Searching for new morphological characters in the systematics of scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific Mussidae

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Abstract

Budd, A.F. and Stolarski, J. 2009. Searching for new morphological characters in scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific Mussidae. — *Acta Zoologica (Stockholm)* **90**: 142–165.

Recent molecular analyses have challenged the traditional classification of scleractinian corals at all taxonomic levels suggesting that new morphological characters are needed. Here we tackle this problem for the family Mussidae, which is polyphyletic. Most of its members belong to two molecular clades composed of: (1) Atlantic Mussidae and Faviidae (except *Montastraea*) and (2) Pacific Mussidae (*Cynarina, Lobophyllia, Scolymia, Symphyllia*) and Pectiniidae. Other Pacific mussids (e.g. *Acanthastrea*) belong to additional clades. To discover new characters that would better serve as phylogenetic markers, we compare the skeletal morphology of mussid genera in different molecular-based clades. Three sets of characters are considered: (1) macromorphology (budding; colony form; size and shape of corallites; numbers of septal cycles), (2) micromorphology (shapes and distributions of septal teeth and granules), and (3) microstructure (arrangement of calcification centres and thickening deposits within costosepta). Although most traditional macromorphological characters exhibit homoplasy, several new micromorphological characters are effective at distinguishing clades, including the shapes and distribution of septal teeth and granules, the area between teeth, and the development of thickening deposits. Arrangements of calcification centres and fibres differ among clades, but the fine-scale structure of thickening deposits does not.

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Introduction

Recent molecular analyses have challenged many long-held notions concerning the systematics and evolution of scleractinian corals. Phylogenetic analyses of mitochondrial (*cytB* and *COI*), and nuclear (β-tubulin) genes have shown that as many as 11 traditional families are polyphyletic (Fukami *et al*. 2004). One example is the family Mussidae, which was originally described by Ortmann (1890) and which, since its inception, has contained a mixture of Atlantic and Pacific taxa. In a recent monograph on scleractinian reef corals (Veron 2000), the coral family Mussidae was described as consisting of 12 modern genera: four are restricted to the western Atlantic (*Isophyllia, Mussa, Mussismilia, Mycetophyllia*),

seven are restricted to the Indo-Pacific (*Acanthastrea, Lobophyllia, Symphyllia, Cynarina, Blastomussa, Micromussa, Indrophyllia*) and one is cosmopolitan (*Scolymia*). Cairns *et al*. (1999) include two additional modern genera in the family: *Acanthophyllia (*restricted to the Indo-Pacific) and *Isophyllastrea* [restricted to the western Atlantic and synonymized with *Isophyllia* by Veron (2000)]. Contrary to this grouping, molecular analyses of these genera (Fukami *et al*. 2004) show that Atlantic and Indo-Pacific members of the family are evolutionarily distinct, and that Atlantic members of the family Mussidae are more closely related to Atlantic members of the family Faviidae (*Colpophyllia, Diploria, Favia, Manicina*) than they are to their Pacific congeners (Fig. 1).
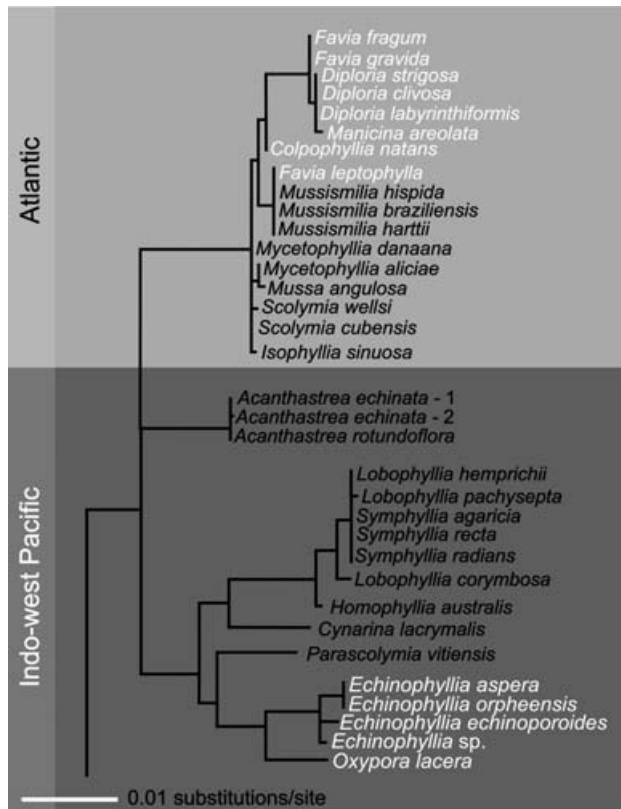
Fig. 1—Molecular tree after Fukami *et al*. (2004) showing the 10 genera of traditional mussids under consideration. Traditional members of the family Mussidae are in black script; traditional members of the family Faviidae (Atlantic) and the family Pectiniidae (Indo-Pacific) are in white script.

Although minor modifications (e.g. Cairns *et al*. 1999; Veron 2000) have been suggested subsequently, the traditional classification system that is most widely used by coral workers today was originally proposed by Vaughan and Wells (1943) and Wells (1956), and is based on skeletal morphology (see discussion in Stolarski and Roniewicz 2001). Three different aspects of skeletal morphology are considered: (1) macromorphology (budding; colony form and integration; size and shape of corallites; numbers of septal cycles), (2) micromorphology (shape and orientation of septal teeth; shape and distribution of granules), and (3) microstructure (arrangement of calcification centres and fibres; development of thickening deposits). In this classification system, the families Mussidae and Faviidae are based on a combination of micromorphological (i.e. septal teeth) and microstructural (i.e. trabeculae) features. The family Mussidae is distinguished by having 'Septa ... formed by several fan systems of large, simple trabeculae, each fan system producing a lobulate dentation,' (Wells 1956; p. F416); whereas the family Faviidae is distinguished by having 'Septa (...) formed by 1 or 2 fan

systems of simple (compound in later forms) trabeculae, more or less regularly dentate marginally,' (Wells 1956; p. F400). However, these two diagnoses are based on the traditional concept of 'trabeculae' (Ogilvie 1897), which does not capture the full range of observed variation at the micromorphological and microstructural levels, including the complex relationships between the mineral and organic phases of the skeleton.

These relationships between the mineral and organic phases of the skeleton are explained by newly proposed models of scleractinian skeletal growth that highlight differences between 'calcification centres' ('Centers of Rapid Accretion' of Stolarski 2003, or 'Early Mineralization Zone' of Cuif and Dauphin 2005) and zones of fibrous, thickening deposits ('stereome' of Vaughan and Wells 1943). Following the new microstructural models, the structure of mussid teeth should be redescribed, distinguishing 'centres of rapid accretion' that are arranged in different ways and surrounded to varying degrees by 'thickening deposits'. Initial attempts at using such redefined, fine-scale morphological characters in combined skeletal–molecular studies have already shown their potential to provide support for molecular-based clades (Cuif *et al*. 2003).

The purpose of this paper is to define and delimit a new set of morphological characters, which reflect skeletal growth, and to determine how well they match molecular data. Special care will be taken to separate different aspects of growth in the definition of different characters. To accomplish this objective, we conduct a comprehensive survey of skeletal variation in (1) costoseptal micromorphology (teeth, granulations) using scanning electron microscopy (SEM) of calicular surfaces and (2) costoseptal microstructure (fibres, calcification centres; including the structure of the corallite wall) using transverse thin sections and SEM of polished and etched sections. We assess homology by comparing states of the newly constructed characters among members of three clades derived from the molecular tree of Fukami *et al*. (2004), which have traditionally been assigned to the family Mussidae. Our emphasis is on the characters that distinguish Atlantic from Pacific mussids. We also compare patterns of variation in the newly constructed characters with those exhibited by traditional macromorphological characters. We use the results to propose a set of morphological characters that can be used in future phylogenetic analyses of this and other related scleractinian groups.

Materials and Methods

Material examined

Our work examines five Atlantic genera (*Isophyllastrea, Isophyllia, Mussa, Mussismilia, Mycetophyllia*), four Indo-Pacific genera (*Acanthastrea, Lobophyllia, Symphyllia, Cynarina*), and one cosmopolitan genus (*Scolymia*), which were treated

in the molecular analyses of Fukami *et al.* (2004). All have been recently placed (Cairns *et al.* 1999; Veron 2000) within the traditional Family Mussidae (Vaughan and Wells 1943; Wells 1956). Representative specimens of the 10 genera are illustrated in Fig. 2. Following Cairns *et al.* (1999), the genera consist of:

Atlantic:
*Genus Isophyllastrea Matthai (1928)
  Type Species: *Astraea rigida* Dana (1846)
  Number of species: one (Cairns *et al.* 1999)
Genus *Isophyllia* Milne Edwards and Haime (1851)
  Type Species: *Madrepora sinuosa* Ellis and Solander (1786)
  Number of species: one (Cairns *et al.* 1999); two (Veron 2000)
Genus *Mussa* Dana (1848)
  Type Species: *Madrepora angulosa* Pallas (1766)
  Number of species: one (Cairns *et al.* 1999); one (Veron 2000)
Genus *Mussismilia* Ortmann (1890)
  Type Species: *Mussa harttii* Verrill (1868)
  Number of species: three (Cairns *et al.* 1999); three (Veron 2000)
Genus *Mycetophyllia* (Milne Edwards and Haime 1848)
  Type Species: *Mycetophyllia lamarckiana* Milne Edwards and Haime (1849)
  Number of species: five (Cairns *et al.* 1999); five (Veron 2000)

Pacific:
Genus *Acanthastrea* (Milne Edwards and Haime 1848)
  Type Species: *Astraea echinata* Dana (1846)
  Number of species: 10 (Cairns *et al.* 1999); 12 (Veron 2000)
Genus *Cynarina* Brüeggemann (1877) [= Acanthophyllia Wells (1937)]
  Type Species: *Caryophyllia lacrymalis* (Milne Edwards and Haime 1848)
  Number of species: two (Cairns *et al.* 1999; including *A. deshayensiana*); one (Veron 2000)
Genus *Lobophyllia* (Blainville 1830)
  Type Species: *Madrepora corymbosa* Forskaal (1775)
  Number of species: seven (Cairns *et al.* 1999); nine (Veron 2000)
Genus *Symphyllia* (Milne Edwards and Haime 1848)
  Type Species: *Mussa recta* Dana (1848)
  Number of species: seven (Cairns *et al.* 1999); seven (Veron 2000)

Cosmopolitan:
Genus *Scolymia* Haime (1852) [= *Homophyllia* Brueggemann, 1877; = *Parascolymia* Wells 1964)
  Type Species*: *Madrepora lacera* Pallas (1766)
  Number of species: five (Cairns *et al.* 1999); three (Veron 2000)

*Note: Veron (2000) synonymized the genus *Isophyllastrea* with *Isophyllia*. He also synonymized *Scolymia lacera* with *Mussa angulosa*, and designated *Scolymia cubensis* as the type species of *Scolymia*. Our morphological observations below reveal significant differences between *Isophyllia sinuosa* and *Isophyllastrea rigida* (but see Fukami *et al.* 2004; who found no genetic differences between *Isophyllia* and *Isophyllastrea*) and between *Scolymia lacera* and *Mussa angulosa*. We therefore follow the diagnosis of Matthai (1928) for *Isophyllastrea* and the Vaughan (1902) designation of *Scolymia lacera* as the type species of *Scolymia*.

Wherever possible, our work focuses on type species. The exceptions are two genera, *Mycetophyllia* and *Scolymia*, whose type species (above) have not yet been genetically characterized. Instead of type species, we have therefore used other species that were analysed by Fukami *et al.* (2004) to represent *Mycetophyllia* and *Scolymia*. These species are: (1) *Mycetophyllia danaana* Milne Edwards and Haime (1849); (2) *Scolymia cubensis* [Milne Edwards and Haime (1849)] (3) *Scolymia australis* [Milne Edwards and Haime (1849)] (the type species of *Homophyllia*), and (4) *Scolymia vitiensis* Brüggemann (1877) (the type species of *Parascolymia*).

The specimens that we studied are listed in Appendix I, and consist of: (1) material that was studied molecularly by Fukami *et al.* (2004) and deposited in the University of Iowa Paleontology Repository or the Florida Museum of Natural History (*Cynarina, Isophyllia, Isophyllastrea, Mussa, Mycetophyllia, Acanthastrea*), (2) material borrowed from the Yale Peabody Museum (*Mussismilia, Scolymia*), (3) material borrowed from the US National Museum of Natural History (*Acanthastrea, Cynarina, Lobophyllia, Symphyllia, Scolymia*), and *(*4) material borrowed from the Florida Museum of Natural History (*Lobophyllia, Symphyllia*).

Characters

Our examination consists of three different groups of skeletal characters, which involve different scales of analysis and preparation methods (Cuif and Perrin 1999).

Macromorphological characters (three-dimensional observations using a regular light microscope). Macromorphology involves the study of many traditional diagnostic features related to colony form (corallite budding and integration, the length and shape of calicular series); the size and shape of the calice; development of the septa (number, spacing, relative thickness and length), the columella (and associated lobes), the corallite wall, endo- and exotheca, and coenosteum.

Micromorphological characters (three-dimensional observations using scanning electron microscopy of calicular surfaces, at magnifications < 200 ×). Micromorphology involves the study of the shapes of teeth along the upper margins of the wall,
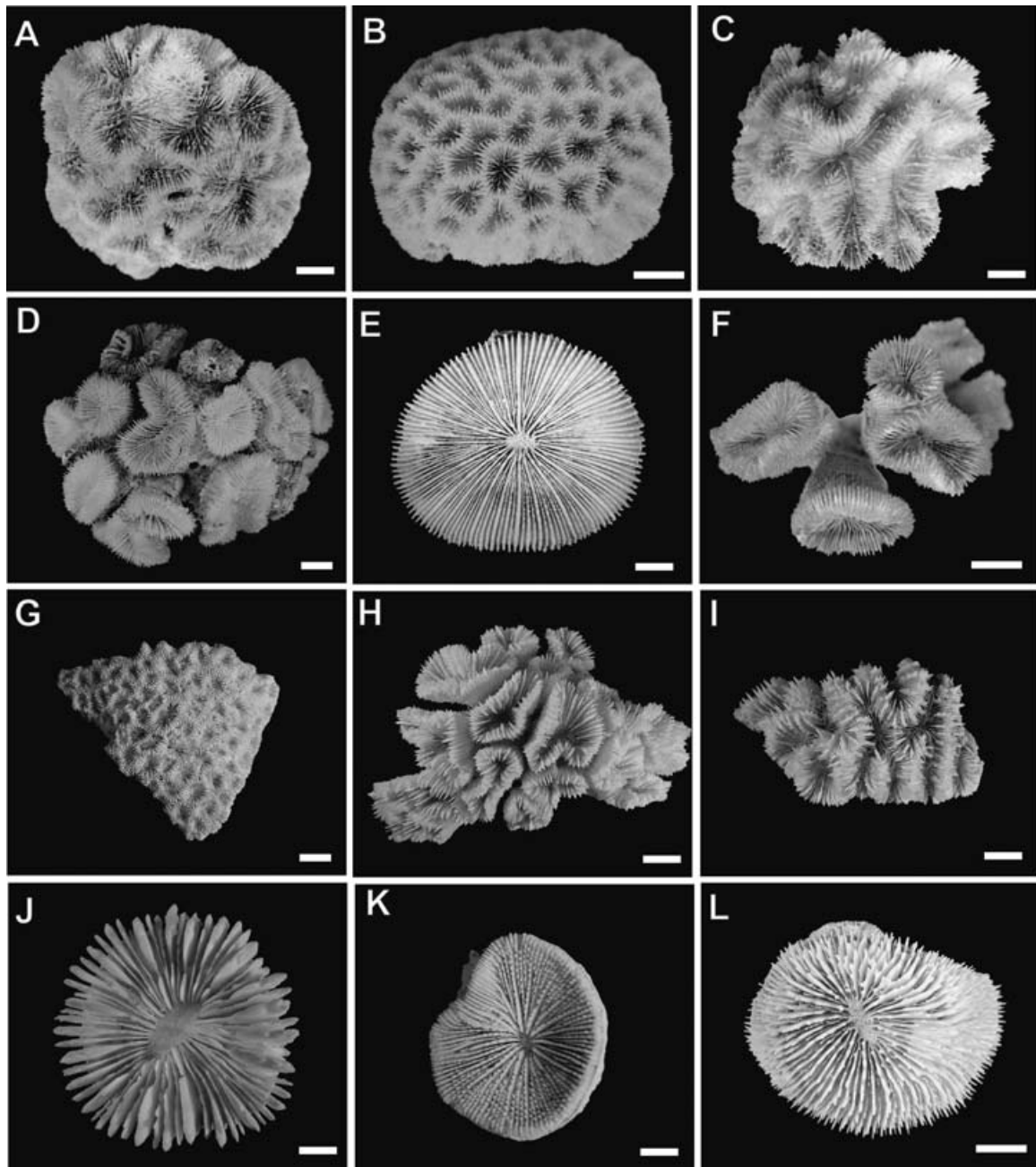
Fig. 2—Representative coralla of the 10 genera under consideration. Growth forms in *Isophyllastrea* and *Acanthastrea* are subcerioid; *Isophyllia*, *Mycetophyllia*, and *Symphyllia* are meandroid; *Mussa* and *Lobophyllia* are phaceloid; *Scolymia* and *Cynarina* are solitary; corallite sizes and numbers of septal cycles vary widely among genera (Table 1). —**A**. *Isophyllia sinuosa*, SUI 102759 (FA1134), Key Largo, Florida (Atlantic). —**B**. *Isophyllastrea rigida*, SUI 102754 (FA1136), Discovery Bay, Jamaica (Atlantic). —**C**. *Mycetophyllia danaana*, SUI 102770 (FA1001), Discovery Bay, Jamaica (Atlantic). —**D**. *Mussa angulosa*, SUI 102763 (FA1135), Key Largo, Florida (Atlantic). —**E**. *Scolymia cubensis*, USNM 84940, Maria Bueno Bay, Jamaica (Atlantic). —**F**. *Mussismilia harttii*, YPM 1468a, syntype, Abrolhos reefs, Brazil (Atlantic). —**G**. *Acanthastrea echinata*, USNM 25, syntype, Fiji (Pacific). —**H**. *Lobophyllia corymbosa*, USNM 89581, Enewetok (Pacific). —**I**. *Symphyllia recta*, USNM 1090898, Samoa (Pacific). —**J**. *Cynarina lacrymalis*, USNM 53145, New Caledonia (Pacific). —**K**. *Scolymia* (= *Homophyllia*) *australis*, USNM 85709, south Australia (Pacific). —**L**. *Scolymia* (= *Parascolmia*) *vitiensis*, USNM 83332, New Caledonia (Pacific). Scale bars are 5 mm.

septa, and columella, and of granulation on septal faces. Samples of selected calices (limited breakage of septal teeth) were mounted on stubs with double-sided adhesive tape and sputter-coated with conductive platinum film for three-diomensional observations using SEM.

Microstructural characters (two-dimensional observations using transverse thin sections and scanning electron microscopy of polished and etched transverse sections, at magnifications < 100 ×). Microstructure involves the study of the internal structure (i.e. the arrangement of calcification centres and fibres) within the wall, septa and columella. Samples of selected calices were cut transversely, impregnated with epoxy, and thin-sectioned to *c.* 30 μm thickness.

To visualize organic and mineral components, samples of selected calices were cut transversely, polished and exposed for *c.* 20 s to 0.1% formic acid solution. The formic acid is known to dissolve not only mineral but also organic components that are not stabilized by covalent bonds (Waite and Anderson 1980). Because etching of mineral and organic components occurs at different rates, the samples yield a distinct negative relief corresponding to regions enriched in organic content (see also Stolarski 2003). The etched samples were rinsed with distilled water and air-dried. After drying, the samples were mounted on stubs with double-sided adhesive tape and sputter-coated with conductive platinum film.

Glossary of skeletal terms

(plural and/or adjective forms are given in parentheses; underlined words are formally defined)

Budding (–). Addition of new corallites to a corallum.

Calice (-*s*; adj. *calicular*). Cup-like structure at the distal end of solitary and outermost surface of solitary and, respectively, colonial coralla. Corresponding to the part of the skeleton occupied by a polyp.

Calcification centre (-*s*). Structure recognized in transverse sections of various skeletal elements as 'dark spot [...] from which fascicles of fibrous crystals radiate toward those of neighbouring centres,' (Vaughan and Wells 1943; p. 32). Calcification centres are built of alternations of two biomineral phases: enriched in mineral and organic components, respectively. A higher concentration of organic components in calcification centres (strong UV autofluorescence) differentiates them from adjacent thickening deposits (much weaker UV autofluorescence). In the layered model of skeletal growth (Stolarski 2003), the calcification centre is considered a well-differentiated region of skeletal rapid accretion. Calcification centres can be recognized on a distal septal margin as small patches that are closely spaced (and even form a more or less continuous zone), or they may be widely separated from each other. The latter results in the formation of teeth on the distal septal margin, or in the development of granulation on septal flanks.

Coenosteum (-*a*; adj. *coenosteal*) or *peritheca* (-*e*; adj. *perithecal*). Skeleton between corallites.

Colline (-*s*). A surficial ridge on the calicular surface of a colony.

Colony (-*ies*). A corallum consisting of two or more corallites whose polyps are integrated to different degrees (Coates and Oliver 1973). Colonies in the family Mussidae may have subcerioid (corallites more or less juxtaposed), meandroid (corallites arranged in series), or phaceloid growth forms.

Columella (-*e*). Vertical axial structure within a corallite or solitary corallum. In the family Mussidae, the columella consists of interwoven threads. The threads may extend from the inner septal margins, or they may form separately. The threads may be loosely to tightly (= spongy) interwoven. Centres of adjacent corallites may be linked by interwoven threads ('trabecular linkage') or by septal plates ('lamellar linkage'); see text for additional description.

Corallite (-*s*). Skeleton of an individual within a colony.

Corallum (-*a*). Entire skeleton of a coral.

Costa (-*e*). Radial structure outside the corallite wall. They may be formed by costal parts of costosepta, as is the case in the Family Mussidae; or they may develop independently from them. Costae may be located along or alternating in position with intracalicular radial elements.

Costoseptum (-*a*). Fan-shaped radial element with outer (costal) and inner (septal) parts. In the family Mussidae, costal parts typically extend beyond the wall forming costa, but in corals with a solely epithecal wall, the entire costoseptum may form inside the calice (e.g. *Gardinera*, see Stolarski 1996).

Dissepiment (-*s*). Small, horizontal domed plate inside ('endothecal') or outside ('exothecal') a corallite. Dissepiments are often formed at regular intervals and stacked more or less regularly on top of each other to form a continuous structure. They may be thickened by stereome.

Epitheca (adj. *epithecal*). Usually thin, external thecal sheath surrounding an individual corallite or corallum (in the case of colonial coralla, it is called 'holotheca'). In the Family Mussidae, epitheca, if present, surrounds the corallum. The calcareous fibres of the outer epithecal part are orientated distally; whereas those of the inner part (epithecal stereome) show centripetal orientation (Barnes 1972). Epitheca may be the only corallum wall, but modern corals typically form composite walls with other skeletal structures [i.e. epithecal–parathecal (= dissepimental); epithecal–trabeculothecal; epithecal–septothecal; epithecal–stereomal walls; Roniewicz and Stolarski (1999)].

Fibre (-*s*). A slender and elongated object, in particular scleractinian coral biocrystal. In comparison to abiotically precipitated calcium carbonate crystals, scleractinian biocrystals have nanocomposite structure with mineral nanograins (*c.* 30–100 nm in diameter) embedded in a thin layer of organic material. (Cuif *et al.* 1998; Stolarski and Mazur 2005).

Granule (-*s*). A small elevation on a septal face or a septal tooth. Granules may be pointed, rounded or bifurcated; they may be scattered over the skeletal surface or aligned.

Granulation. The pattern produced by granules.

Paratheca (adj. *parathecal*). Wall consisting of intercostal or epicostal dissepiments. May form composite wall structure with epitheca (i.e. epithecal–parathecal wall).

Phaceloid growth form. A branching corallum whose branches are each formed by an individual corallite or corallite series. The corresponding polyps are not connected by soft tissue. Corals with phaceloid growth forms, which lack integration between polyps in the adult growth phase, are considered 'pseudocolonies' (Coates and Jackson 1985).

Radial elements. Skeletal structures that radiate towards the axis of a calice (mainly septa, costae, costosepta, paliform lobes, septal spines).

Septal lobe (-*s*). A lobe on the distal margin of a septum, which is formed by an additional fan system of calcification centres.

Septotheca (adj. *septothecal*). Wall formed by fusion of outer parts of septa, which are typically thickened during ontogeny.

Septum (-*a*). Radially arranged vertical partition within a calice. In a fully developed costoseptum, the inner part (i.e. septal part of costoseptum).

Series (–). Corallites or corallite centres arranged in straight or meandering rows ('valleys').

Stereome (or *stereoplasm*). See thickening deposit.

Solitary. A corallum consisting of a single centre (monocentric) or corallite.

Thickening deposit (-*s*). Fibrous skeletal structure deposited outside the calcification centre (i.e. outside area of rapid skeletal accretion). Thickening deposits differ from calcification centres by having significantly fewer organic components. There are several formal or informal terms that are alternatively used to describe fibrous deposits, e.g. 'stereoplasm', 'secondary thickening' (see Ogilvie 1897), 'stereome' (see Vaughan and Wells 1943; Sorauf 1972), or 'tectura' (Stolarski 1995).

Tooth (pl. *teeth*). Projections along the septal margins, and/or upper ends of columellar threads. Septal teeth extend from the septa and are not formed by septal substitution. Columellar teeth may or may not differ in shape from septal teeth. Teeth may be spine-like, lobate, paddle-shaped, lacerate, beaded, or acute in shape. They may have circular or elliptical outlines.

Trabecula (-*e*). Pillars or rods of calcareous fibres radiating from centres of calcification that are aligned in axes (but see Stolarski 2003).

Wall (-*s*) or *theca* (-*e*). Skeletal structure uniting the outer edges of septa in a corallite.

Museum abbreviations

SUI, University of Iowa Paleontology Repository, Iowa City, IA, USA.

UF, Florida Museum of Natural History, Gainesville, FL, USA.

USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

YPM, Yale Peabody Museum, New Haven, CT, USA.

ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

Results

Macromorphological characters

Coralla and calices. The 10 selected mussid genera consist of both colonial and solitary forms (Table 1). In both forms, new corallites may be created by asexual budding within the wall of the parent corallite (asexual reproduction of solitary forms is less frequent). In all cases except the Atlantic genera *Mycetophyllia*, *Isophyllastrea* and *Isophyllia*, budding is multidirectional (i.e. lacking any preferred direction). In the genera *Mycetophyllia*, *Isophyllastrea* and *Isophyllia*, colonies are initially formed by circumoral budding (i.e. budding around a central parent corallite). Also colonies of one species of the Pacific genus *Lobophyllia* (*L. hataii*, which was not studied molecularly) are formed by circumoral budding.

Colony shapes in the selected genera are primarily branching and massive (Table 1). Three main types of colony forms occur in both Atlantic and Pacific genera: (1) some genera have branching, phaceloid colony shapes (i.e. one corallite or corallite series per branch; Fig. 2D,F,H); (2) some genera have massive, subcerioid colony shapes (i.e. walls of adjacent corallites are more or less juxtaposed; Fig. 2B,G); and (3) some genera have massive, meandroid colony shapes (i.e. corallites arranged in series; Fig. 2A,C,I). Some genera contain species that have different colony forms; for example, the genus *Mussismilia* contains species with both phaceloid (*Mussismilia harttii*) and subcerioid (*Mussismilia hispida*, *Mussismilia brasiliensis*) colony forms, and *Mycetophyllia* contains foliaceous species with multiserial meandroid colonies (*Mycetophyllia aliciae*, *Mycetophyllia lamarckiana*). In general, in subcerioid forms, walls of adjacent corallites are not completely anastomosed, but are separated by a limited amount of coenosteum. The similarities in colony form between Atlantic and Pacific colonial forms are so striking that *Isophyllia* has sometimes been referred to as the Atlantic counterpart of *Symphyllia*, and *Mussa* has been referred to as the Atlantic counterpart of *Lobophyllia* (Verrill 1902; Matthai 1928; Wells 1964). Among meandroid forms, the number of corallites per series ranges from few (5–10 corallites; Fig. 2A,C) to many (> 10 corallites; Fig. 2I). Both Atlantic and Pacific mussids also include taxa with solitary (i.e. monocentric) coralla (Fig. 2E,J–L), which were previously thought to be early monocentric forms of colonial genera but have recently been interpreted as distinct genera (Wells 1964).

One character that shows possible differences between Atlantic and Pacific genera is the linkage between centres either within corallite series or during budding of daughter from parent corallites (Table 1; Fig. 3). In all 10 genera, centres are distinct in mature corallites, and columellae do not continue between centres. In general, Atlantic taxa have

Table 1 Comparison of macromorphological characters among Atlantic and Pacific mussids (Figs 2, 3)

	Coralla and calices			Radial elements									Other features		
Species	Corallum shape & arrangement of calices	Symmetry of bud geometry	Number of centres per series	Centre linkage	Epitheca	Calice or valley width	Calice relief	No. of septal cycles	Relative costoseptal thickness	Septal spacing (per 5 mm)	Minor septa*	Confluent costae	Septal lobes	Columella size (relative to calice width)	Endothecal dissepiments
Atlantic															
Isophyllia sinuosa	massive, meandroid (uniserial)	circumoral	5–10	trabecular	reduced	large (10–15 mm)	high (4–10 mm)	> 3	equal	< 6	present	present	absent	≤ 1/4	medium
Isophyllastrea rigida	massive, subcerioid	circumoral	1–2	trabecular	reduced	large (10–15 mm)	high (4–10 mm)	> 3	unequal	6–12	present	present	absent	≤ 1/4	medium
Mycetophylla danaana	massive, meandroid (uniserial)†	circumoral	5–10	lamellar	absent	large (10–15 mm)	very high (> 10 mm)	3	equal	6–12	present	present	absent	feeble	abundant
Mussa angulosa	branching, phaceloid	multidirectional	1–3	trabecular	absent	huge (> 30 mm)	high (4–10 mm)	≥ 4	unequal	< 6	present	not applicable	absent	≤ 1/4	abundant
Scolymia cubensis	solitary	multidirectional	one	trabecular	absent	huge (> 30 mm)	high (4–10 mm)	≥ 5	unequal	< 6	present	not applicable	absent	≤ 1/4	medium?
Mussismilia harttii	branching, phaceloid	multidirectional	one	trabecular	reduced	medium (4–10 mm)	high (4–10 mm)	≥ 4	equal	6–12	present	not applicable	absent	≤ 1/4	abundant
Pacific															
Acanthastrea echinata	massive, subcerioid	multidirectional	1–2	lamellar	reduced	medium (4–10 mm)	medium (2–4 mm)	3	equal	< 6	present	present	absent	1/2	medium
Lobophyllia corymbosa	branching, phaceloid	multidirectional‡	1–5	lamellar	reduced	very large (15–30 mm)	very high (> 10 mm)	3	unequal	< 6	present	not applicable	absent	≤ 1/4	abundant
Symphyllia recta	massive, meandroid (uniserial)	multidirectional	> 10	lamellar	absent	medium (4–10 mm)	high (4–10 mm)	> 3	unequal	6–12	absent	absent	absent	≤ 1/4	abundant
Cynarina lacrymalis	solitary	multidirectional	one	lamellar	reduced	huge (> 30 mm)	very high (> 10 mm)	≥ 4	unequal	< 6	present	not applicable	well-developed	≤ 1/4	medium
Scolymia australis	solitary	multidirectional	one	lamellar	reduced	very large (15–30 mm)	medium (2–4 mm)	≥ 5	equal	6–12	present	not applicable	absent	≤ 1/4	medium
Scolymia vitiensis	solitary	multidirectional	one	lamellar	reduced	huge (> 30 mm)	high (4–10 mm)	≥ 5	equal	< 6	present	not applicable	absent	≤ 1/4	medium?

*Minor septa' refer to short septa of higher cycles that do not extend to the columella. †Some species of *Mycetophyllia* (e.g. *M. aliciae*, *M. ferox*) are foliaceous and form multiserial meandroid colonies with long series (> 10 centres). ‡Some species of *Lobophyllia* (e.g. *L. hataii*) have circumoral budding.
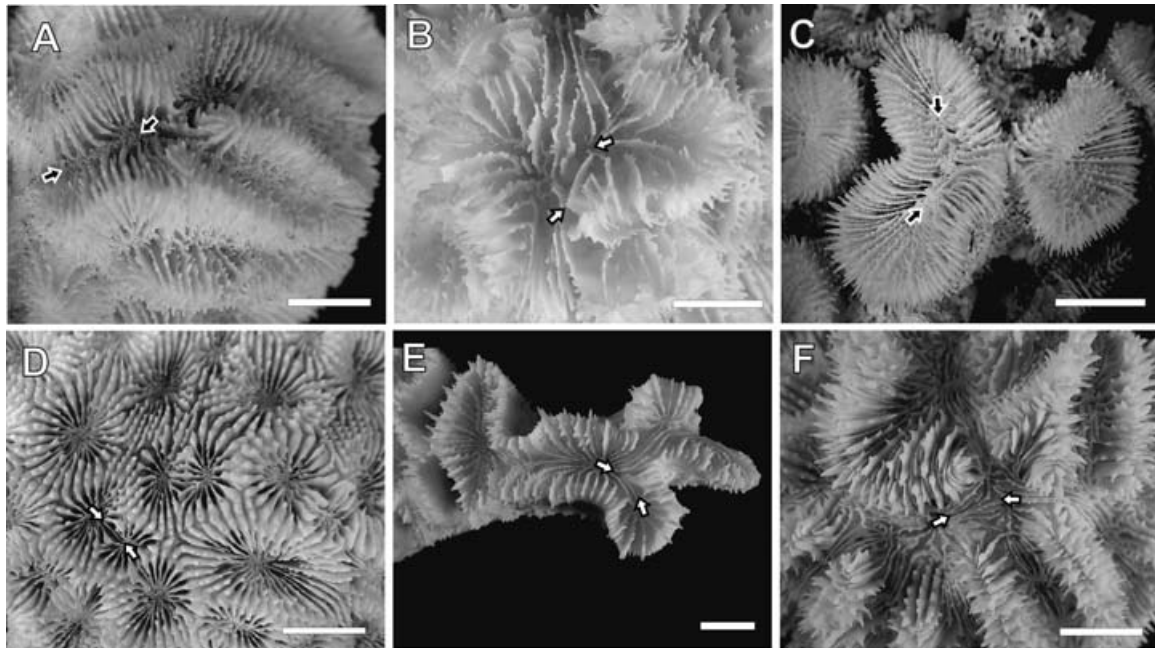
Fig. 3—Calicular surfaces of three Atlantic and three Pacific colonial genera showing trabecular (black arrows) versus lamellar (white arrows) linkage between corallite centres. Linkage is typically trabecular in Atlantic mussids (except *Mycetophyllia*), and lamellar in Pacific mussids. —**A**. *Isophyllia sinuosa*, SUI 102758 (FA1137), Crocus Bay, Anguilla (Atlantic). —**B**. *Mycetophyllia danaana*, SUI 102772 (FA1003), Bocas del Toro, Panama (Atlantic). —**C**. *Mussa angulosa*, SUI 102763 (FA1135), Key Largo, Florida (Atlantic). —**D**. *Acanthastrea echinata*, USNM 25, syntype, Fiji (Pacific). —**E**. *Lobophyllia corymbosa*, USNM 47110, Palau (Pacific). —**F**. *Symphyllia recta*, USNM 91129, Indonesia (Pacific). Scale bars are 5 mm.

indirect or trabecular (i.e. formed by intermingling threads, which extend from the inner septal margins) linkage, whereas Pacific taxa have direct or lamellar (i.e. formed by a plate, which originates by elongation of the dorsal directive protoseptum along the corallite axis) linkage. The one exception is the Atlantic genus *Mycetophyllia*, which has lamellar linkage.

Epitheca (as defined above) is absent or reduced in the 10 genera (Table 1). In general, epitheca is absent in Atlantic mussids and present (albeit reduced) in Pacific mussids. The exceptions are *Isophyllia*, *Isophyllastrea* and *Mussismilia* in the Atlantic; and *Symphyllia* in the Pacific.

Lastly, calices in the 10 genera are generally large and high in relief in comparison with other reef-building taxa such as the family Faviidae (Table 1). No distinct differences can be detected between Atlantic and Pacific taxa. Solitary (and some phaceloid) genera generally tend to have larger calices than genera with massive colony shapes. High calice relief is associated with the presence of collines in *Mycetophyllia* (Fig. 2C), septal lobes in *Cynarina* (Fig. 2J), and corallite walls (phaceloid–meandroid clumps) in *Lobophyllia* (Fig. 2H).

Radial elements. No consistent differences could be detected between Atlantic and Pacific genera in number of septal cycles, relative thicknesses of costae or septa in different cycles, or septal spacing (Table 1), characters which have been traditionally used in scleractinians to distinguish species as opposed to higher taxa (Vaughan 1902, 1907). All but one of the genera under consideration (*Symphyllia*) have short cycles of higher septa that do not extend to the columella. All but one of the subcerioid and meandroid genera under consideration (*Symphyllia*, and possibly some *Acanthastrea* and *Mycetophyllia*) have costae that are confluent from one calice to the next. Only one of the 10 genera (*Cynarina*) possesses a crown of septal lobes, which encircle the columella (Fig. 2J).

Columella, wall, endo- and exotheca. Columellae are formed by intermingling threads, which extend from the inner septal margins (trabecular) in all genera. They are relatively small (i.e. their diameter is less than one-quarter the calice width), with two exceptions: (1) *Acanthastrea*, which has a relatively thick columella, and (2) *Mycetophyllia*, which has a relatively thin columella, sometimes consisting of a single thin thread.

Corallite walls are generally thin in all 10 genera, and formed from dissepimental tissue (i.e. parathecal). Of the taxa with subcerioid or meandroid colony forms, coenosteum is present in *Isophyllia*, *Acanthastrea* and *Symphyllia*, but not in *Mycetophyllia*. In *Symphyllia* it forms a distinctive groove (ambulacrum) on the calicular surface between adjacent series. Endothecal dissepiments range from moderate to abundant, and both moderate and abundant dissepiments occur in Atlantic and Pacific genera.

Summary. No single macromorphological character or combination of macromorphological characters distinguishes Atlantic from Pacific mussid genera. In the traditional classification system of Vaughan and Wells (1943), mussid genera are distinguished primarily by a combination of colony form and centre linkage. The same range of colony forms exists in both Atlantic and Pacific mussids. Centre linkage differs among Atlantic and Pacific clades; however, there are exceptions.

Micromorphological characters

Septal teeth and granulation. Scanning electron microscopy reveals significant differences in the shape of septal teeth between Atlantic and Pacific mussids (Figs 4–6). In Atlantic genera, septal teeth, especially those of lower septal cycles, are usually circular in outline (or spine-like in shape), whereas in Pacific genera, septal teeth are elliptical in outline (or triangular in shape). This difference is particularly visible in Atlantic versus Pacific species of *Scolymia* (Fig. 7).

Atlantic and Pacific mussids also differ in differentiation among septal teeth in different septal cycles. In Atlantic genera, septal teeth in different septal cycles do not differ in shape, although size differences were detected in two genera (*Scolymia*, *Isophyllastrea*, see Figs 5B and 7A). In some Pacific taxa [*Lobophyllia*, *Symphyllia*, *Scolymia australis* (= *Parascolymia*)], the teeth in different septal cycles differ significantly in shape (Figs 4H,I,L and 5C). However, this differentiation was not observed in *Acanthastrea* and *Scolymia vitiensis* (= *Homophyllia*) (Figs 4G,K and 5A).

In both Atlantic and Pacific genera, the lower level architecture (i.e. granulation) of septal teeth consists of rounded or pointed granules that are arranged multidirectionally (Figs 4 and 6; Table 2). Granules form at the growing edge of the septa and their axes consist of calcification centres, which are secondary to primary calcification axes along the septal plane that form the teeth themselves (see below). Typically, in Atlantic genera, granules are pointed (i.e. spines), whereas in Pacific genera they are rounded (i.e. blunt tips). For example, pointed granules are developed in Atlantic species of *Scolymia* (Fig. 7A–D); whereas septal faces of Pacific species are either covered with scattered rounded granules (*Scolymia australis*, Fig. 7E) or they are smooth (*Scolymia vitiensis*, Fig. 7F).

The septal micromorphology of septal faces is also better developed (more distinctive) in Atlantic genera than in Pacific genera because of less extensive development of thickening deposits (Figs 4 and 6). In Atlantic genera, granules on septal teeth are well developed, particularly along one preferential axis that is perpendicular to the septal plane (Fig. 6A–E). In *Mussismilia*, a particularly distinct spiked ridge, perpendicular to the septal plane, is associated with each tooth (Figs 6F and 8A–C). Such 'paddle-shaped' teeth are common in many Atlantic faviid corals such as *Favia fragum* (Fig. 8D–F; see Cuif and Perrin 1999; Cuif *et al.*

2003), suggesting that they may be the closest relatives of *Mussismilia*. In Pacific genera, granules are less prominent and more evenly distributed on the surface of the septal teeth, and near the base of septal teeth, they are faint because of the development of extensive, smooth thickening deposits (for example Fig. 6L).

In Atlantic genera, the area between teeth contains distinct horizontal bands (Fig. 4A–F), whereas in Pacific genera, this area is either smooth [*Acanthastrea*, *Scolymia* (= *Homophyllia*)] or formed by vertical pillars ('palisade') [*Lobophyllia*, *Symphyllia*, *Cynarina*, *Scolmia* (= *Parascolymia*)] (Fig. 4H–J,L). Sometimes, in Pacific genera, the area between teeth is not evenly filled with skeletal deposits resulting in the formation of a 'pore' that is filled during further growth of the septum (Fig. 4F,H,L).

Columella shape and columella teeth. Few consistent differences exist between Atlantic and Pacific genera in the development of the columella (Table 2). The columella is spongy (consisting of > 12 threads) in all five Pacific genera, and in three Atlantic genera (*Mussa*, *Scolymia*, *Mussismilia*) (Fig. 9). In two Atlantic genera (*Isophyllia*, *Mycetophyllia*) it is loose (consisting of < 12 threads). Columella teeth differ from septal teeth in all 10 genera, except *Mycetophyllia (*columella composed of loose threads) and *Acanthastrea* (columella spongy). In the four Pacific genera that have vertical 'palisade' structures in the area between septal teeth (*Lobophyllia*, *Symphyllia*, *Cynarina*, *Parascolymia*), the same palisade structure is visible in the columella teeth (Fig. 9H–J,L). In comparison to septal teeth, columella teeth are typically twisted (often in a clockwise direction).

Summary. Atlantic and Pacific mussids differ in tooth shape, tooth and septal granulation, and the structure of the area between teeth. Granules are better developed in Atlantic genera and thickening deposits are more extensive in Pacific genera. Granulation in Atlantic genera consists of distinct and pointed granules (tiny spines), whereas granulation in Pacific genera consists of rounded granules.

Microstructural characters

Wall structure and coenosteum. The structure of the corallite wall and coenosteum are best observed in transverse thin section, and are therefore treated herein as microstructural, although relatively coarse in scale. In all 10 mussid genera, corallite walls are primarily parathecal (formed by dissepiments). In Atlantic genera, corallite walls are usually thin (Fig. 10; Table 3). In *Isophyllia*, *Mycetophyllia* and Atlantic *Scolymia*, they are partially septothecal. In Pacific genera, walls are thickened by layers of thickening deposits or stereome (Fig. 11; Table 3). Excluding solitary and phaceloid forms which do not form coenosteum by definition, porous costate coenosteum occurs in both Atlantic and Pacific genera (except *Mycetophyllia*). As is the case with the corallite wall, costae are thickened by layers of thickening deposits in Pacific genera.
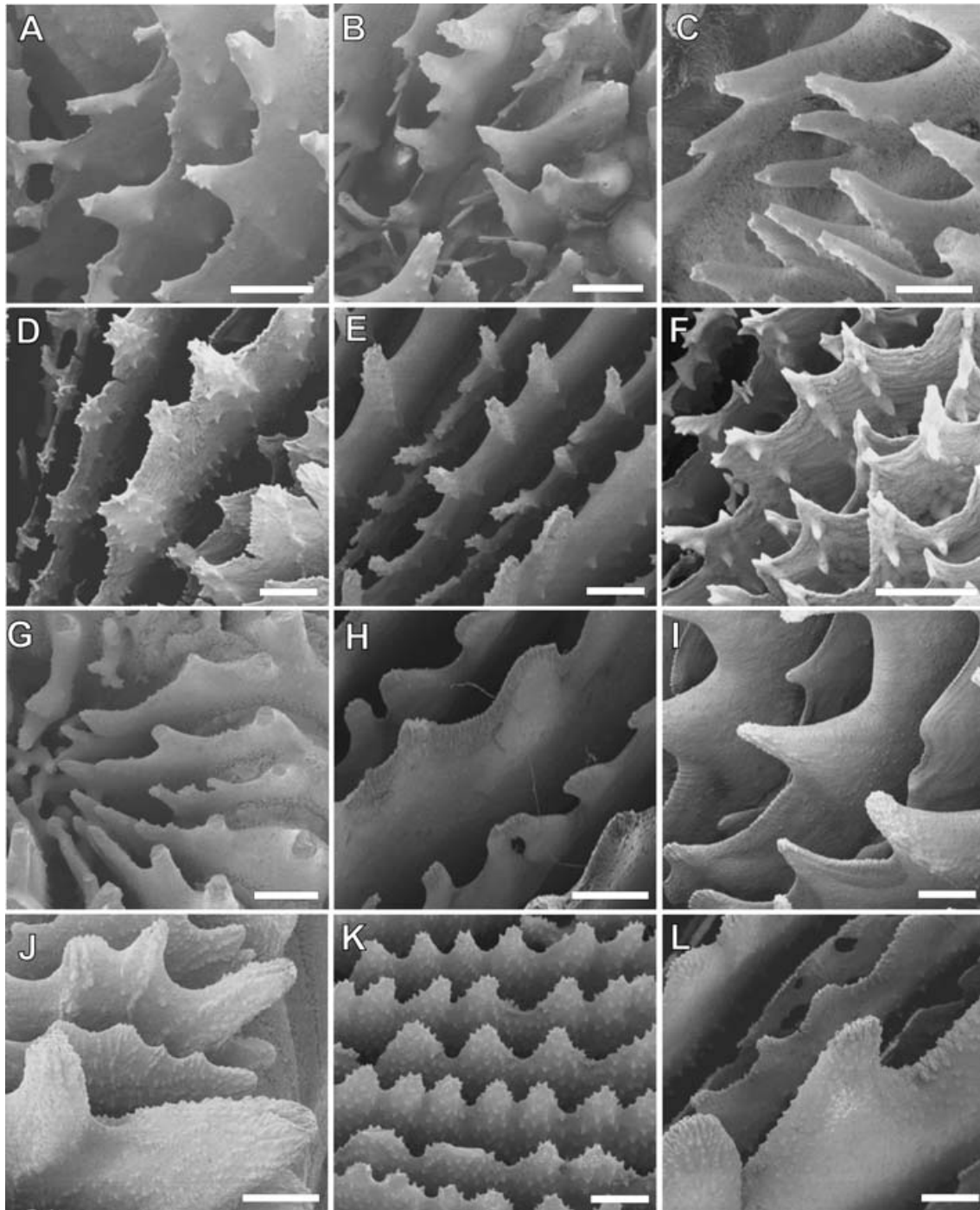
Fig. 4—Micromorphological characters (septal teeth, granulation) of mid-septa of the 10 genera under consideration. Teeth in Atlantic genera (A–F) are circular in outline, whereas teeth in Pacific genera (G–L) are elliptical. Granules are pointed in Atlantic genera, whereas they are rounded in Pacific genera. —**A**. *Isophyllia sinuosa*, SUI 102757 (FA1014), Bocas del Toro, Panama (Atlantic). —**B**. *Isophyllastrea rigida*, SUI 102753 (FA1074), Bocas del Toro, Panama (Atlantic). —**C**. *Mycetophyllia danaana*, SUI 102770 (FA1001), Discovery Bay, Jamaica (Atlantic). —**D**. *Mussa angulosa*, SUI 102770 (FA1012), Bocas del Toro, Panama (Atlantic). —**E**. *Scolymia cubensis*, USNM 84940, Maria Bueno Bay, Jamaica (Atlantic). —**F**. *Mussismilia harttii*, YPM 4516, Maria Farinha, Pernambuco, Brazil (Atlantic). —**G**. *Acanthastrea echinata*, USNM 83348, Malaysia (Pacific). —**H**. *Lobophyllia corymbosa*, USNM 100561, Madagascar (Indian Ocean). —**I**. *Symphyllia recta*, USNM 91129, Indonesia (Pacific). —**J**. *Cynarina lacrymalis*, USNM 93865, Papua New Guinea (Pacific). —**K**. *Scolymia* (= *Homophyllia*) *australis*, USNM 85709, south Australia (Pacific). —**L**. *Scolymia* (= *Parascolymia*) *vitiensis*, USNM 91254, Gt. Palm Island, Australia (Pacific). Scale bars are 1 mm.
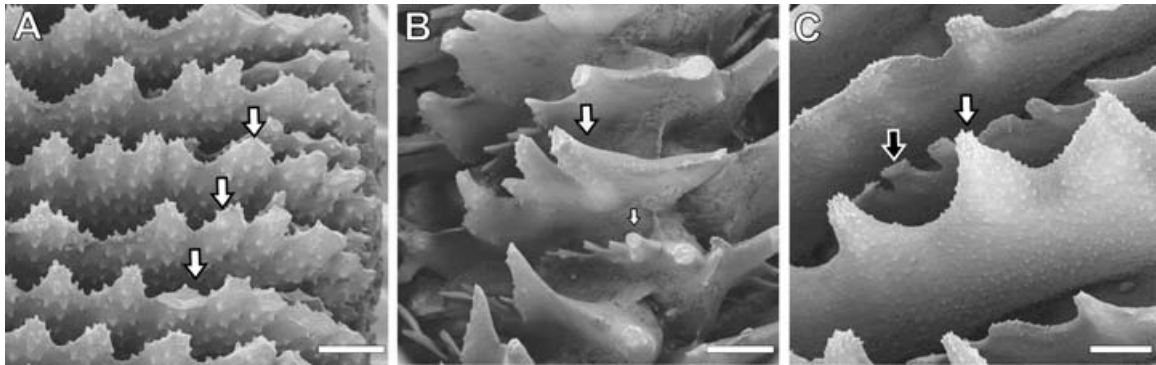
Fig. 5—Differentiation in septal teeth among septal cycles. Teeth in different septal cycles may differ in size in Atlantic genera; but they differ in shape in Pacific genera. —**A**. *Scolymia* (= *Homophyllia*) *australis*, USNM 85709, south Australia (Pacific), not differentiated (equal arrows). —**B**. *Isophyllastrea rigida*, SUI 102753 (FA1074), Bocas del Toro, Panama (Atlantic), differentiated in size but not shape (small versus large arrow). —**C**. *Lobophyllia* sp., USNM 92382, Palau (Pacific), different shapes among septal cycles (black vs. white arrow). Scale bars are 1 mm.

Calcification centres and thickening deposits. Atlantic and Pacific mussids differ in the distinctiveness of calcification centres within septa, and in the development of thickening deposits in the corallite wall and septa. In Atlantic genera, the costosepta are composed of discrete calcification centres that are aligned to form a medial line; clusters of calcification centres form periodically along the line. Weak concentric rings are visible in thickening deposits of *Isophyllastrea* (Fig. 10B,E), *Mussa* (Fig. 10G,J), and *Scolymia* (Fig. 10H,K) but were not observed in *Isophyllia* (Fig. 10A,D), *Mycetophyllia* (Fig. 10C,F), or *Mussismilia* (Fig. 10I,L).

In Pacific genera, the calcification centres within the costosepta are faint and irregular. Well-developed medial lines are present in *Cynarina* (Fig. 11G,J), and the higher septal cycles of *Symphyllia* (Fig. 11C,F). Well-developed concentric rings are visible in thickening deposits of most genera (*Acanthastrea*, *Lobophyllia*, *Symphyllia* and *Homophyllia*), but were not observed in *Cynarina* or *Scolymia* (= *Parascolymia*).

In all 10 genera, the fine-scale structure of the thickening deposits is similar. These deposits are organized into superimposed layers composed of bundles of fibres that were formed during consecutive biomineralization cycles (Fig. 12).

Summary. Although fine-scale structure is similar in the 10 genera under consideration, differences can be observed between Atlantic and Pacific mussids in the distinctiveness of calcification centres and development of thickening deposits within costosepta.

Discussion and conclusions

New diagnostic characters

The present study represents a first step in delineating a set of morphological characters that can be used in phylogenetic analyses of the Family Mussidae and related taxa. It recognizes several new micromorphological characters for the first time, involving the shapes of septal teeth, the relative development of secondary calcification axes and corresponding granulation on septal teeth and septal faces, the shape of the area between teeth, and the development of thickening deposits. Moreover, it shows that most macromorphological characters that have traditionally been used to distinguish scleractinian families, genera and species exhibit homoplasy. Although the distinctiveness of calcification centres within costosepta appears to be informative, the fine-scale structure

Fig. 6—Close-ups of septal teeth showing granulation in Atlantic (A–F) and Pacific (G–L) mussids; granules correspond to the position of calcification centres (= Centers of Rapid Accretion). The septal plane is marked with white dashed line. Primary directions of growth of granules are marked with white arrows; whereas black arrows indicate other (not dominating) directions. Length of the arrow (shorter, longer) is proportional to the relative protrusion of the granules. Arrows repeated in all/some directions indicate that granules are distinct in the lower portions of septal teeth, or they fade in deeper parts of septa because they are covered with smooth thickening deposits). —**A**. *Isophyllia sinuosa*, SUI 102755 (FA1007), Bocas del Toro, Panama (Atlantic). —**B**. *Isophyllastrea rigida*, SUI 102752 (FA1009), Bocas del Toro, Panama (Atlantic). —**C**. *Mycetophyllia danaana*, SUI 102772 (FA1003), Bocas del Toro, Panama (Atlantic). —**D**. *Mussa angulosa*, SUI 102761 (FA1012), Bocas del Toro, Panama (Atlantic). —**E**. *Scolymia cubensis*, USNM 84940, Maria Bueno Bay, Jamaica (Atlantic). —**F**. *Mussismilia harttii*, YPM 4516, Maria Farinha, Pernambuco, Brazil (Atlantic). —**G**. *Acanthastrea echinata*, SUI 102778 (FA1094), Taiwan (Pacific). —**H**. *Lobophyllia corymbosa*, USNM 92382, Palau (Pacific). —**I**. *Symphyllia recta*, USNM 91129, Indonesia (Pacific). —**J**. *Cynarina lacrymalis*, USNM 93865, Papua New Guinea (Pacific). —**K**. *Scolymia* (= *Homophyllia*) *australis*, USNM 85709, south Australia (Pacific). —**L**. *Scolymia* (= *Parascolymia*) *vitiensis*, UF 2130, Palau (Pacific). Scale bars are 500 μm. See also Table 2.
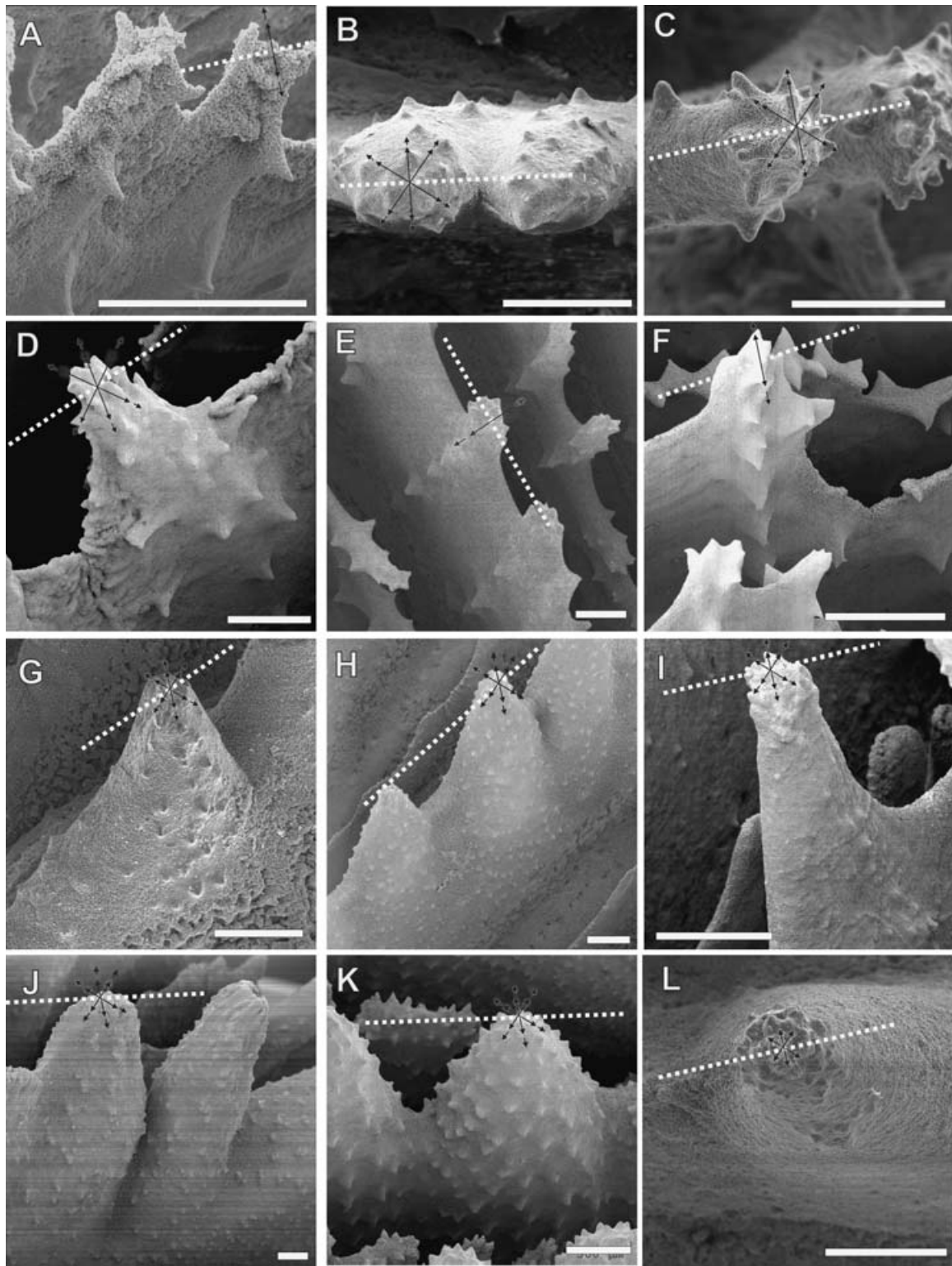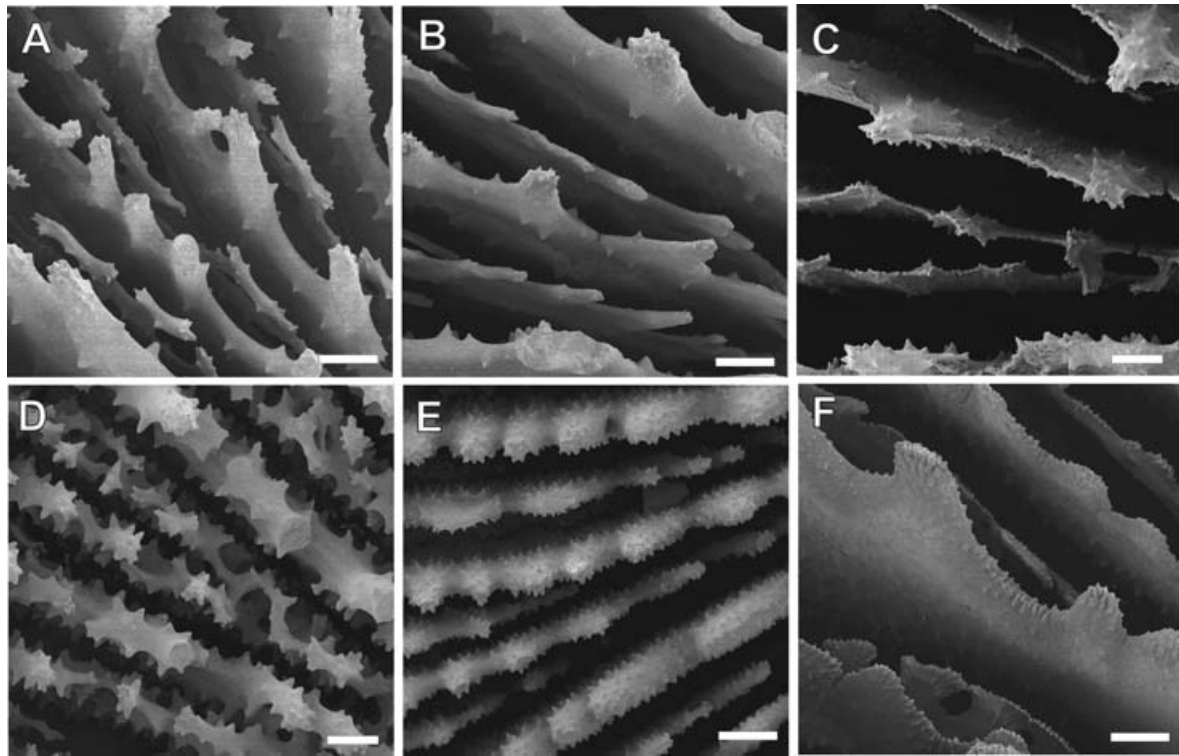
Fig. 7— Micromorphological diversity (septal teeth, granulation) of mid-septa in Atlantic (A–D) and Pacific (E–F) species of *Scolymia* and *Scolymia*-like genera (SEM micrographs). Differences in the shapes of teeth and granules between Atlantic and Pacific *Scolymia* suggest that *Scolymia* from the two different oceans are unrelated. —**A**. *Scolymia cubensis*, USNM 84940, Maria Bueno Bay, Jamaica (Atlantic). —**B**. *Scolymia lacera*, USNM 84920, Maria Bueno Bay, Jamaica (Atlantic). —**C**. *Mussa angulosa* (sometimes synonymized with *Scolymia lacera*), SUI 102761 (FA1012), Bocas del Toro, Panama (Atlantic). —**D**. *Scolymia wellsii*, USNM 84926, Angel Reef, Trinidad and Tobago (Atlantic). —**E**. *Scolymia* (= *Homophyllia*) *australis*, USNM 85709, south Australia (Pacific). —**F**. *Scolymia* (= *Parascolymia*) *vitiensis*, USNM 91254, Gt. Palm Island, Australia (Pacific). Scale bars are 1 mm.

of the thickening deposits is not effective at distinguishing clades in the examined taxa (see also Jell 1974).

The importance of features associated with septal teeth was previously recognized by Vaughan and Wells (1943) and Wells (1956), who recognized large, 'lobulate' teeth as being diagnostic of the family Mussidae. They used the term 'lobulate' to refer to fan systems of 'simple trabeculae', whose centres are orientated roughly parallel to the septal plane. By contrast, septal teeth in the family Faviidae were interpreted as having been formed by 'simple trabeculae' that are not organized into fans (except for septal lobes, e.g. in *Manicina*). Despite the use of teeth in classification, Vaughan and Wells (1943) and Wells (1956) did not distinguish between different shapes of teeth and granules, characters which we have found to be essential to distinguishing molecular-based clades. Our study benefits from advances in electron microscopy over the past few decades, which allow not only shapes of granules and teeth to be observed with higher resolution, but also the centres and fibres that form them. We are therefore able to observe and interpret the shape variation in teeth

and granules using up-to-date models of septal growth (Stolarski 2003), which focus on the complex interplay between the rapid accretion front (where primary and secondary calcification axes form) and the surrounding thickening deposits.

More specifically, the most definitive diagnostic differences between Atlantic and Pacific mussids involve: (a) the spine-shaped teeth of Atlantic mussids vs. the triangular-shaped teeth of Pacific mussids (more precisely, circular tooth outlines in Atlantic mussids vs. elliptical tooth outlines in Pacific mussids), and (b) the granules in Atlantic mussids are distinct and pointed (tiny spines), whereas the granules in Pacific mussids are rounded. These shape differences can be attributed to the relative pace of growth of primary and secondary calcification centres (axes) and thickening deposits.

In both Atlantic and Pacific mussids, septal teeth are formed by calcification axes in multiple directions. The primary axis in both groups is along the septal plane. Secondary axes are better developed in the teeth of Atlantic mussids;

Table 2 Comparison of micromorphological characters among Atlantic and Pacific mussids

| Species	Septal tooth outline (Fig. 4)	Differentiation in teeth amond septal cycles (Fig. 5)	Secondary axes (Fig. 6)	Distribution of septal tooth granulation (Fig. 6)	Septal face granulation (Fig. 4)	Area between teeth (Fig. 4)	Thickening deposits (Figs 4 and 6)	Columella shape (Fig. 9)
Atlantic								
Isophyllia sinuosa	circular	none	strong; axis perpendicular to septal plane well-developed	secondary axis well developed	diffuse, pointed	weakly banded	less extensive	loose threads, teeth different from septa
Isophyllastrea rigida	circular	size but not shape	strong	multi-directional	diffuse, pointed	weakly banded/-smooth	less extensive	loose threads, teeth different from septa
Mycetophyllia danaana	circular	none	strong	multi-directional	diffuse, pointed	weakly banded/-smooth	less extensive	loose threads, teeth same as septa
Mussa angulosa	circular	none	strong	multi-directional	diffuse, pointed	banded	less extensive	spongy, teeth different from septa
Scolymia cubensis	circular	size but not shape	strong; axis perpendicular to septal plane well-developed	secondary axis well developed	diffuse, pointed	weakly banded	less extensive	spongy, teeth different from septa
Mussismilia harttii	circular	none	strong; axis perpendicular to septal plane very well-developed	secondary axis well developed	evenly scattered to aligned, pointed	banded	less extensive	spongy, teeth different from septa
Pacific								
Acanthastrea echinata	elliptical	none	weak	multi-directional	diffuse, rounded	weakly palisade/-smooth	more extensive	spongy, teeth same as septa
Lobophyllia corymbosa	elliptical	shape difference between septal cycles	weak	multi-directional	diffuse, rounded	palisade	more extensive	spongy, teeth different from septa
Symphyllia recta	elliptical	shape difference between septal cycles	weak	multi-directional	diffuse, rounded	palisade	more extensive	spongy, teeth different from septa
Cynarina lacrymalis	elliptical	shape difference between septal cycles	weak	multi-directional	diffuse, rounded	palisade	more extensive	spongy, teeth different from septa
Scolymia australis	elliptical	none	weak	multi-directional	evenly scattered, rounded	smooth	more extensive	spongy, teeth different from septa
Scolymia vitiensis	elliptical	shape difference between septal cycles	weak	multi-directional	diffuse, rounded	palisade	more extensive	spongy, teeth different from septa
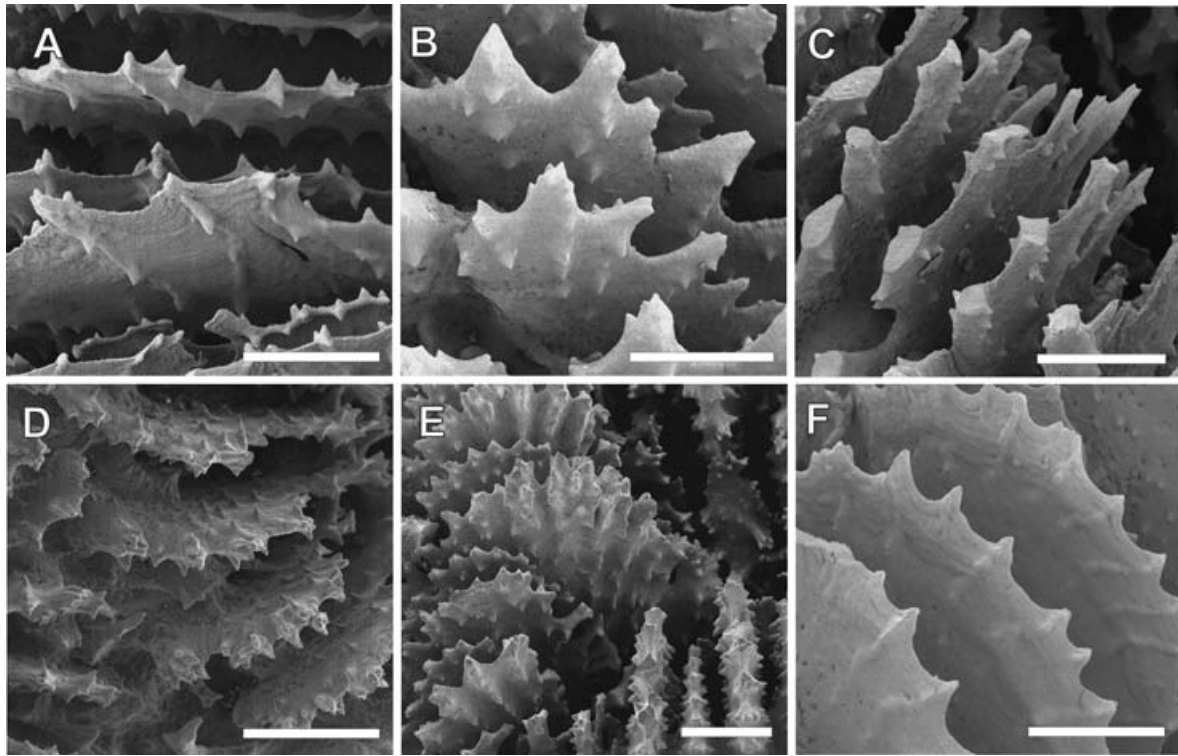
Fig. 8—SEM micrographs of micromorphological characters of mid-septa in three *Mussismilia* species (A–C) with selected members of the family Faviidae (D–F). The teeth and granules of *Mussismilia* are more similar to *Favia leptophylla* and other Atlantic faviids than they are to Atlantic mussids. —**A**. *Mussismilia harttii*, YPM 4516, Maria Farinha, Pernambuco, Brazil (Atlantic). —**B**. *Mussismilia brasiliensis*, YPM 9104, Abrolhos reefs, Brazil (Atlantic). —**C**. *Mussismilia hispida*, YPM 4515, Periperi, Bahia, Brazil (Atlantic). —**D**. *Favia leptophylla*, SUI 99645, Abrolhos reefs, Brazil (Atlantic). —**E**. *Favia fragum*, SUI 83695 Bocas del Toro, Panama (Atlantic). —**F**. *Colpophyllia natans*, SUI 102823 (FA1071), Bocas del Toro, Panama (Atlantic). Scale bars are 500 μm.

whereas thickening deposits are more extensive in Pacific mussids. Our observations suggest that granules are more pronounced and pointed in Atlantic mussids, because they are not engulfed in thickening deposits, which are less extensively developed than in Pacific mussids. For the same reason, the septal teeth in Atlantic genera are thinner at their base. Conversely, enhanced growth of thickening deposits in Pacific mussids may be responsible for their thicker septal teeth and their low, rounded granules.

The taxonomic importance of the relative development of calcification axes and thickening deposits was highlighted by researchers working on microstructures of Cenozoic corals (Alloiteau 1957; Chevalier 1971, 1975; for review see Stolarski and Roniewicz 2001). For example, Alloiteau (1957) distinguished between 'fibreux', 'granuleux' and 'lamellaire' costoseptal histological structure based on the size and arrangement of calcification centres and fibres observed in transverse thin section (Alloiteau 1957; p. 21). In fact, he removed the family Meandrinidae from the suborder Faviina, which also contains the families Faviidae and Mussidae, and raised it to subordinal rank on the basis

of its lack of 'ornamentation' (e.g. teeth, granulation). In addition to differences in the shapes of teeth and granules, the present study shows that Atlantic mussids have a distinctive costoseptal microstructure, which consists of discrete calcification centres, which are aligned forming medial septal lines and which form clusters at regular intervals along the lines. Costoseptal structure in Pacific mussids varies from faint irregular centres to continuous, well-developed medial septal lines (e.g. *Cynarina*), but never forms clusters.

One of the first studies to show that tooth shape is indeed diagnostic of family level molecular clades was that of Cuif *et al.* (2003), who mapped the shapes of septal teeth onto a 28rRNA phylogeny. Cuif *et al.* (2003) found that 'paddle-shaped' septal teeth were diagnostic of a clade composed of faviid/mussid 'robust' corals. A 'paddle-shaped' tooth is formed by a short series of calcification centres (a secondary calcification axis) that is transverse to the direction of the septal plane. Our study further extends these micromorphological observations to a larger number of mussid genera, and shows that such secondary axes are well-developed in Atlantic mussids and may occur in multiple orientations.
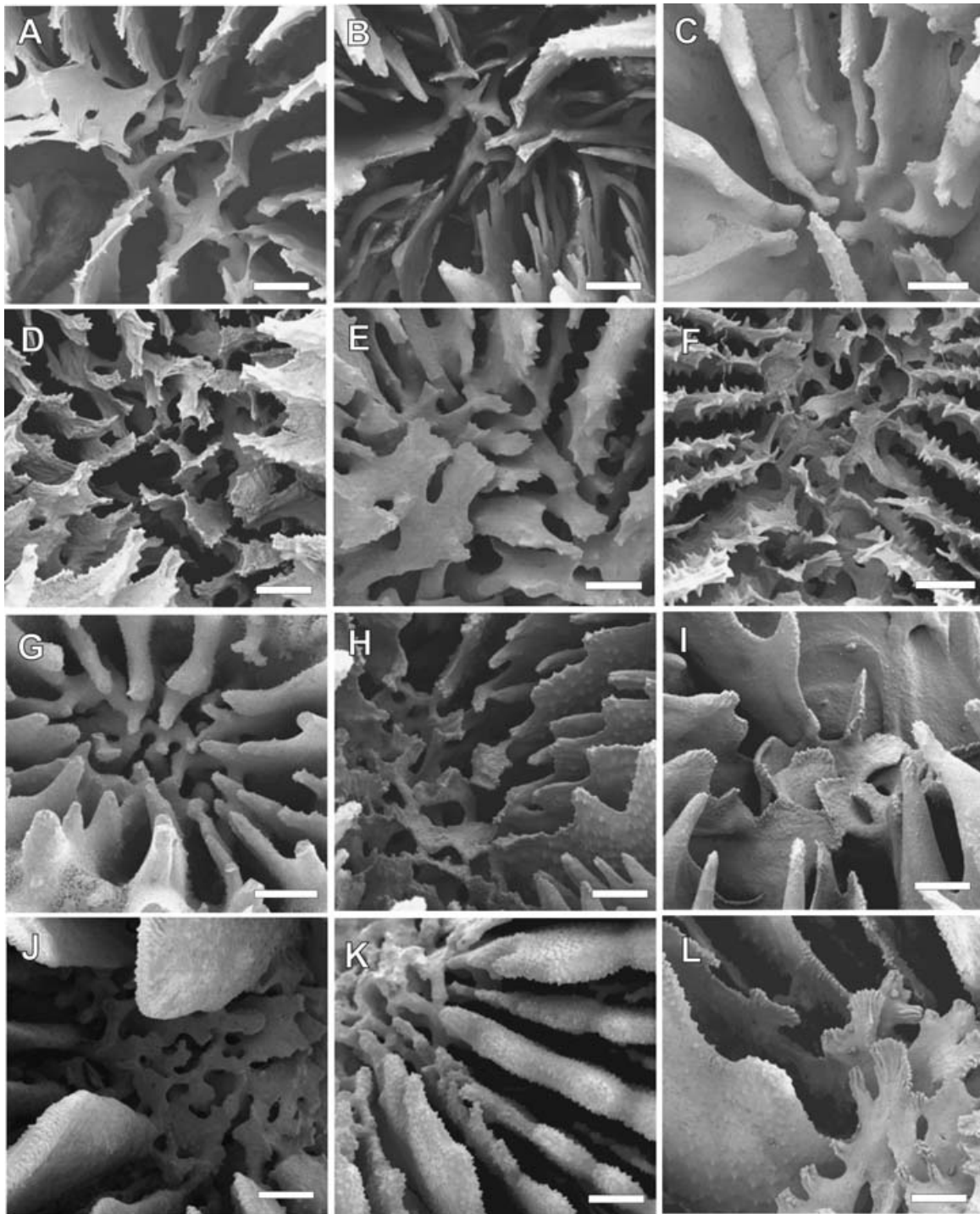
Fig. 9—Columellae in the 10 genera under consideration. All SEM micrographs. *Isophyllia*, *Isophyllastrea* and *Mycetophyllia* have columellae consisting of loose threads; columellae are spongy in the other seven genera. —**A**. *Isophyllia sinuosa*, SUI 102757 (FA1014), Bocas del Toro, Panama (Atlantic). —**B**. *Isophyllastrea rigida*, SUI 102753 (FA1074), Bocas del Toro, Panama (Atlantic). —**C**. *Mycetophyllia danaana*, SUI 102771 (FA1002), Bocas del Toro, Panama (Atlantic). —**D**. *Mussa angulosa*, SUI 102761 (FA1012), Bocas del Toro, Panama (Atlantic). —**E**. *Scolymia cubensis*, USNM 84939, Maria Bueno Bay, Jamaica (Atlantic). —**F**. *Mussismilia harttii*, YPM 4516, Maria Farinha, Pernambuco, Brazil (Atlantic). —**G**. *Acanthastrea echinata*, USNM 83348, Malaysia (Pacific). —**H**. *Lobophyllia corymbosa*, UF 4090, Cook Islands (Pacific). —**I**. *Symphyllia recta*, USNM 91129, Indonesia (Pacific). —**J**. *Cynarina lacrymalis*, USNM 93865, Papua New Guinea (Pacific). —**K**. *Scolymia* (= *Homophyllia*) *australis*, USNM 85709, south Australia (Pacific). —**L**. *Scolymia* (= *Parascolymia*) *vitiensis*, USNM 91254, Great Palm Island, Australia (Pacific). Scale bars are 1 mm.
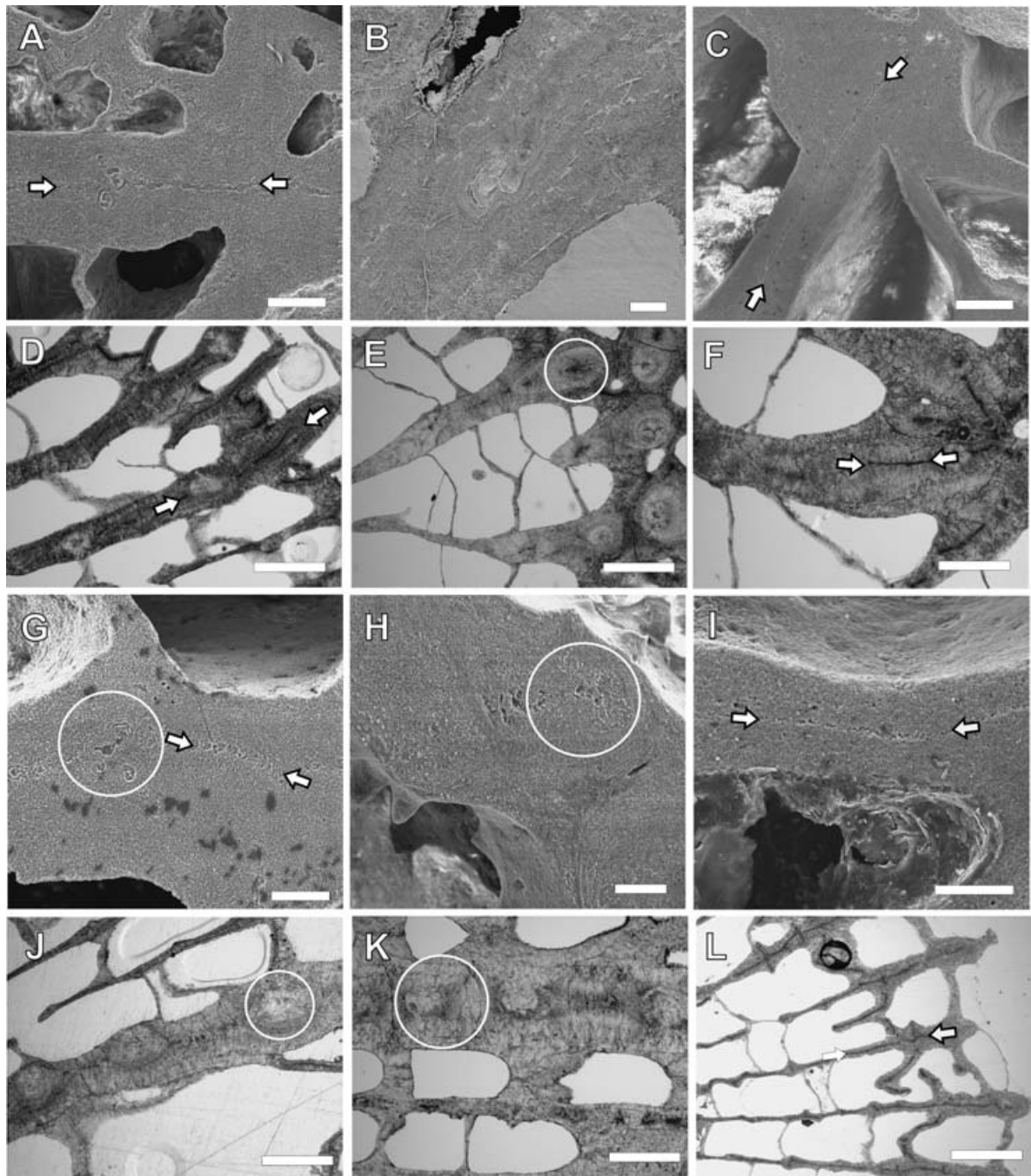
Fig. 10—Transverse polished, etched sections (A–C, G–I; SEM micrographs) and thin sections (D–F, J–L) of six Atlantic mussids. Calcification centres are discrete and aligned, forming a medial line (arrows); small clusters of calcification centres form along the line and are encircled by concentric rings of thickening deposits (white circles). —**A**. *Isophyllia sinuosa*, SUI 102755 (FA1007), Bocas del Toro, Panama (Atlantic). —**B**. *Isophyllastrea rigida*, SUI 102753 (FA1074), Bocas del Toro, Panama (Atlantic). —**C**. *Mycetophyllia danaana*, SUI 102771 (FA1002), Bocas del Toro, Panama (Atlantic). —**D**. *Isophyllia sinuosa*, SUI 102757 (FA1014), Bocas del Toro, Panama (Atlantic). —**E**. *Isophyllastrea rigida*, SUI 102752 (FA1009), Bocas del Toro, Panama (Atlantic). —**F**. *Mycetophyllia danaana*, SUI 102771 (FA1002), Bocas del Toro, Panama (Atlantic). —**G**. *Mussa angulosa*, SUI 102752 (FA1013), Bocas del Toro, Panama (Atlantic). —**H**. *Scolymia cubensis*, USNM 84940, Maria Bueno Bay, Jamaica (Atlantic). —**I**. *Mussismilia harttii*, YPM 1468c, syntype, Abrolhos reefs, Brazil (Atlantic). —**J**. *Mussa angulosa*, SUI 102751 (FA1012), Bocas del Toro, Panama (Atlantic). —**K**. *Scolymia cubensis*, USNM 84940, Maria Bueno Bay, Jamaica (Atlantic). —**L**. *Mussismilia harttii*, YPM 4516, Maria Farinha, Pernambuco, Brazil (Atlantic). Scale bars in A, B, C, G, H, I are 1 mm; scale bars in D, E, F, J, K, L are 500 μm.

Table 3 Comparison of microstructural characters among Atlantic and Pacific mussids.

Species	Coenosteum*	Corallite wall	Calcification centres	Structure of thickening deposits
Atlantic				
Isophyllia sinuosa	present	mostly parathecal, partially septothecal	clusters of centres along a medial line	well-developed layers (no rings)
Isophyllastrea rigida	present	mostly parathecal, partially septothecal	clusters of centres along a medial line	layers and concentric rings
Mycetophyllia danaana	absent	mostly parathecal, partially septothecal	clusters of centres along a medial line	well-developed layers (no rings)
Mussa angulosa	not applicable	parathecal only	clusters of centres along a medial line	layers and concentric rings
Scolymia cubensis	not applicable	mostly parathecal, partially septothecal	clusters of centres along a medial line	layers and concentric rings
Mussismilia harttii	not applicable	parathecal only	clusters of centres along a medial line	well-developed layers (no rings)
Pacific				
Acanthastrea echinata	present	parathecal with thickening deposits (stereome)	faint irregular centres	layers and concentric rings
Lobophyllia corymbosa	not applicable	parathecal with thickening deposits (stereome)	faint irregular centres	layers and concentric rings
Symphyllia recta	present	parathecal with thickening deposits (stereome)	faint irregular centres; with a continuous medial line in higher septal cycles	layers and concentric rings
Cynarina lacrymalis	not applicable	parathecal with thickening deposits (stereome)	continuous well-developed medial line	well-developed layers (no rings)
Scolymia australis	not applicable	parathecal with thickening deposits (stereome)	faint irregular centres	layers and concentric rings
Scolymia vitiensis	not applicable	parathecal with thickening deposits (stereome)	faint irregular centres	well-developed layers (no rings)

*Phaceloid and solitary forms do not have coenosteum by definition; subcerioid forms may have limited coensteum.

Well-developed transversal axes are present in *Isophyllia* and Atlantic *Scolymia cubensis* (Fig. 6A,E), and are particularly strong in *Mussismilia* (Figs 6F and 8A–C), whose teeth more closely resemble Atlantic faviids than Atlantic mussids, matching the molecular phylogeny in Nunes *et al.* (2008). However, we did not observe well-developed transversal axes in Pacific mussids. Transversal axes are well developed in Pacific faviids (e.g. *Favia stelligera*, see Cuif *et al.* 2003), suggesting that this character may be either convergent or plesiomorphic and therefore requires further study.

Taxonomic implications

Pacific 'Scolymia'. The taxonomic implications of the present study are many. First, contrary to Veron (2000), our results indicate that Atlantic and Pacific *Scolymia* are unrelated and that Pacific *Scolymia australis* and *Scolymia vitiensis* are unrelated, supporting the assignment by Wells (1964) of *Scolymia australis* to the genus *Homophyllia* and of *Scolymia vitiensis* to *Parascolymia*. As originally defined, *Scolymia* is distinguished from the genus *Homophyllia* on the basis of number of teeth per centimetre and calice size.

Scolymia is distinguished from *Parascolymia* on the basis of lamellar linkage among centres during asexual budding and thick granules. Our results further indicate that the granules of *Scolymia australis* are thicker and more narrowly scattered than the granules of *Scolymia vitiensis* (Fig. 7). There is no differentiation among teeth in different septal cycles in *Scolymia australis*, and the area between teeth is distinctively palisade in *Scolymia vitiensis*, resembling *Lobophyllia* and *Symphyllia*.

Atlantic 'Scolymia'. Moreover, our results suggest that *Scolymia lacera* and *Mussa angulosa* may not be the same species as indicated by Matthai (1928) and Veron (2000). In addition to macromorphology (especially the high frequency of intramural budding and fewer septal cycles observed in *Mussa*), our observations show no differentiation among septal teeth in different septal cycles in *Mussa* in contrast to the strong size differentiation among septal teeth reported in *Scolymia lacera* (Fig. 7B,C). Granulations are also abundant and pointed (spiny) in *Scolymia wellsii* (Fig. 7D), supporting its recognition as a separate species. Strangely, the shape of its septal teeth and granulation is in many ways similar to
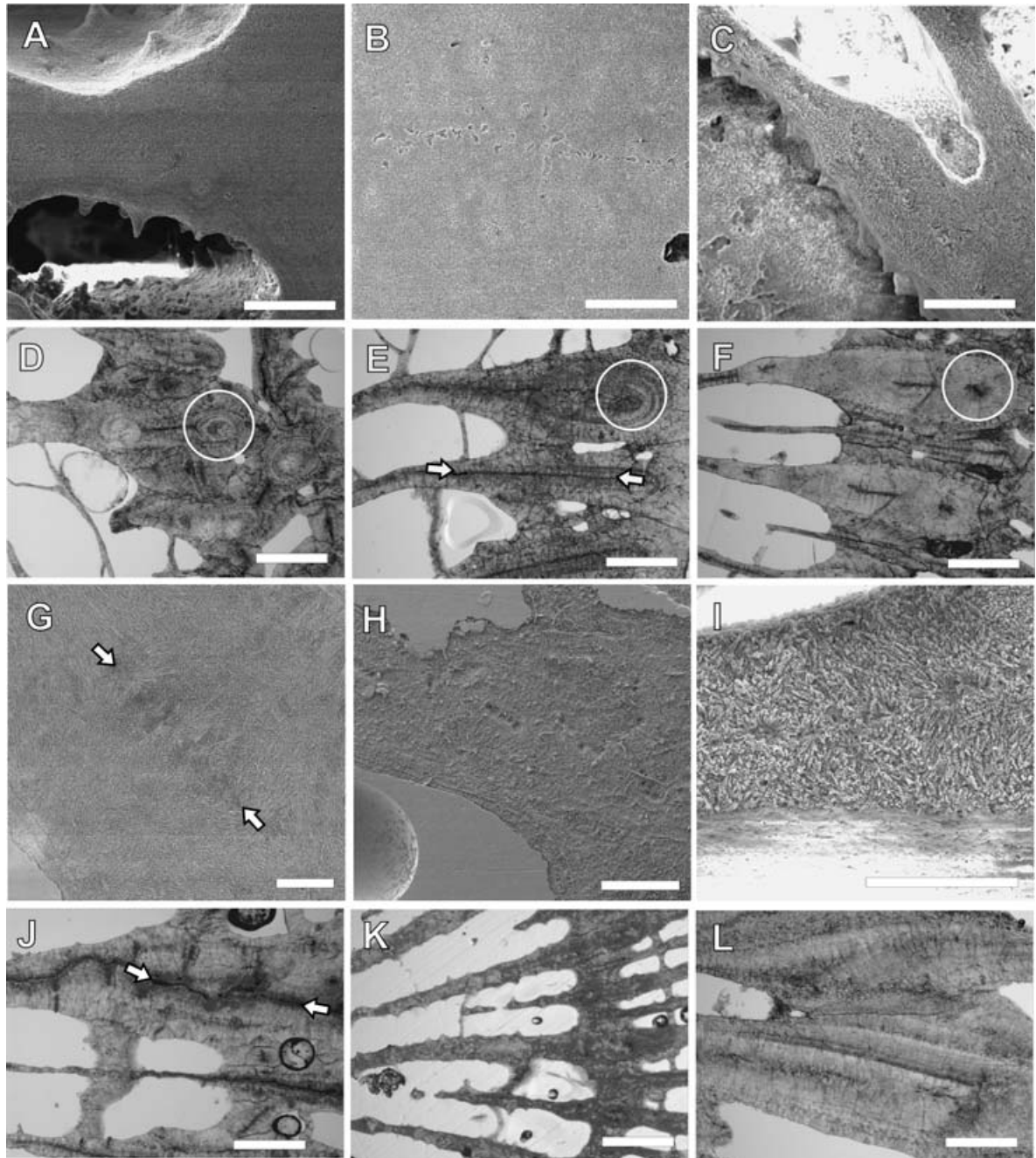
Fig. 11—Transverse polished, etched sections (A–C, G–I; SEM micrographs) and thin sections (D–F, J–L) of six Pacific mussids. The calcification centres may be aligned forming a mid-septum medial line (arrows), or they may be arranged in clusters that are clearly separated from each other and encircled by concentric rings of thickening deposits (white circles). —**A**. *Acanthastrea echinata*, SUI 102778 (FA 1094), Taiwan (Pacific). —**B**. *Lobophyllia corymbosa*, USNM 100561 (FA 1045), Madagascar (Pacific). —**C**. *Symphyllia recta*, SUI 102779 (FA 1028), Lizard Island, Asutralia (Pacific). —**D**. *Acanthastrea echinata*, SUI 102778 (FA 1094), Taiwan (Pacific). —**E**. *Lobophyllia corymbosa*, USNM 100561 (FA 1045), Madagascar (Pacific). —**F**. *Symphyllia recta*, USNM 93794, Papua New Guinea (Pacific). —**G**. *Cynarina lacrymalis*, USNM 93865, Papua New Guinea (Pacific). —**H**. *Scolymia* (= *Homophyllia*) *australis*, USNM 85709, south Australia (Pacific). —**I**. *Scolymia* (= *Parascolymia*) *vitiensis*, UF 2130 (FA 1057), Palau (Pacific). —**J**. *Cynarina lacrymalis*, USNM 93862, Papua New Guinea (Pacific). —**K**. *Scolymia* (= *Homophyllia*) *australis*, USNM 85709, south Australia (Pacific). —**L**. *Scolymia* (= *Parascolymia*) *vitiensis*, USNM 91254, Great Palm Island, Australia (Pacific). Scale bars in A, B, C, G, H, I are 1 mm; scale bars D, E, F, J, K, L are 500 μm.
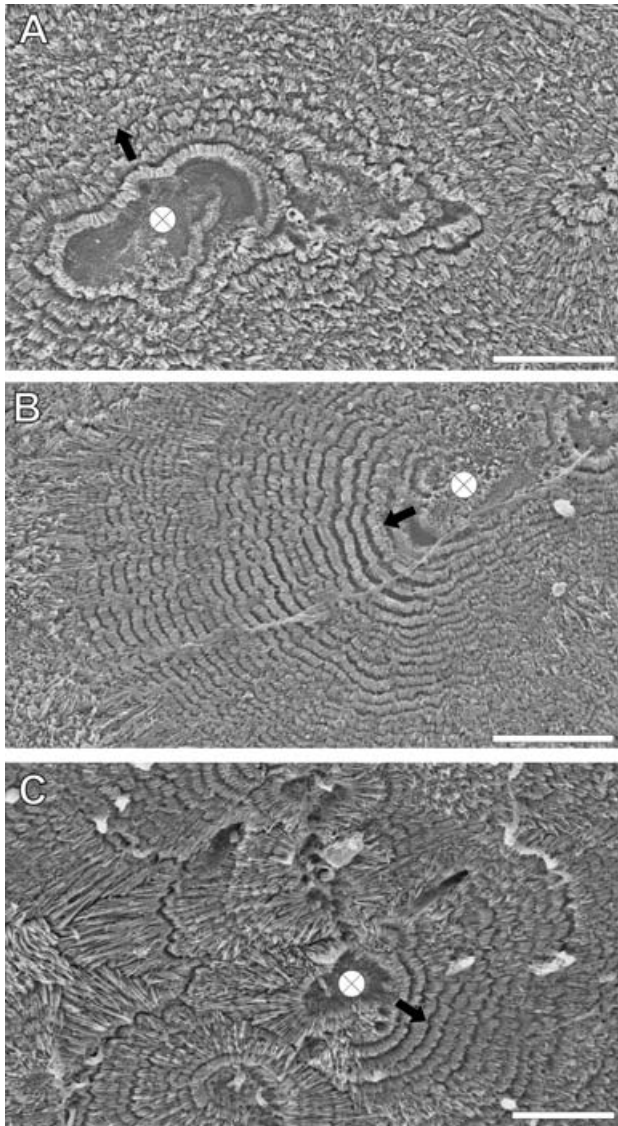
Fig. 12—SEM micrographs of etched surfaces of the skeleton of Atlantic *Isophyllia sinuosa* (A), and Pacific *Acanthastrea bowerbanki* (B) and *Symphyllia radians* (C). The thickening deposits (black arrow) are organized in superimposed layers composed of bundles of fibres formed during consecutive biomineralization cycles. Calcification centres are marked with crossed circles. —**A**. *Isophyllia sinuosa*, SUI 102757 (FA1014), Bocas del Toro, Panama (Atlantic). —**B**. *Acanthastrea bowerbanki*, ZPAL (Pacific). —**C**. *Symphyllia radians*, USNM 93797, Papua New Guinea (Pacific). Scale bars are 50 μm.

Mussismilia, suggesting that Atlantic *Scolymia*, like Pacific *Scolymia*, may also be polyphyletic.

Mussismilia. As described above, our results indicate that the septal teeth and granulation of *Mussismilia* is more similar to *Favia leptophylla* and other Atlantic faviids than it is to

Atlantic mussids. Specifically it has 'paddled-shaped' teeth and aligned granules on septal faces (Fig. 8). *Mussismilia* is distinguished from *Mussa*, on the basis of it more numerous, sometimes perforate, septa and multicentred, lacerate teeth (consisting of twisted threads) with abundant spiny granulation (Laborel 1969). Atlantic faviids form a separate sub-clade in the molecular tree of Fukami *et al.* (2004) (Fig. 1), with *Mussismilia* being more closely allied to this subclade than to Atlantic mussids (see also Nunes *et al.* 2008). Our micromorphological observations support these relationships.

Isophyllastrea. The genus *Isophyllastrea* was originally distinguished from *Isophyllia* on the basis of its subcerioid growth form and it mono- to di-centric corallites (Matthai 1928). Our observations show that the characters that distinguish *Isophyllastrea* from *Isophyllia* are in many ways similar to those that distinguish *Mussa angulosa* from *Scolymia lacera*. There is no differentiation among septal teeth in different septal cycles in *Isophyllia* in contrast to the strong size differentiation among septal teeth in *Isophyllastrea*. Moreover the septal teeth of *Isophyllia* possess well-developed transversal secondary axes, which were not observed in *Isophyllastrea*. It is unclear whether the observed differences indicate that *Isophyllastrea rigida* and *Isophyllia sinuosa* belong to different genera. The same is true of *Scolymia lacera* and *Mussa angulosa*.

Acanthastrea. Much of the present study has focused on discovering morphological characters that distinguish Atlantic from Pacific mussids; however, the genetic results (Fukami *et al.* 2004) also show that species of *Acanthastrea* belong to one or more distinct clades that are separate from other Pacific mussids and that the genus *Acanthastrea* may not be monophyletic. Most of the micromorphological and microstructural characters treated herein reveal similarities between *Acanthastraea* and other Pacific mussids. However, *Acanthastraea* also differs from other Pacific mussids in the structure of its columella, in addition to macromorphological characters (its subcerioid colony form and relatively smaller calices). Clearly the structure of the columella warrants further investigation in future work.

Future work

The present study provides the groundwork for future morphological work on the systematics of the Family Mussidae: (1) performing morphology-based phylogenetic analyses and quantitatively comparing morphological and molecular data, (2) formally revising the taxonomy of this polyphyletic group, and (3) incorporating fossils into phylogenetic analyses and examining the divergence of Atlantic and Pacific mussids within a geological context.

One question that remains unresolved is the effect of environment on the new diagnostic characters. Foster (1979) found that the thickness of the costosepta and associated corallite wall in *Montastraea annularis* changed in response to

transplantation between fore-reef and lagoon environments. Cursory examination of thin-sections of the transplanted colonies has shown that arrangements of calcification centres do not change in response to transplantion, but that thickening deposits are better developed in fore-reef environments. However, the amount of variation observed in transplanted colonies is far less than that reported herein. Moreover, the colonies in the present study were collected in a range of reef environments at varied geographical locations (Appendix I) and represent a broad spectrum of the variation that exists within Atlantic and Pacific mussids. This sampling and the observed agreement between morphological and molecular data indicate that the reported morphological differences are genetic in origin and not caused solely by phenotypic plasticity in response to environmental factors. Support for environmental stability of some microstructural features is also provided by experiments showing that even drastic differences in seawater geochemistry (carbonate-ion concentrations), which cause the suppression of calcification rate, do not affect the gross microarchitecural and microstructural features of corals. For example, Marubini *et al.* (2002) showed that scale-like fibrous units typical of the skeleton surface of *Acropora* develop in corals cultured in seawater with normal and low carbonate-ion concentrations.

Acknowledgements

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Appendix I List of specimens examined

Museum	Catalogue no	Genus	Species	Type status	Collector	Collecting year	Location	Ocean
SUI (U.Iowa)	102752	*Isophyllastrea*	*rigida*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102753	*Isophyllastrea*	*rigida*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102754	*Isophyllastrea*	*rigida*	non-type	Budd	1974	Discovery Bay, Jamaica	Atlantic
SUI (U.Iowa)	102755	*Isophyllia*	*sinuosa*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102756	*Isophyllia*	*sinuosa*	non-type	Budd	1974	Discovery Bay, Jamaica	Atlantic
SUI (U.Iowa)	102757	*Isophyllia*	*sinuosa*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102758	*Isophyllia*	*sinuosa*	non-type	Budd	1989	Crocus Bay, Anguilla	Atlantic
SUI (U.Iowa)	102759	*Isophyllia*	*sinuosa*	non-type	Heckel	1975	Key Largo, Florida	Atlantic
SUI (U.Iowa)	102761	*Mussa*	*angulosa*	non-type	Budd	1974	Discovery Bay, Jamaica	Atlantic
SUI (U.Iowa)	102762	*Mussa*	*angulosa*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102763	*Mussa*	*angulosa*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102763	*Mussa*	*angulosa*	non-type	Heckel	1975	Key Largo, Florida	Atlantic
SUI (U.Iowa)	102843	*Mussa*	*angulosa*	non-type	Budd	1974	Discovery Bay, Jamaica	Atlantic
YPM	9104	*Mussismilia*	*braziliensis*	non-type	Laborel	1964	Brazil	Atlantic
YPM	9105	*Mussismilia*	*braziliensis*	non-type	Laborel	1964	Brazil	Atlantic
SUI (U.Iowa)	102764	*Mussismilia*	*harttii*	non-type	Amaral	1989	Abrolhos, Brazil	Atlantic
SUI (U.Iowa)	102765	*Mussismilia*	*harttii*	non-type	Amaral	1989	Abrolhos, Brazil	Atlantic
YPM	1468A	*Mussismilia*	*harttii*	syntype	Hartt	1867	Brazil	Atlantic
YPM	1468B	*Mussismilia*	*harttii*	syntype	Hartt	1870	Brazil	Atlantic
YPM	1468C	*Mussismilia*	*harttii*	syntype	Hartt	1870	Brazil	Atlantic
YPM	1469	*Mussismilia*	*harttii*	syntype	Hartt	1867	Brazil	Atlantic
YPM	4514	*Mussismilia*	*harttii*	syntype (var. conferta)	Rathbun	1870	Brazil	Atlantic
YPM	4516	*Mussismilia*	*harttii*	non-type	Hartt	1875	Brazil	Atlantic
YPM	4551	*Mussismilia*	*harttii*	syntype (var. intermedia)	Derby & Wilmot	1870	Brazil	Atlantic
SUI (U.Iowa)	102766	*Mussismilia*	*hispida*	non-type	Amaral	1989	Abrolhos, Brazil	Atlantic
YPM	4284	*Mussismilia*	*hispida*	paratype	Dana	1838	Brazil	Atlantic
YPM	4287	*Mussismilia*	*hispida*	holotype	Dana	1838	Brazil	Atlantic
YPM	4515	*Mussismilia*	*hispida*	non-type	Rathbun	1870	Brazil	Atlantic
YPM	4545	*Mussismilia*	*hispida*	non-type	Derby & Wilmot	1870	Brazil	Atlantic
YPM	4542	*Mussismilia*	*tenuisepta*	syntype	Derby & Wilmot	1870	Brazil	Atlantic
YPM	4543	*Mussismilia*	*tenuisepta*	syntype	Derby & Wilmot	1870	Brazil	Atlantic
SUI (U.Iowa)	102767	*Mycetophyllia*	*aliciae*	non-type	Budd	1974	Discovery Bay, Jamaica	Atlantic
SUI (U.Iowa)	102768	*Mycetophyllia*	*aliciae*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102768	*Mycetophyllia*	*aliciae*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102770	*Mycetophyllia*	*danaana*	non-type	Budd	1974	Discovery Bay, Jamaica	Atlantic
SUI (U.Iowa)	102771	*Mycetophyllia*	*danaana*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102772	*Mycetophyllia*	*danaana*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
SUI (U.Iowa)	102773	*Mycetophyllia*	*lamarckiana*	non-type	Budd	1974	Discovery Bay, Jamaica	Atlantic
SUI (U.Iowa)	102774	*Mycetophyllia*	*lamarckiana*	non-type	Budd	1974	Discovery Bay, Jamaica	Atlantic
SUI (U.Iowa)	102775	*Mycetophyllia*	*lamarckiana*	non-type	Budd	1974	Discovery Bay, Jamaica	Atlantic
SUI (U.Iowa)	102777	*Scolymia*	*cubensis*	non-type	Fukami	2003	Bocas del Toro, Panama	Atlantic
USNM	84939	*Scolymia*	*cubensis*	non-type	Goreau	~1969	Maria Buena Bay, Jamaica	Atlantic
USNM	84940	*Scolymia*	*cubensis*	non-type	Goreau	~1969	Maria Buena Bay, Jamaica	Atlantic
USNM	84919	*Scolymia*	*lacera*	non-type	Goreau	~1969	Maria Buena Bay, Jamaica	Atlantic
USNM	84920	*Scolymia*	*lacera*	non-type	Goreau	~1969	Maria Buena Bay, Jamaica	Atlantic
USNM	1090899	*Scolymia*	*lacera*	non-type	Antonius	1971	Colombia	Atlantic
SUI (U.Iowa)	102776	*Scolymia*	*wellsii*	non-type	Amaral	1989	Abrolhos, Brazil	Atlantic
USNM	84926	*Scolymia*	*wellsii*	non-type	Hubbard	–	Trinidad & Tobago	Atlantic
YPM	8117	*Scolymia*	*wellsii*	paratype	Laborel	1964	Brazil	Atlantic
YPM	8118	*Scolymia*	*wellsii*	paratype	Laborel	1964	Brazil	Atlantic
YPM	9102	*Scolymia*	*wellsii*	non-type	Laborel	1964	Brazil	Atlantic
YPM	9103	*Scolymia*	*wellsii*	non-type	Laborel	1964	Brazil	Atlantic
UF	2137	*Acanthastrea*	cf. *rotundoflora*	non-type	Fukami	2003	Palau	Pacific

Appendix I *Continued*

Museum	Catalogue no	Genus	Species	Type status	Collector	Collecting year	Location	Ocean
UF	2142	*Acanthastrea*	cf. *rotundoflora*	non-type	Fukami	2003	Palau	Pacific
USNM	83348	*Acanthastrea*	echinata	non-type	Phillippi	–	Malaysia (Wells 373757)	Pacific
UF	2065	*Acanthastrea*	echinata	non-type	Fukami	2003	Palau	Pacific
SUI (U.Iowa)	102778	*Acanthastrea*	echinata	non-type	Fukami	2003	Taiwan	Pacific
USNM	25	*Acanthastrea*	echinata	syntype	Dana	1846	Fiji	Pacific
USNM	91115	*Acanthastrea*	echinata	non-type	Hoeksema	1991	Indonesia	Pacific
USNM	45070	*Acanthastrea*	hemprichii	hypotype	Wells	1947	Bikini Atoll	Pacific
USNM	89888	*Acanthastrea*	ishigakiensis	non-type	Paulay	1984	Cook Islands	Pacific
UF	1382	*Cynarina*	lacrymalis	non-type	Fukami	2003	Palau	Pacific
USNM	93862	*Cynarina*	lacrymalis	non-type	Hoeksema	1992	Papua New Guinea	Pacific
USNM	93865	*Cynarina*	lacrymalis	non-type	Hoeksema	1992	Papua New Guinea	Pacific
USNM	53145	*Cynarina*	lacrymalis	non-type	Catala	1958	New Caledonia	Pacific
USNM	89580	*Lobophyllia*	corymbosa	non-type	–	1955	Enewetak	Pacific
USNM	89581	*Lobophyllia*	corymbosa	non-type	–	1955	Enewetak	Pacific
UF	4090	*Lobophyllia*	corymbosa	non-type	Paulay	1984	Cook Islands	Pacific
UF	566	*Lobophyllia*	corymbosa	non-type	Paulay	2002	Guan	Pacific
USNM	43	*Lobophyllia*	costata	holotype	Dana	1846	Tahiti	Pacific
USNM	47110	*Lobophyllia*	costata	non-type	Faulkner	1979	Palau	Pacific
USNM	89588	*Lobophyllia*	costata cf.	non-type	Veron	1976	Enewetak	Pacific
USNM	89583	*Lobophyllia*	costata cf.	non-type	Best & Veron	1976	Enewetak	Pacific
UF	2023	*Lobophyllia*	hataii	non-type	Paulay	2003	Palau	Pacific
UF	4088	*Lobophyllia*	hemprichii	non-type	Paulay	1991	Niue Islands	Pacific
UF	4089	*Lobophyllia*	hemprichii	non-type	Paulay	1991	Niue Islands	Pacific
USNM	41	*Lobophyllia*	multilobata	holotype	Dana	1846	Fiji	Pacific
USNM	45431	*Lobophyllia*	multilobata	hypotype	Faustino	1927	Philippines	Pacific
USNM	91024	*Lobophyllia*	pachysepta	non-type	Kropp	1984	Guam	Pacific
USNM	45515	*Lobophyllia*	pachysepta	non-type	Mayer	1918	Murray Islands, Australia	Pacific
USNM	92382	*Lobophyllia*	sp.	non-type	Potts	1993	Palau	Pacific
USNM	92380	*Lobophyllia*	sp.	non-type	Potts	1993	Palau	Pacific
USNM	100561	*Lopophyllia*	corymbosa	non-type	Humes	1963	Madagascar [Mozambique Channel (Nossi Be, Sakatia)]	Pacific
USNM	91271	*Lopophyllia*	hemprichii	non-type	Rosso	1955	Heron Island, Queensland	Pacific
USNM	83368	*Palauphyllia*	sp.	non-type	Weber	1975	Palau	Pacific
USNM	85709	*Scolymia*	australis	non-type	Zeidler & Growlett-Holmes	1986	South Australia	Pacific
UF	2100	*Scolymia*	sp.	non-type	Fukami	2003	Palau (HF-Palau-84, loc.737)	Pacific
UF	2130	*Scolymia*	vitiensis	non-type	Fukami	2003	Palau (HF-Palau-116, loc740)	Pacific
USNM	83332	*Scolymia*	vitiensis	non-type	Humes & Halverson	1971	New Caledonia	Pacific
USNM	91254	*Scolymia*	vitiensis	non-type	Hoeksema	1991	Gt Palm Island, Australia	Pacific
USNM	90798	*Symphyllia*	agaricia	non-type	Hoeksema	1991	Philippines	Pacific
USNM	1090898	*Symphyllia*	nobilis (= recta)	non-type	Mayor	1920	Samoa	Pacific
USNM	93797	*Symphyllia*	radians	non-type	Hoeksema	1992	Papua New Guinea (Madang)	Pacific
USNM	93796	*Symphyllia*	radians	non-type	Hoeksema	1992	Papua New Guinea	Pacific
USNM	90863	*Symphyllia*	radians	non-type	Kropp	1984	Caroline Islands	Pacific
UF	398	*Symphyllia*	radians	non-type	Paulay	1999	Oman	Pacific
UF	4091	*Symphyllia*	radians	non-type	Paulay	1992	Gilbert Islands	Pacific
SUI (U.Iowa)	102779	*Symphyllia*	recta	non-type	Budd	1988	Lizard Island, Australia	Pacific
USNM	93794	*Symphyllia*	recta	non-type	Hoeksema	1992	Papua New Guinea	Pacific
USNM	91129	*Symphyllia*	recta	non-type	Hoeksema	1991	Indonesia	Pacific
USNM	93792	*Symphyllia*	valenciennesi	non-type	Hoeksema	1992	Papua New Guinea	Pacific
USNM	89594	*Symphyllia*	valenciennesi	non-type	–	1955	Marshall Islands (Ralik Chain, Enewetak, MPML #319)	Pacific