue & de Watteville, 1935 and *C. dispersa* O'Donoghue & de Watteville, 1937. With regard to the former, O'Donoghue & de Watteville (1935, p. 210) remarked: "Careful examination of all the colonies in the collection, some of which are of a fair size, and presumably age also, failed to reveal any ooecia…".

In conclusion, *Antoniettella exigua* developed small colonies usually on the undersides of platy corals inhabiting muddy reefs during the late Early Miocene in the region that is now East Kalimantan. Some aspects of this cribrimorph cheilostome seem to match those of a classical spot colony adapted to the exploitation of short-lived substrates. However, it is more likely that the corals encrusted provided long-lived substrates, and that the small size of *A. exigua* was an adaptation to low food supply (Okamura et al., 2001) in the cryptic recesses beneath the reef corals, or an adaptation to the high sedimentation rates and turbidity usually regarded as detrimental to the growth of encrusting bryozoans (Berning et al., 2009), along with a strategy of occupying and defending a tiny patch of substrate against lateral overgrowth and fouling.

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