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Journal of Natural History

ISSN: 0022-2933 (Print) 1464-5262 (Online) Journal homepage: www.tandfonline.com/journals/tnah20

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Journal of Natural History
Vol. 45, Nos. 31–32, August 2011, 1905–1924

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(Received 1 October 2010; final version received 14 March 2011; printed 3 June 2011)

Three new species of *Astreopora* (Hexacorallia: Scleractinia: Acroporidae), from Cenderawasih Bay in West Papua, exhibit morphological innovations for this conservative genus, extant since the Cretaceous. Two species are fully branching, a condition never previously described for *Astreopora*: *Astreopora cenderawasih* sp. nov. has dendritic branching, also seen in the confamilial genus *Montipora*, whereas branches of *A. acroporina* sp. nov. possess an axial corallite, regarded as the key morphological innovation facilitating rapid diversification and dominance of reefs in the younger, confamilial and most diverse genus *Acropora* (staghorn corals). We propose that these novel characters may be parallelisms indicating deep familial homologies. The third species, *Astreopora montiporina* sp. nov., has expansive coenosteum, reminiscent of plating *Montipora*. The new species form part of the most species-rich *Astreopora* assemblage reported to date, comprising 14 species. The unique tectonic and eustatic history of Cenderawasih Bay may have played a role in the evolution of these new species.

Keywords: coral reefs; axial growth; diversification; speciation; hexacorals, coral triangle

Introduction

Astreopora is a small and extremely conservative genus of the reef-building coral family Acroporidae. Family members also include *Acropora* and *Montipora*, the most species-rich genera of reef-building corals: because of these, Acroporidae dominates diversity and abundance on most modern Indo-Pacific coral reefs (Wallace 1999; Veron 2000). Living *Astreopora* species occur only in the Indo-Pacific: Lamberts (1982) revised the living members and recognized 10 species, one of which (*Astreopora elliptica*) was later synonymized with the type species *Astreopora myriophthalma* by Veron and Wallace (1984). One new species was described by Moll and Best (1984) and two by Veron and Wallace (1984), bringing the number of modern species to 13 (12 reported in Veron 2000 plus *Astreopora lambertsi* Moll and Best 1984). Many more species have been recorded from the fossil record throughout Europe and the Middle East (28 species listed in Felix 1925), the Americas (at least seven species; Vaughan 1919; Frost and Langenheim 1974; Budd et al. 1994) and the Indo-Pacific (at least three species; Hoffmeister 1932, 1945).

Living species of *Astreopora* recorded to date exhibit only three simple, non-branching colony forms: massive, encrusting (laminar) or plating (listed in Table 1), with some intermediates and only a suggestion of branching in some encrusting forms

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ISSN 0022-2933 print/ISSN 1464-5262 online

DOI: 10.1080/00222933.2011.573098
http://www.informaworld.com

Table 1. *Astreopora* species recorded in Cenderawasih Bay.

Species	No. of sites	Mean Calice Diameter (mm)*	Colony form
Living, Cenderawasih Bay:			
A. myriophthalma (Lamarck, 1816) R	31	1.79	massive
A. gracilis Bernard, 1896 R	27	1.25	massive
A. listeri Bernard, 1896 R	29	1.72	massive
A. ocellata Bernard, 1896 R,P	5	2.51	massive
A. suggesta Wells, 1954 R	15	1.34	encrusting to massive
A. cucullata Lamberts,1980 R	6	1.54	submassive, encrusting, plates
A. incrustans Bernard, 1896 R,P,S	9	1.75	submassive, encrusting, plates
A. macrostoma Veron and Wallace, 1984 R	3	to 3.3	submassive, encrusting, plates
A. randalli Lamberts, 1980 R,P,S	9	1.45	submassive, encrusting, plates
A. expansa Brüggemann, 1877 R,P,S	13	1.47	plates with epitheca
A. montiporina sp. nov. R,P,S	4	1.18	plates with epitheca
A. moretonensis Veron and Wallace, 1984 R,P	1	2.2	encrusting with upright tubes
A. cenderawasih sp. nov. R,P,S	2	1.40	dendritic branching
A. acroporina sp. nov. R,P,S	4	1.15 (radials)	axial branching
Living, elsewhere Indo-Pacific:			
A. scabra Lamberts, 1982	–	~2.0	massive (glomerate)
A. lambertsi Moll and Best, 1984	–	1.35	massive (glomerate)

Notes: R, recorded in the field; P, confirmed from photograph; S, confirmed from specimen(s).
*From Veron and Wallace (1984), Moll and Best 1984, Lamberts (1982, 1980), Bernard (1896) and this study.

because of folded edge-zones or the influence of commensal organisms. Only one additional distinct form is seen in the fossil species *Astreopora goethalsi* Vaughan, 1919, *Astreopora antiguensis* Vaughan, 1919 and *Astreopora portoricensis* Vaughan, 1919 (which may be synonyms, C.W. personal observation of types) from the Americas, have upright cuneate or club-like plates similar to those seen in another Acroporidae genus, *Isopora* (Wallace et al. 2007). Additionally, two fossil species (*Astreopora hexaphylla* Felix, 1906 and *Astreopora esperanzae* Frost and Langenheim, 1974 from late Cretaceous to Middle Eocene sites) are reported as sometimes being ramose (Baron-Szabo 2006), but very little information is available on the nature of this branching. A form termed "reptoid" for some early fossils seems to describe an early growth stage of a laminar form (Frost and Langenheim 1974). Remarkably little variety is shown in the main skeletal features of corallite shape and size and coenosteal fine structure among both living and fossil *Astreopora* species (Lamberts 1982; Veron and Wallace 1984; Frost and Langenheim 1974).

In contrast to the known fossil and extant *Astreopora*, all species of the confamilial genus *Acropora* share a key morphological feature, axial branching, similar to that seen in the flowering plants (Gould 2002; Donoghue 2005). This is thought to have contributed to early and continued diversification of *Acropora* (Dauget 1991; Wallace 1999, 2008; Wallace and Rosen 2006; Chen et al. 2009). This feature is also present in some species of the genus *Isopora*, which has been distinguished from *Acropora* by genetic distance, reproductive mode, and skeletal morphology and microstructure (Fukami et al. 2000; Wallace et al. 2007). About half the species of *Acropora* have indeterminate growth, allowing a single colony to occupy large areas of reef and sometimes to increase population size by breakage and redistribution of branches. Other species have determinate growth, in which colonies grow into more or less symmetrical shapes, although this shape is sometimes repeated in a layering process (Wallace 1999). Before the present study, neither determinate nor indeterminate branching growth had been described for *Astreopora*, although indeterminate growth by layering of unbranched plates is reported in *Astreopora expansa* (e.g. Veron 2000: 435).

In this paper we describe three new species from Cenderawasih Bay in the Papuan Bird's Head Seascape and examine the significance of characters previously not recorded for *Astreopora*, in relation to the evolution of Acroporidae and of reef corals in general.

Materials and methods

Location, field methods and biodiversity analysis

Cenderawasih Bay, Papua, Indonesia (Figure 1), is a large north-facing bay of ca. 68,000 km^2 and depths up to 2140 m. The bay has fringing coral reefs along coastlines and islands, and patch reefs within open waters. Approximately 20% of the bay is designated National Park (Taman Nasional Teluk Cenderawasih, TNTC) (Figure 1). In February 2006, a survey of coral species diversity (herein meaning "richness" per se, rather than a diversity index) was conducted at 33 sites, each comprising deep (10–40 m) and shallow (<10 m) components in this bay. A full description of sites, methods and species diversities is given in Turak and DeVantier (forthcoming). Species present in each site were assessed by two 45-minute surveys conducted using SCUBA (cf DeVantier et al. 1998). All easily recognizable species of *Astreopora* were recorded. Unknown species and colonies that were difficult to identify *in situ* were photographed, and representative specimens were collected for microscopic examination at the Museum of Tropical Queensland (MTQ). Identifications made in the field were reassessed using binocular microscopy and reference to type and mentioned specimens of all *Astreopora* species in MTQ and some on loan, as well as descriptions in Lamberts (1980, 1982), Veron and Wallace (1984) and Veron (2000). For comparison of colony shapes with modern material, fossil types from Vaughan (1919) were examined and photographed in the United States Natural History Museum (NHNM) Washington DC in 2008 and 2009.

Taxonomic analysis

Specimens of the new species described here and comparative material from other species were examined, and characters were measured, using a Wild M8 binocular

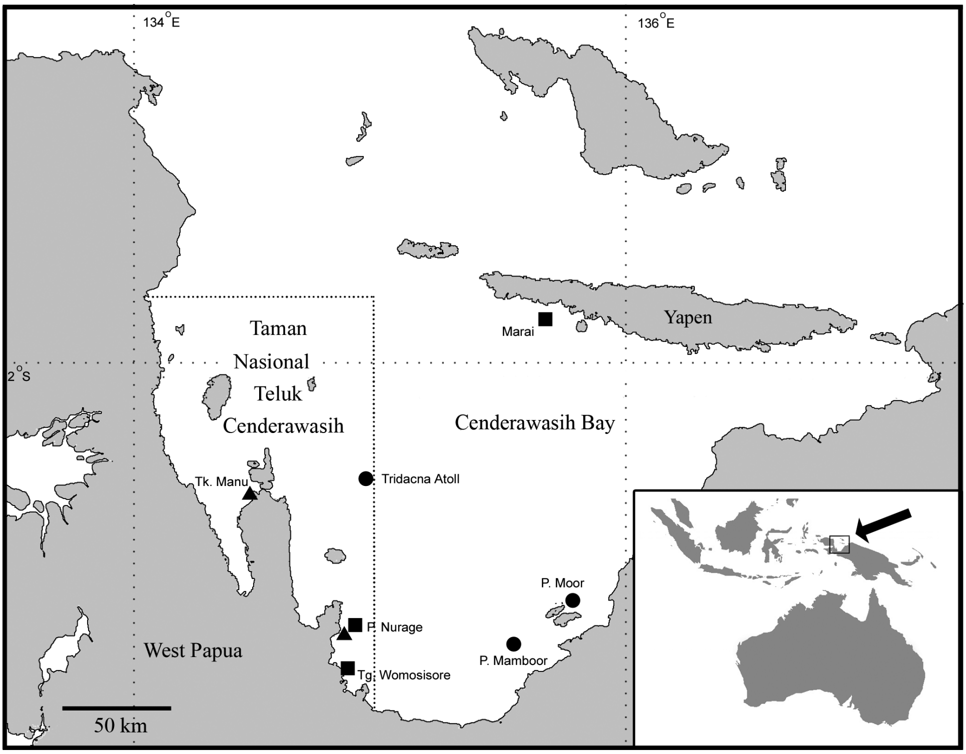

Figure 1. Map of Cenderawasih Bay, West Papua, showing locations for new *Astreopora* species. Symbols: triangles, *Astreopora cenderawasih*; squares, *Astreopora acroporina*; circles, *Astreopora montiporina*; (see Turak and DeVantier, forthcoming, for locations of all sample sites).

microscope with measuring graticule. Scanning electron micrographs, prepared using the JEOL JSM-5410LV scanning electron microscope at James Cook University and commercially prepared geological thin sections were used for comparison and illustration. Measurements of quantitative characters were taken for 10 corallites per specimen. Types of the new species are deposited in MTQ. Duplicate specimens of each of the three species are deposited in the Fisheries department, State University of Papua, Manokwari, West Papua (UNIPA), but these were not examined.

Results

Species diversity

Our study confirmed that 14 species of *Astreopora* were present in Cenderawasih Bay, including 11 of the 13 currently valid species and three which are described as new to science (Table 1). Species richness of *Astreopora* in Cenderawasih Bay exceeds previous records of six species during the Snellius-II Expedition in Eastern Indonesia (Best et al. 1989), nine from the Great Barrier Reef (Veron and Wallace 1984; Veron 2000) and up to 10 species for the entire Indonesian archipelago (based on Veron 2000), the most *Astreopora*-rich locations known to date. It also exceeds species counts of 10 and nine species respectively in neighbouring parts of the Bird's Head seascape: Raja Ampat (60,000 km^2) and FakFak-Kaimana (20,000 km^2) (Turak and DeVantier forthcoming). No fossil deposits have yielded as many as 10 species of *Astreopora* (Felix 1925; Vaughan 1919; Budd et al. 1994; Stemann 2004; Johnson and Kirby 2006). Cenderawasih Bay is therefore significant in both time and space for the presence of such an unusually high number of species.

Local richness was also exceptional in Cenderawasih Bay, with individual reef sites hosting up to nine species of *Astreopora* (Turak and DeVantier forthcoming). *Astreopora* usually occurs with a diversity of fewer than four species per whole reef (Lamberts 1982; Veron and Wallace 1984; Veron 2000).

Systematics

Family **ACROPORIDAE** Verrill, 1901

Massive or ramose colonies by extratentacular budding; corallites small, synapticulothecate, pseudo-costate, slightly differentiated from coenosteum. Septa non-exert, in two cycles, formed by simple spiniform trabeculae projecting inward and upward from vertical mural trabeculae, commonly fusing to form laminae. Columella absent or trabecular and weak. Dissepiments thin and tabular when developed. Coenosteum extensive, light reticulate, flaky, generally spinose or striate on surface. Polyps hermaphrodite with internal or external fertilization followed by internal or external larval development respectively.

Occurrence: Upper Cretaceous to Recent.

Genus ***Astreopora*** De Blainville, 1830

Colony massive, encrusting, plating or ramose. Axial corallite rarely present. Columella absent, but pseudo-columella, formed by trabecular extensions of the septa, may be present. Coenosteum reticular, formed by outwardly inclined trabeculae, with spinose surface. Dissepiments tabular.

Occurrence: Upper Cretaceous to Recent; Europe, Caribbean and Indo-Pacific.

Astreopora cenderawasih sp. nov.
(Figures 2A, 3)

Type locality

Cenderawasih Bay, West Papua.

Material examined

Holotype. MTQ G60697 Indonesia, West Papua, Cenderawasih Bay, Pulau Nurage TNTC 3°1.8′S, 134°50.1′ E; depth 2 m, collected E. Turak 19 February 2006.

Paratypes. MTQ: G60695 Indonesia, West Papua, Cenderawasih Bay, Pulau Nurage TNTC 3°1.8′S, 134°50.1′E; depth 4 m, collected L. DeVantier 19 February 2006; G60696 Indonesia, West Papua, Cenderawasih Bay, Teluk Manu TNTC 2°28.9′ S, 134°33.8′ E, depth 4 m, collected L. DeVantier 22 February 2006; G60698 Indonesia, West Papua, Cenderawasih Bay, Pulau Nurage TNTC 3°1.8′ S, 134°50.1′ E, 2 m collected E. Turak 19 February 2006.

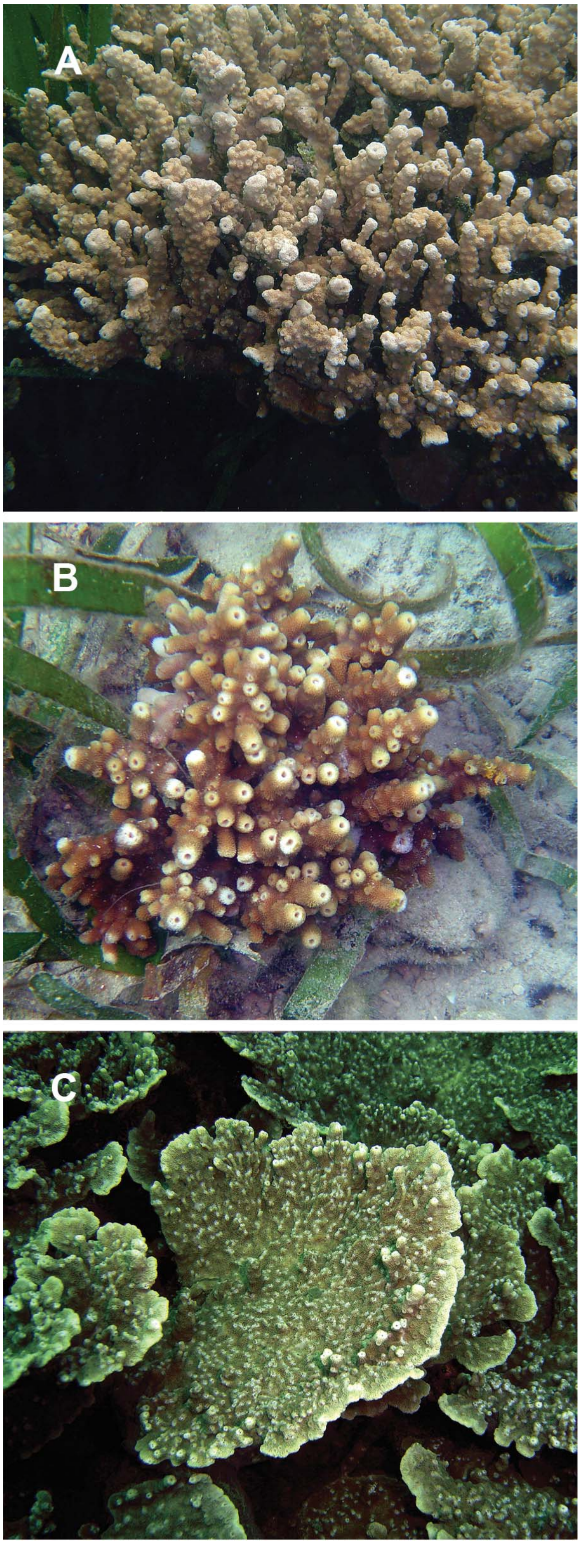

Figure 2. Field appearance of the three new *Astreopora* species in Cenderawasih Bay, West Papua. (A) *Astreopora cenderawasih*; (B) *Astreopora acroporina*; (C) *Astreopora montiporina*.

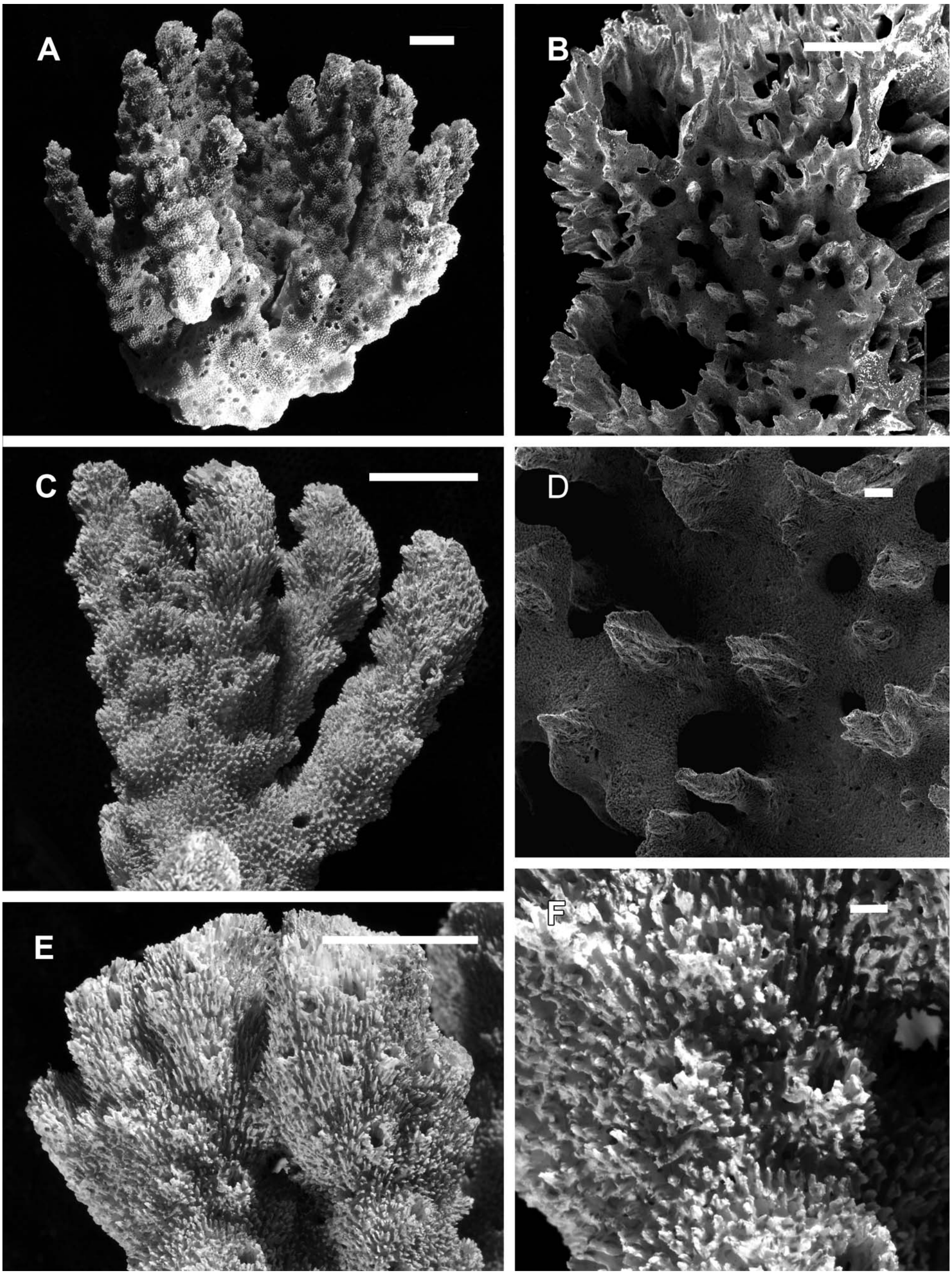

Figure 3. *Astreopora cenderawasih* sp. nov. (A–C) Holotype MTQ G60697; (D–F) paratype MTQ G60695. (A) Whole specimen; (B) scanning electron micrograph (SEM) of coenosteal spinules; (C) close up of group of branches formed by dendritic division of basal branch; (D) SEM of branch tip, coenosteum with no axial corallite; (E) branch tip; (F) SEM showing radial corallite detail. Scale bars: A, C, E: 10 mm; B, F: 1 mm; D: 100 μm.

Etymology

Named for the bay in which it was found, “bird of paradise” in Indonesian.

Diagnosis

Colony indeterminate in growth, mostly consisting of vertical branching units, but some small plates may occur at the base; branching units develop from a thick basal branch that divides into several branchlets, which may also divide; corallites occur up to the tip, which is formed of coenosteum. Corallites tubular, immersed, conical or appressed, with round to oval openings, irregularly scattered on branch surface and mostly not touching; outer diameter of opening 1.5–3.0 mm; inner diameter 0.8–2.0 mm; primary septa all present as laminae to 1/3R, forming a pseudo-columella deeper in corallite; secondary septa some to all present as laminae or points. Coenosteum evenly distributed spinules which are tall, irregular cone-shaped with blade-like ridges running lengthwise; tips of branches formed by irregular reticulate growth without spinules.

Skeletal characteristics

Holotype. Part of colony, 100 mm greatest width and 86 mm height. Corallum is an irregular arrangement of vertical palmate branching units, flattened in cross-section, without axial corallites, given off from an irregular basal region. In each palmate unit, a basal branch divides into two to several branches towards its tips. Corallites tubular, immersed, conical or appressed, with round to oval openings, irregularly scattered on branch surface and mostly not touching; outer diameter of opening 1.75–2.17 mm, inner diameter 0.88–1.98 mm; primary septa all present as irregular vertical laminae, with some to all extending to form a pseudo-columella; secondary septa present as points or narrow plates up to 1/4R. Coenosteum evenly distributed spinules which are tall, irregular cone-shaped with blade-like ridges running lengthwise; tips of branches formed by irregular reticulate growth without spinules.

Variations shown in paratypes. Branching diverges from the palmate mode in some colonies, with branches sometimes thickening towards their centre and sometimes extending at angles from each other; branches are sometimes in the form of chimney-like columns (similar to those occasionally seen in *Astreopora moretonensis*).

Field characteristics

Colour pale to dark brown and purple-grey, colonies spreading to around 1 m diameter.

Habitat

Sandy reef flat and upper reef slope at 2–5 m.

Distribution

To date, recorded from Cenderawasih Bay only; see Figure 1.

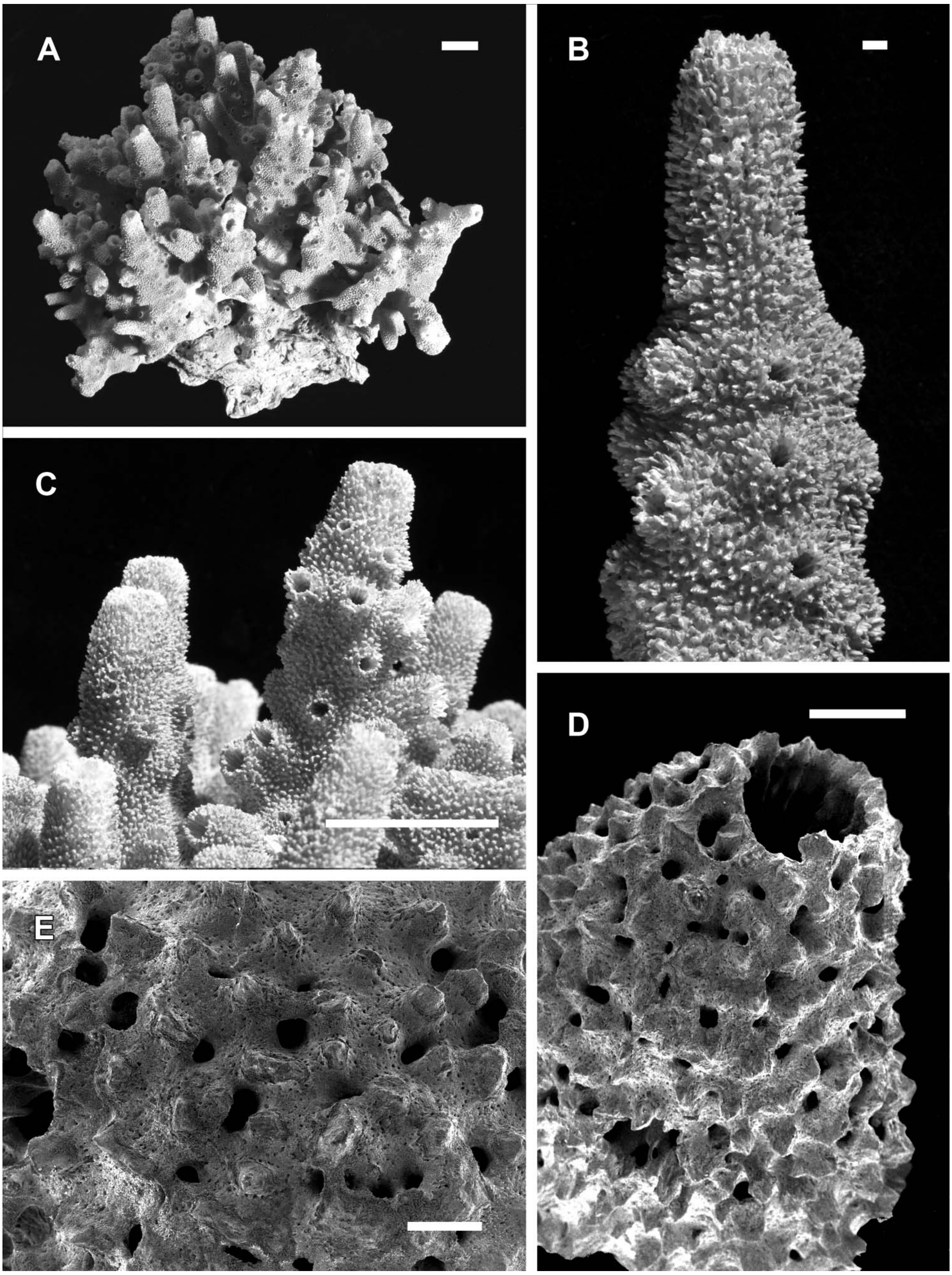

Figure 4. *Astreopora acroporina* sp. nov. Holotype (A–C) MTQ G60692; (D, E) MTQ G60691; (A) Whole corallum; (B) branch tip showing axial and radial corallites; (C) group of branches; (D) scanning electron micrograph (SEM) showing coenosteal spinules; (E) SEM showing axial corallite. Scale bars: A, C: 10 mm; B, D: 1 mm; E: 500 μm.

Astreopora acroporina sp. nov.
(Figures 2B, 4)

Type locality

Cenderawasih Bay, West Papua.

Material examined

Holotype. MTQ: G60692 Indonesia, West Papua, Cenderawasih Bay, Pulau Nurage TNTC 3°1.8′ S, 134°50.1′ E; depth 3 m collected L. DeVantier 19 February 2006.
Paratypes. MTQ: G60691, G60693 Indonesia, West Papua, Cenderawasih Bay, Tanjung Womosisore TNTC 3°5.9′ S, 134°50.3′ E, depth 1 m, collected E. Turak 18 February 2006; G60694 Indonesia, West Papua, Cenderawasih Bay, South Yapen, Marai, 1°43.9′ S, 135°46.3′ E, depth 1 m, collected E. Turak 14 February 2006.

Etymology

Named for its central or axial corallite, as in *Acropora*.

Diagnosis

Colony consisting of irregular vertical branching units with an axial corallite and a greater or lesser degree of secondary branching, the secondary branches also having an axial corallite. Basal areas of one smaller colony have some solitary corallites on a roughly hemispherical structure, from which only a few branches are given off. Axial corallites extend throughout the extent of branches. Radial corallites have a similar appearance to axial corallites, without the extended axis, i.e. they are tubular with round openings. These occur scattered and not touching on both branches and branchlets, the longer radials only distinguished from axials by the absence of radial corallites. Coenosteum of evenly distributed spinules, which are low conical with irregular blade-like tops.

Skeletal characteristics

Holotype. Part of colony, 125 mm greatest width and 100 mm height, with 10 supplementary fragments 14–53 mm long and nine smaller fragments. Corallum consists of numerous branches, irregular in shape and length, given off from an irregular base. Branches up to 70 mm long, 11–15 mm basal width but in some cases wider further up the branch. Branchlets and incipient branchlets are given off in an irregular arrangement along the extent of the branch. Each branch or branchlet has an axial corallite running from base to tip. Axial corallite diameters: outer 2.58–4.45 mm, inner 1.5–2.51 mm; six primary septa present, as complete or incomplete vertical plates, flaky in appearance, sometimes broken into segments, all or some twisting to form a trabecular pseudo-columella towards the base of the corallite; secondary septa all present, up to 1/4R. “Radial” corallites occur scattered and not touching on both branches and branchlets; the longer radials only distinguished from axials by the absence of radial corallites. Corallite shape conical to tubular with round opening; outer diameter

1.47–1.56 mm, inner diameter 1.06–1.25 mm; radial septa vertical laminae or broken laminae, some to all meeting deep within the corallite; secondary septa present up to 1/4R as laminae to broken laminae. Coenosteum the same on and between corallites: evenly distributed spinules which are low conical with an irregular blade-like top.
Variations shown in paratypes. Two of the paratypes (G60691 and G60694) have about half of the corallum with very little branching, the corallites being of varying heights and some appearing to be incipient axial corallites, while the other half of the corallum is fully branching.

Field characteristics

Colour pale brown-grey, colonies mostly no more than 200 mm in diameter.

Habitat

Sandy reef flat and upper reef slope at 1–2 m.

Distribution

To date, recorded from Cenderawasih Bay only; see Figure 1.

Astreopora montiporina sp. nov.
(Figures 2C, 5)

Type locality

Cenderawasih Bay, West Papua.

Material examined

Holotype. MTQ: G60711 Indonesia, West Papua, Nabire, southeast Moor, 2°56.1′S, 135°44.9′ E; depth 12 m collected E. Turak 15 February 2006.
Paratypes. MTQ: G60710 Indonesia, West Papua, Nabire, southeast Moor, 2°56.1′S, 135°44.9′ E; depth 12 m collected E. Turak 15 February 2006; G60712 Indonesia, West Papua, Tridacna Atoll, 2°29.7′S, 134°59.0′ E; depth 25 m collected E. Turak 20 February 2006.

Other material. MTQ 60715, -16 Indonesia, West Papua, Nabire, northeast Mamboor, 3°4.3′S, 135°36.2′ E; depth 9–34 m collected L. DeVantier 16 February 2006.

Etymology

Named for its superficial resemblance to plating species of *Montipora*, because of immersed corallites, small corallite size and extensive coenosteum.

Diagnosis

Colony indeterminate in growth, with numerous thin plates given off in an irregular fashion. Most of undersurface is covered by epitheca. Corallite diameters: outer

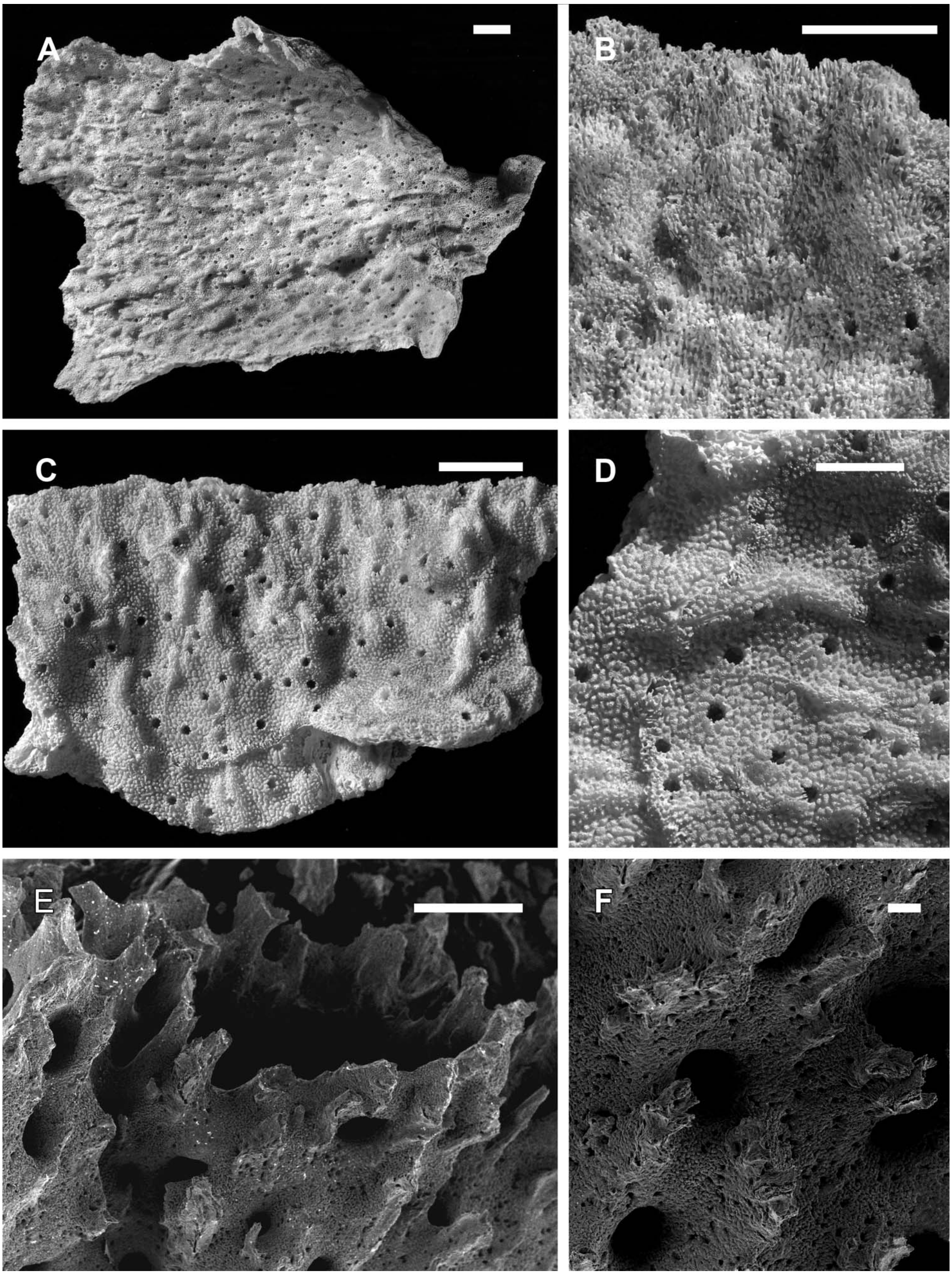

Figure 5. *Astreopora montiporina* sp. nov. (A, B, E, F) Holotype MTQ G60711; (C, D) paratype MTQ G60712. (A, C) Whole specimen; (B, D) close up of plate surface; (E, F) scanning electron micrographs showing corallites and coenosteum spinules. Scale bars: A–C: 10 mm; D: 5 mm; E: 500 μm; F: 100 μm.

1.00–2.00 mm; inner 0.99–1.50 mm; primary and secondary septa present as narrow laminae to < 1/4R; pseudo-columella present. Small projecting branchlets may be developed on the plates. Coenosteum reticulate and flaky, with evenly distributed elaborate spinules.

Skeletal characteristics

Holotype. Part of colony, thin plate 155 mm greatest width by 90 mm, with corallites only on upper surface; an additional 10 pieces of corallum, 13–63 mm width, are included with holotype. Epitheca covers lower surface to within 15 mm of edge. Corallites immersed to sub-immersed, diameters: outer 1.22–1.71 mm; inner 0.99–1.37 mm; six primary and six secondary septa present, as narrow laminae to < 1/4R; in some corallites, primary septa can be seen meeting to form a loose pseudo-columella. Coenosteum reticulate and flaky, with evenly distributed elaborate spinules. Upper surface shows presence of abundant worm tubes just below the coenosteum, and has a small number of small protrusions bearing two or three corallites.

Variations shown in paratype. Upper surface of paratype has small projecting branchlets to just under 10 mm long, given off irregularly at an angle to the surface: these have up to 10 corallites.

Field characteristics

Colour pale green to brown or grey, colonies spreading to around 2 m diameter.

Habitat

Mid to lower reef slope on fringing reefs.

Distribution

To date, recorded from Cenderawasih Bay only; see Figure 1.

Discussion

Novel characters for Astreopora

The new species display several characters never before recorded for *Astreopora* and hence identified as "novel" for *Astreopora*, although known in other Acroporidae genera. Two species, *A. cenderawasih* sp. nov. and *A. acroporina* sp. nov., have a predominantly branching growth mode (Figure 2A,B). No previously named living *Astreopora* has branching colonies, although two (*A. moretonensis* and *A. macrostoma*) can have occasional branch-like developments, caused by up-growth and rolling of portions of a flat plate (e.g. Veron and Wallace 1984: fig. 1082; Veron 2000: 436, 447) and epifauna can cause secondary elongation of some corallites in some massive species, including *A. myriophthalma* and *A. gracilis* (personal observation ET, LD).

In *A. cenderawasih* sp. nov., the branches take a dendritic form (see Figure 3A,C), that appears homologous to the branching mode seen in some species of the confamilial genus *Montipora*, e.g. *M. digitata* and *M. tortuosa* (see Stobart 2000: fig. 1).

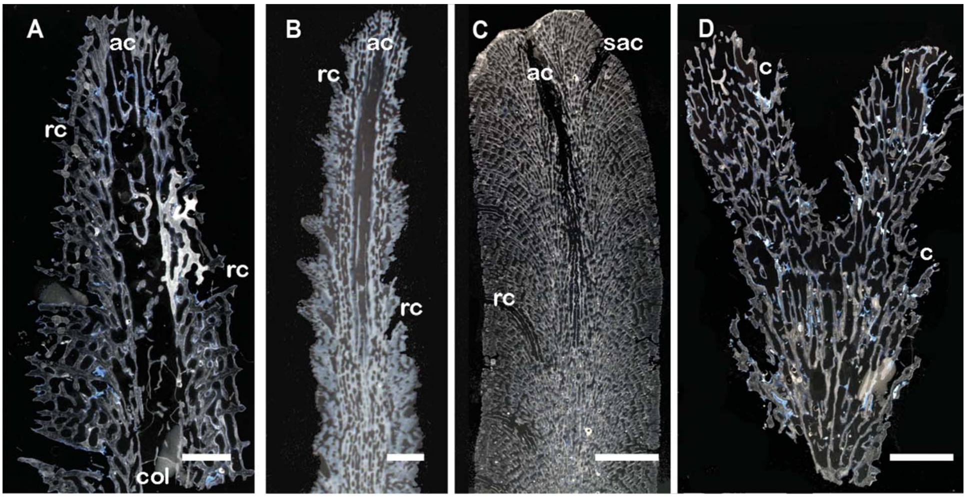

Figure 6. Thin sections of branching Acroporidae showing presence (A–C) and absence (D) of an axial corallite; (A) *Astreopora acroporina* sp. nov.; (B) *Acropora muricata*, type species of *Acropora*; (C) *Isopora togianensis*, showing a supplementary axial corallite (sac) as well as the main axial; (D) *Astreopora cenderawasih* sp. nov., which has dendritic branching with no axial corallite. ac, axial corallite; col, pseudocolumella; rc, radial corallite; sac, supplementary axial corallite. Scale bars: A, B, 1 mm; C, D, 5 mm.

A thick basal branch divides into several branches, which grow upwards: these may divide again, in a more irregular fashion. This form of growth introduces to the genus the potential to cover three-dimensional space on the reef relatively quickly and also to reproduce asexually by breakage and redistribution of colonies, as is seen in some branching *Montipora* (e.g. Heyward and Collins 1985; Kayannei et al. 2002) as well as *Anacropora* and some indeterminately growing *Acropora* (Wallace 1999).

Most remarkable among the characters shown by the new species is the branching mode in *A. acroporina* sp. nov. Branches of this species have a central or axial corallite that continues throughout the length of the branch to open at the tip. Other, "radial", corallites are budded off around this corallite from below the tip, as can be seen in Figure 4B. Despite the presence of the axial corallite, *A. acroporina* sp. nov. has a rudimentary columella (referred to as a pseudo-columella), formed by the entanglement of primary septa deep in the corallite. The skeletal architecture is formed by an open trabecular structure without synapticular rings, also seen in *A. cenderawasih* sp. nov. (Figures 6A,D). Most importantly, the "radial" corallites of *A. acroporina* sp. nov. (i.e. the corallites formed on the side of the axial corallite) are typical of *Astreopora* corallites, without any shape or coenosteal differentiation from the axial, apart from its far longer extent. This differs from the situation with *Acropora*, in which a variety of characters and character states have developed exclusively in radial corallites, accentuating the difference between axial and radial corallites and allowing morphological species groups to be recognized among both modern and fossil species (Wallace 1999; Wallace and Rosen 2006).

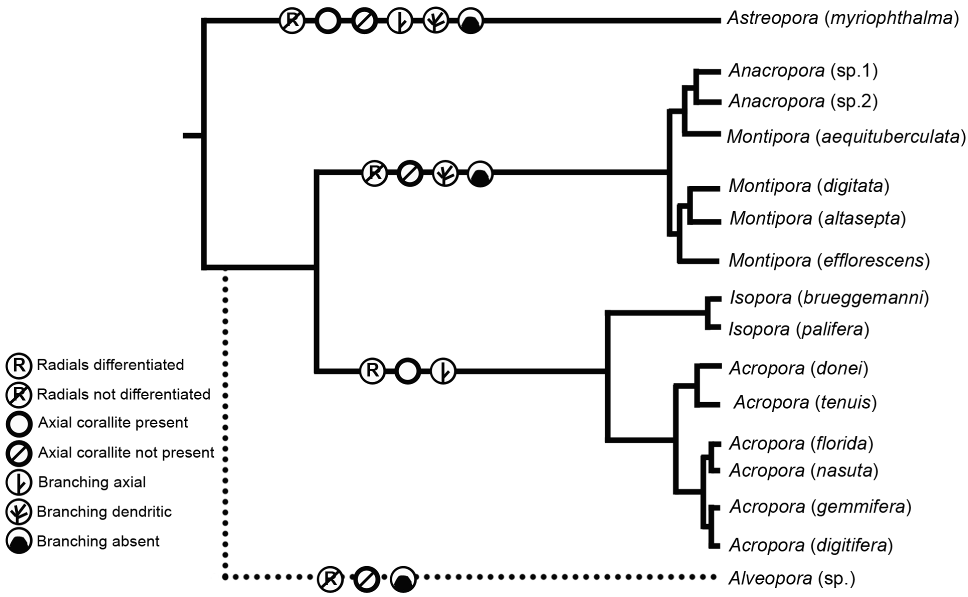

Figure 7. Branching and corallite features of Acroporidae, including the novel *Astreopora* characters, on a molecular phylogeny of modern family relationships after Fukami et al. (2000: solid lines), adding *Alveopora* after Fukami et al. (2008: dotted line). Six of seven character states are present in the basal genus *Astreopora*. [Note: Species names of species from the initial molecular cladogram are bracketed and do not always indicate the range of species bearing the skeletal characters.]

Source of novelty

In Acroporidae, the single axial corallite as the basis of branching, long thought to be the exclusive characteristic of *Acropora*, also occurs in some species of its sister genus *Isopora* (albeit accompanied by “supplementary” axials: Wallace et al. 2007; Budd and Wallace 2008; Wallace and Budd 2009), and now is seen in one species of *Astreopora*. The dendritic form of branching, previously only described by Stobart (2000) for the genus *Montipora*, is also herein recorded for the first time in a species of *Astreopora.* This genus is usually interpreted as basal to the family in molecular phylogenies (Figure 7, Fukami et al. 2000, 2009; Le Goff Vitry et al. 2004; Kitahara et al. 2010), although the position of a fossil genus *Dendracis* is uncertain. The finding of two different branching forms in this basal genus, while similar but more diversified characters occur in more recently derived members of Acroporidae (Figure 7), suggests that the origins of these characters might be earlier in the family lineage than previously thought.

The axial corallite as expressed in each of the genera *Astreopora*, *Acropora* and *Isopora* is shown in thin section in Figures 6A–C. In *Acropora*, as well as leading to a variety of colony forms, the axial corallite has developed along with a suite of other variable characters such as highly differentiated and sometimes dimorphic radial corallites and coenosteal microstructure (Figure 6B, Wallace 1999: figs. 34, 35, respectively). This has resulted in a high degree of morphological variation and intense species-level diversification, including the beginnings of at least 10 species groups by the Mid to Late Eocene (49–34 million years ago), and the current high species diversity and species-group diversity of that genus (Wallace and Rosen 2006; Wallace 2008). In the other two genera (*Isopora* and *Astreopora*), the axial corallite is not associated with extensive differentiation of other characters. In *A. acroporina* sp. nov., the axial corallite retains a pseudo-columella formed of twisted spines (Figure 6A), a feature seen only in *Astreopora* and another genus *Alveopora*, newly transferred to the family following recent molecular studies (Figure 7; Fukami et al. 2008; Dai and Horng 2009). *Astreopora* also has a distinctive coenosteal microstructure, which is retained in the three new species discussed here. In *Isopora*, sister genus to *Acropora*, the axial corallite occurs in multiples, or as a single large corallite with small supplementaries within the branch (Figure 6C). It does not have a columella and is more similar in appearance to the axial corallite of *Acropora*. There is also a small amount of differentiation of the other corallites in *Isopora* colonies, sufficient to separate them as radial corallites.

For plants, it has been proposed that apparent convergences of some characters may actually be indicative of deep ancestral programming within a clade, which places constraints on the way in which variations can be formed in clade members: characters or character states might re-appear in combination with a different set of other characters (Donoghue and Ree 2000; Donoghue 2005).The presence of an axial corallite, now seen first in *Astreopora* and later in *Acropora* and *Isopora*, may be a parallelism in the sense described by Donoghue (2005; also quoting from Gould 2002), that is, it results from "historical constraints in the evolving system—the same condition originates again and again within a lineage owing to something about the structure and development of the shared ancestor". A similar parallelism may also apply to the dendritic branching in *A. cenderawasih* sp. nov. (Figure 6D). Remarkably, no other recorded species of *Astreopora* from any other region of the Indo-Pacific has evolved either of these branching patterns and little or no branching is seen in fossil forms from other regions.

At present, we do not have molecular evidence to indicate whether these new species are recently derived, or remnants of previously wider-ranging populations, however as *Astreopora* is considered the basal living genus, it appears that the potential for both these forms of branching is present at the base of the clade (Figure 7). With regard to the character of axial branching, its full potential to work in concert with a suite of other characters (radial corallites, colony shape, skeletal micromorphology) to produce an estimated 120 to 150 living species and 20 living species groups is seen in *Acropora* (Veron and Wallace 1984; Wallace 1999, 2008) but in *A. cenderawasih* sp. nov., the same character has the appearance of an experimental deviation from the typical *Astreopora* form, not supported by other character changes. Another hypothesis, still to be explored, is that this species may have cross-generic hybrid origins.

Biodiversity of the type locality

Astreopora is one of a number of coral genera displaying greater than usual species diversity in Cenderawasih Bay, although other family members *Acropora*, *Isopora* and *Montipora* show high, but not exceptional diversity, including as yet undescribed species (Turak and DeVantier forthcoming). Despite extensive work in the Bird's Head Peninsular and surrounding regions, we have not found the two branching *Astreopora* species elsewhere. Similarly, six species of reef-associated fish have been described that are, for the present, considered endemic to Cenderawasih Bay (Allen and Erdmann 2009). The apparently restricted distribution of some fish and corals may possibly be attributable to the tectonic and eustatic history of the Indo-Papuan region (Hall 1998; Polhemus 2007; Allen and Erdmann 2009). Cenderawasih Bay is unusually deep and has a wide mouth that is partially blocked by high islands. It persisted as part of a broader Mollucca Sea deepwater basin throughout successive periods of tectonic change, with its western side fringed by shallower carbonate platforms (Hall 1998), while being episodically blocked, either partially or totally, from outside seas by an amalgamation of islands and exposed sea floor or shallow waters during low sea stands in the Plio-Pleistocene (e.g. Potts 1984; Polhemus 2007). This would have seen it alternatively open to or isolated from surrounding seas, which may have been conducive to localized speciation events as well as the accumulation of widespread species. Another possibility would be that the evolutionary novelty seen here is a consequence of edge-zone processes, such as hybridization and parapatric or peripatric speciation (Van Oppen et al. 2002; Willis et al. 2006; Budd and Pandolfi 2010).

Both of the branching characters described here as novel for *Astreopora* have played a role in the evolution and diversification of one or more other genera of Acroporidae. Their appearance in *Astreopora*, thought to be a basal genus to the family (Fukami et al. 2000, 2008; Kitahara et al. 2010) suggests that the underlying basis for axial and dendritic branching was present even at the basal stage of evolution of the family and saw expression in the diversification of other genera, especially *Acropora* and *Montipora*. Alternatively, the appearance of these characters in *Astreopora* may exemplify novel evolutionary pathways for the genus, occurring in small, isolated populations and leading to the recent divergence of these restricted range species. An apparently independent evolution of an axial corallite has, for example, also occurred in the unrelated faviid *Cyphastrea decadia* (Moll and Best 1984). In the light of these questions some explanation might be found for apparently contradictory phenomena such as the diversification of *Acropora* both early (Wallace and Rosen 2006) and late (Fukami et al. 2000; van Oppen et al. 2001) in its history and the apparent misalignment of genetic and morphological boundaries in *Acropora* (van Oppen et al. 2002), as well as similar questions relating to other coral taxa.

Acknowledgements

We thank the Indonesian Department of Nature Conservation (PHKA), Indonesian Ministry of Marine Affairs and Fisheries (DKP) and Mr M.G. Nababan, Head of Cenderawasih National Park Authority for sponsoring the rapid biodiversity assessment that led to these discoveries; the citizens and governments of Papua and Papua Barat provinces for hosting and warmly receiving the expedition; the Indonesian Institute of Sciences (LIPI) and Dr Suharsono for permission to carry out taxonomic research on the specimens; the staff of UNIPA for fruitful discussions while onboard the boat and for curating the duplicate specimens; Citra Pelangi captain and crew; the Walton Family Foundation and Gordon and Betty Moore Foundation for financial support; Conservation International Indonesia Program, M. Erdmann and M. Lazuadi for field and logistic support; P. Muir (MTQ) for electron microscopy, laboratory photography and figure preparation; the Advanced Analytical centre, James Cook University for electron microscope preparation and use; B. Done (MTQ) for registration of material; D. Richardson for thin sectioning; M. Trenerry for valued assistance; and three anonymous reviewers for suggestions on the manuscript.

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