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The first modern solitary Agariciidae (Anthozoa, Scleractinia) revealed by molecular and microstructural analysis

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Abstract. *Dactylotrochus cervicornis* (= *Tridacophyllia cervicornis* Moseley, 1881), which occurs in Indo-Pacific waters between 73 and 852 m, was originally described as an astraeid but was later transferred to the Caryophylliidae. Assumed to be solitary, this species has no stolons and only one elongated fossa, and is unique among azooxanthellate scleractinians in often displaying extremely long thecal extensions that are septate and digitiform. Based on both molecular phylogenetic analyses (partial mitochondrial CO1 and 16S rDNA, and partial nuclear 28S rDNA) and morphological characteristics, we propose the transfer of *D. cervicornis* from the Caryophylliidae to the Agariciidae, making it the first extant representative of the latter family that is solitary and from deep water (azooxanthellate). The basal position of *D. cervicornis* within the agariciids implied by our analyses strengthens the case for inclusion of fossil species that were solitary, such as *Trochoseris*, in this family and suggests that the ancestor of this scleractinian family, extant members of which are predominantly colonial and zooxanthellate, may have been solitary and azooxanthellate.

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Introduction

The coral family Agariciidae is widely distributed, agariciid species being common on all major shallow-water coral reefs and some reported in waters deeper than 100 m (Fricke *et al*. 1987). The family is defined by common morphology from the level of the whole colony to that of septal microstructure (Wells 1954, 1956; Nemenzo 1955; Veron 2000), and comprises a total of 47 extant species falling into seven genera (Veron 2000; Glynn *et al*. 2001; Licuanan and Aliño 2009). *Agaricia* and *Helioseris* are restricted to the western Atlantic, *Pavona*, *Coeloseris*, *Gardineroseris* and *Pachyseris* occur in the Indo-Pacific, and the genus *Leptoseris* contains both Indo-Pacific and Caribbean species. Without exception, extant agariciids are zooxanthellate and form massive, laminar or frondose colonies and, based on morphological similarity to extant corals, the same appears to hold for most, but not all, of the 27 fossil genera assigned to this family (Wells 1956; Chevalier 1961, 1968; Budd and McNeill 1998; Baron-Szabo 2002, 2008; Pandey and Fürsich 2005; Pandey *et al*. 2007). By contrast, two fossil genera (*Trochoseris* and *Vaughanoseris*, from the Middle and Upper Cretaceous respectively) are atypical in being solitary and most likely also azooxanthellate.

The (admittedly limited) available molecular data imply that, with the possible exception of *Pachyseris* (Fukami *et al*. 2008; Kitahara *et al*. 2010*a*), Agariciidae is a valid 'Complex' coral family (Romano and Palumbi 1996; Romano and Cairns 2000; Le Goff-Vitry *et al*. 2004; Kerr 2005; Fukami *et al*. 2008; Barbeitos *et al*. 2010; Kitahara *et al*. 2010*a*, 2010*b*; Stolarski *et al*. 2011), which in molecular phylogenetic analyses has as its sister group a clade comprising shallow-water acroporids and the poritid *Alveopora* sp. In contrast with most other scleractinian families whose members are predominantly azooxanthellate, the Caryophylliidae appears not to be a valid taxon, members of this family being scattered across both 'Complex' and 'Robust' coral clades in molecular analyses (Kitahara *et al*. 2010*a*). Apart from *Caryophyllia* and related genera (see Kitahara

et al. 2010*b*), most caryophylliids will ultimately comprise new families or be included in existing ones. One implication of the broad survey carried out by Kitahara *et al*. (2010*a*) is a close relationship between *Dactylotrochus cervicornis*, a solitary, deep-water coral until now classified into the Caryophylliidae, and members of the family Agariciidae. This unexpected grouping is of particular interest as it suggests a link between extant agariciids, which are colonial and zooxanthellate, and fossil taxa, which are solitary and azooxanthellate. However, at this time, the support for such a grouping was based on a single molecular marker, part of the mitochondrial CO1 gene.

Dactylotrochus cervicornis occurs in Indo-Pacific waters between 73 and 852 m, and was originally described as an astraeid (*Tridacophyllia* Moseley, 1881) but later transferred to the Caryophylliidae (see Wells 1954). This monotypic genus is characterised by a solitary, trochoid, and attached corallum, with calicular edge flaring outward as four to eight thecal extensions, some of which are bifurcate. Its wall is septothecate, with costae that are detectable only near the calicular edge, fainting towards the pedicel. The septal faces bear well developed menianes (ledge-like features), but pali and columella are absent. The transfer of *Dactylotrochus* to the caryophylliids and its position with this family (Wells 1954: 470) were based on 'the constancy of development of thecal extensions and the lack of prominent septal dentitions as in pectiniids', and especially on the similarity of young stages to the 'typical' caryophylliid genus *Desmophyllum*.

In the present study, the relationship between the caryophylliid *Dactylotrochus* and Agariciidae is confirmed using a range of additional molecular markers and, in the light of strong molecular support for this relationship, supporting morphological criteria were sought and also identified. This approach illustrates the reciprocally informative and complementary nature of molecular and morphological approaches to coral systematics. Furthermore, the transfer of *D. cervicornis* to the Agariciidae makes it the first extant genus and species in this family that is azooxanthellate (deep water). The basal position of *D. cervicornis* among the extant Agariciidae included in our analyses, together with the fact that the fossil agariciids from the Middle Cretaceous were also solitary, suggests that the ancestor of this coral family, which is today predominantly colonial and zooxanthellate, was solitary and azooxanthellate.

Materials and methods

DNA preparation, amplification and sequence analyses

French expeditions around New Caledonian waters collected 144 specimens of the solitary scleractinian *D. cervicornis* between depths of 215 and 852 m using warren-dredge and beam-trawl. A small thecal extension fragment was removed from the specimen collected at station Norfolk 2 DW 2135 (23°02′S, 168°21′E – 295–330 m sampling depth), which was preserved in absolute ethanol, and from it genomic DNA was extracted using DNeasy Tissue and Blood Kit (QIAGEN, Valencia, CA, USA) following the manufacturer's instructions. PCR amplification of mitochondrial (16S rDNA and CO1) and nuclear (28S rDNA) markers were carried out following Kitahara *et al*. (2010*a*, 2010*b*) and Stolarski *et al*. (2011). Amplicons were purified using Mo-Bio Ultra Clean (PCR Clean Up) spin columns (Mo Bio Laboratories, Inc., Carlsbad, CA, USA) and submitted to direct sequencing at Macrogen (Seoul, South Korea).

For each marker analysed herein, sequences from selected agariciids were aligned with at least one representative of each scleractinian family; in many cases, reference sequences were available in GenBank, but in others sequences were obtained in the present study. The alignments consisted of totals of 22 families for 16S rDNA, 21 for CO1 and 15 for 28S rDNA (Table 1). Sequences were initially aligned using ClustalW ver. 2 (Larkin *et al*. 2007), manually edited using JalView version 8.0 (Clamp *et al*. 2004), and are provided as fasta format in Supplementary Material 1. Each alignment was tested to find the most appropriate models of nucleotide substitution by the hierarchical likelihood ratio test implemented in MrModeltest (Nylander 2004). Phylogenetic analyses were performed using PhyML (Guindon and Gascuel 2003) for maximum likelihood (ML) and MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) for Bayesian Inference (BI), under the GTR model. The ML analyses were performed with a non-parametric Shimodaira–Hasegawa-like procedure (see Anisimova and Gascuel 2006) and with 100 bootstrap replicates. For the BI, two runs each of 10 million generations were calculated for each marker with topologies saved at each 1000 generations. Average standard deviation of split frequencies between runs of each marker converged to or less than 0.01. The first 2500 saved topologies were discarded as burnin, and the remaining were used to calculate the posterior probability.

Skeleton preparation and analysis

Specimens illustrated in this study were subjected to various destructive analyses and the resulting thin sections and skeletal fragments attached to microscope stubs are housed at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (ZPAL), or at the School of Pharmacy and Molecular Sciences, James Cook University, Townsville (JCU). Skeletons of agariciids and *Dactylotrochus* were selected and tissue was extracted from ethanol-preserved specimens by removing the soft tissue by overnight immersion in 3% sodium hypochlorite (NaOCl) solution. Small pieces of dried skeleton were removed from the respective colony. Skeletons were rinsed in ultra-pure water and washed in an ultrasonic cleaner for 2 min. All specimens were studied with transmitted light microscope (TLM) and scanning electron microscope (SEM). Thin (~30 µm thick) sections of various skeletal elements were observed and photographed with a Nikon Eclipse 80i TLM. Skeletal microarchitectural and microstructural features were visualised with Philips XL 20 or Jeol JSM5410 LV SEM microscopes. Specimens were observed intact (septal surfaces), as broken but not etched skeletal samples, or as broken/polished and etched samples. Transverse or longitudinal polished or broken sections of septa were exposed for ~20 s etching in 0.1% formic acid solution, following Stolarski (2003). The etched samples were rinsed with distilled water and air-dried. Once dried, samples were mounted on stubs and sputter coated with gold or conductive platinum film.

Table 1. Family and GenBank accession numbers of each scleractinian representative included in the phylogenetic reconstruction

An asterisk indicates previous family of *D. cervicornis*. A hash symbol (#) indicates that the species position in its family is unresolved (see Fukami *et al.* 2008)

Taxonomy			Markers		
Family	Genus	Species	CO1	16S rDNA	28S rDNA
Acroporidae	*Acropora*	*hemprichii*	–	AF550359	–
		palmata	AB441246	–	–
	Isopora	*palifera*	AB441248	–	–
Agariciidae	*Agaricia*	*agaricites*	AY451366	–	–
		fragilis	AY451368	–	–
		humilis	AB441219	–	–
		lamarcki	AY451369	–	–
		tenuifolia	AY451372	–	–
		undata	–	–	EU262789
	Dactylotrochus	*cervicornis*	HM018624	HQ439697	HQ439630
	Gardineroseris	*planulata*	AB441218	–	–
	Helioseris	*cucullata*	AB441220	–	–
	Leptoseris	*incrustans*	–	L76012	–
		sp.	AY451373	–	EU262806
	Pachyseris	*speciosa* #	AB441222	–	–
	Pavona	*cactus*	AB441216	–	–
		varians	–	L76016	EU262847
Anthemiphylliidae	*Anthemiphyllia*	*costata*	HM018604	–	HQ439609
		spinifera	–	HQ439685	–
Astrocoeniidae	*Stephanocoenia*	*michelinii*	AB441228	AF265581	–
Caryophylliidae *	*Caryophyllia*	*lamellifera*	HM018616	–	–
		inornata	–	AF265599	–
		smithii	–	–	AF549216
	Thalamophyllia	*gasti*	–	AF265590	–
Dendrophylliidae	*Astroides*	*calycularis*	–	–	AF549248
	Dendrophyllia	*alternata*	–	AF550366	–
		sp.	AB441239	–	–
	Tubastraea	*micranthus*	–	–	AF549219
	Turbinaria	*peltata*	AB441240	–	–
Euphylliidae	*Euphyllia*	*ancora*	AB441204	AF265598	–
Faviidae	*Cyphastrea*	*ocellina*	–	L76132	–
	Echinopora	*lamellosa* #	–	L76003	–
	Favia	*fragum* #	AY451351	FFU40295	–
		stelligera #	–	–	AF549223
Flabellidae	*Flabellum*	*angulare*	–	AF550363	–
		tuthilli	HM018643	–	HQ439664
Fungiacyathidae	*Fungiacyathus*	*marenzelleri*	–	EF589061	–
		turbinolioides	HM018648	–	HQ439679
Fungiidae	*Cycloseris*	*fragilis*	–	L75998	–
	Lobactis	*scutaria*	AB441224	–	–
Guyniidae	*Guynia*	*annulata*	–	AF265580	–
Meandrinidae	*Dichocoenia*	*stokesi*	AB117298	AF265607	–
	Meandrina	*brasiliensis*	AB11797	–	–
		pectinata	–	–	AF549234
Merulinidae	*Merulina*	*scabricula* #	AB117284	L76014	–
Mussidae	*Cynarina*	*lacrymalis* #	AB117246	–	–
		sp. #	–	AF265613	–
	Mussa	*angulosa* #	–	–	EU262869
	Mussismilia	*braziliensis* #	AB117231	–	–
Oculinidae	*Galaxea*	*fascicularis* #	AB441201	L76006	–
	Madrepora	*oculata* #	–	HQ439760	HQ439680
Pectiniidae	*Echinophyllia*	*aspera* #	–	–	AF549241
	Pectinia	*alcicornis*	AB117385	L76017	–
Pocilloporidae	*Pocillopora*	*damicornis*	–	L76019	–
		verrucosa	AB441230	–	AF549252

(*continued next page*)

Table 1. (*continued*)

Family	Taxonomy Genus	Species	Markers CO1	16S rDNA	28S rDNA
Poritidae	*Porites*	*compressa*	–	L76020	–
		porites	DQ643837	–	EU262878
Rhizangiidae	*Astrangia*	sp.	NC008161	NC008161	–
Siderastreidae	*Psammocora*	*stellata* #	–	L76021	–
	Siderastrea	*radians*	–	–	EU262861
		stellata	AB441213	–	–
Turbinoliidae	*Tropidocyathus*	*labidus*	–	AF265585	–
		lessoni	HM018669	–	HQ439683

Results

Molecular analyses

For each gene analysed, the sequence obtained from *D. cervicornis* was aligned with published sequences from species representing most scleractinian families (Table 1). In general, the sequences for each marker were from different specimens or species; hence, rather than concatenating sequences, each gene was analysed separately enabling the observation of the effects of different genes on the phylogenetic reconstruction of the family. Furthermore, it was also avoided the assembly of chimeras. The final sequence alignments consisted of 514 positions in the case of 16S rDNA, 595 positions for CO1, and 693 positions for the 28S rDNA, of which 218, 214 and 238 were variable, and 136, 121 and 182 were parsimony informative respectively. The average nucleotide composition values were 31% (T), 13.6% (C), 31.9% (A) and 23.5% (G) for 16S, 37.6% (T), 17.7% (C), 21.7% (A) and 22.9% (G) for CO1, and 22% (T), 26.6% (C), 17.5% (A) and 33.8% (G) for 28S. The base composition of these three genes was remarkably constant among agariciids and *D. cervicornis*, diverging less than 1% for each base. Estimates of evolutionary distances between sequences for each marker are provided as Supplementary Material 2. Alignment of the CO1 sequences did not require any substantial insertion/deletions; however, as has been found in previous studies (Romano and Palumbi 1997; Romano and Cairns 2000; Le Goff-Vitry *et al*. 2004; Kitahara *et al*. 2010*b*; Stolarski *et al*. 2011), alignment of 16S rDNA required an indel of nearly 120 bp within representatives of the 'Robust clade'. Interestingly, while the size of the 28S rDNA fragment generated was constant across all scleractinians analysed, two short base insertions (MGCT in the first domain and AA in the second) were present in each of the sequences from agariciids and *D. cervicornis*, but not in any other scleractinian species.

For each marker, near identical topologies resulted from the application of ML (using the Shimodaira–Hasegawa test and bootstrap) and BI methods of phylogenetic analysis, and the trees did not differ significantly between markers (Fig. 1). Irrespective of the phylogenetic method applied, the 'Complex' and the 'Robust' coral clades were always recovered. As in previous study (Kitahara *et al*. 2010*a*), the 'Complex' clade was formed by representatives of the following families: Acroporidae; Agariciidae (including *D. cervicornis*); Astrocoeniidae; Caryophylliidae* (*Thalamophyllia gasti*); Dendrophylliidae; Euphyllidae (*Euphyllia ancora*); Flabellidae; Fungiacyathidae; Guyniidae; Oculinidae* (*Galaxea fascicularis*); Poritidae; Siderastreidae*; and Turbinoliidae. The 'Robust' clade comprised all other scleractinian families examined together with additional representatives of those families above marked with an asterisk (*). In addition, there was strong statistical support in ML and BI analyses of both 16S rDNA and 28S rDNA sequences (and in BI analyses of CO1 sequences) for *D. cervicornis* clustering with all of the agariciids. However, the ML analysis of CO1 data differed slightly in the placement of two *Leptoseris* representatives. Given that all of the other analyses performed grouped *Leptoseris* within the clade composed of other agariciids and *D. cervicornis*, we believe the CO1 ML topology to be incorrect with respect to this fine detail. A trait found by Kitahara *et al*. (2010*a*), and also recovered in our CO1 based phylogeny is the interesting position of agariciids in relation to 'Robust' corals. Apparently, the partial sequence of CO1 does not have enough phylogenetic signal to separate 'Complex' and 'Robust' corals. Nonetheless, the 'Robust' corals diverge from agariciids.

Morphological analyses

Macromorphology

D. cervicornis is an intriguing deep-water scleractinian that has numerous unique morphological characters. All specimens examined to date are firmly attached to the substrate, and most (>150) have only one fossa (Fig. 2*A*, 3*A*). However, 'aberrant' specimens collected from New Caledonian waters (e.g. Norfolk 2 station DW 2023) suggest a propensity of this genus for coloniality, as two or three interconnected fossae (and presumably mouths) are readily distinguished in each of them (Supplementary Material 3). The corallum is attached by a robust pedicel (up to 15 mm in diameter) that expands into a thin, polycyclic, encrusting base (Fig. 2*A*, 3*I*). Sometimes larger specimens display a base almost twice as large as the pedicel, suggesting that this species may have the ability to colonise regions that have strong currents. The lower corallum has thin transversal ridges encircling the base. Costae are flat, usually detectable only near calicular edge, becoming inconspicuous towards pedicel. Each costa bears 2 or 3 small rounded granules. Shallow and narrow intercostal striae separate each adjacent costa. Above the pedicel, the theca and corresponding internal septa divide into several, elongate, tapered and sometimes bifurcating thecal extensions (Fig. 2*A*, *B*). The

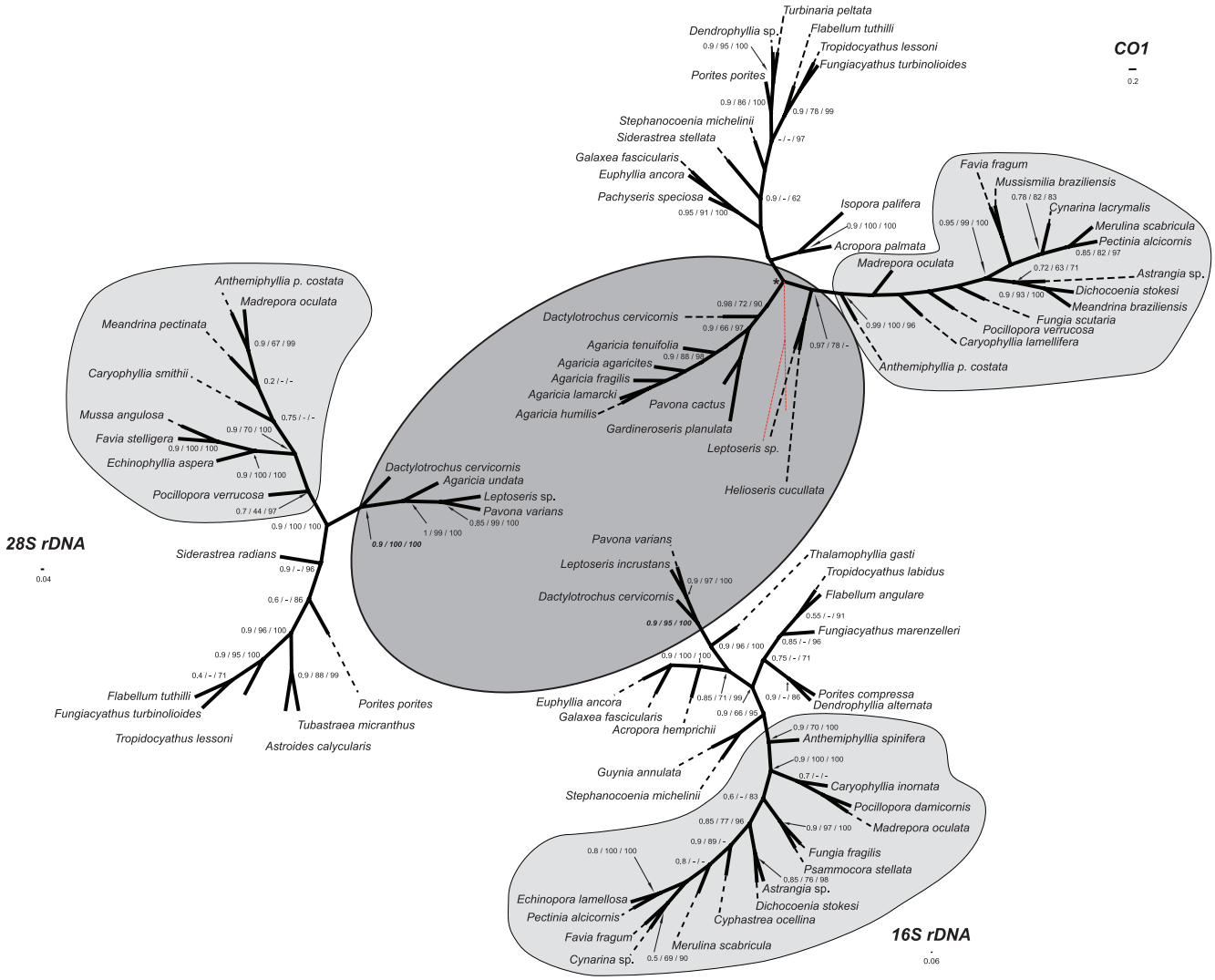

Fig. 1. Unrooted most likely trees derived from maximum likelihood analysis of partial 16S rDNA, partial CO1, and partial 28S rDNA nucleotide sequences. Values near each node indicate the maximum likelihood (ML) Shimodaira–Hasegawa-like statistical support followed by bootstrap (100 replicate) analyses, and Bayesian Inference (BI) posterior probability (7500 topologies). An asterisk (*) in the CO1 reconstruction indicates discrepancy between the ML and BI (different branching from BI is indicated in red). Dark shaded area indicates Agariciidae clade and light shaded areas indicate the 'Robust' coral clades. Dashed lines bridge the end of each branch and its respective species name.

largest thecal extensions originate on the plane of the lesser calicular diameter and often attain up to 20 mm in basal width. Slightly beyond their base, the main thecal extensions bifurcate into two or more smaller extensions. Several other extensions (usually nonbifurcating) are oriented outward from calicular edge (see Cairns 1999). The largest specimen examined (DW 2023) was 27.7 × 19.1 mm in calicular diameter, 37.6 mm in height, and 15.1 × 14.2 mm in pedicel diameter. Septal symmetry was difficult to determine. Larger coralla have up to 470 closely spaced septa, usually progressively narrowing in higher septal cycles and originating closer to calicular edge. Septal faces bear well developed menianes oriented parallel to slightly oblique in relation to upper septal edge (Fig. 2*C*, *D*, *E*) (for meniane definition see Gill 1967 and Morycowa and Roniewicz 1995). Meniane edges are always beaded (Fig. 3*B*, *D*). Fossa deep and narrow, columella always absent. All specimens examined have a white corallum.

Micromorphology and microstructure

The following micromorphological and microstructural characters are herein described and provide clues about the phylogenetic relationships of *Dactylotrochus*: (1) features of the corallum base (septa-wall relationship); (2) skeleton microtexture and corresponding microstructure of thickening deposits (TD); and (3) arrangement of septal rapid accretion deposits (RAD).

Polished bases of coralla show polycyclic development. Initial theca (prototheca) is encircled with concentric thecal rings (Fig. 3*I*, *J*). Prototheca RAD form a zone (~10–20 µm thick in transverse sections) of closely spaced centers (Fig. 3*J*), which

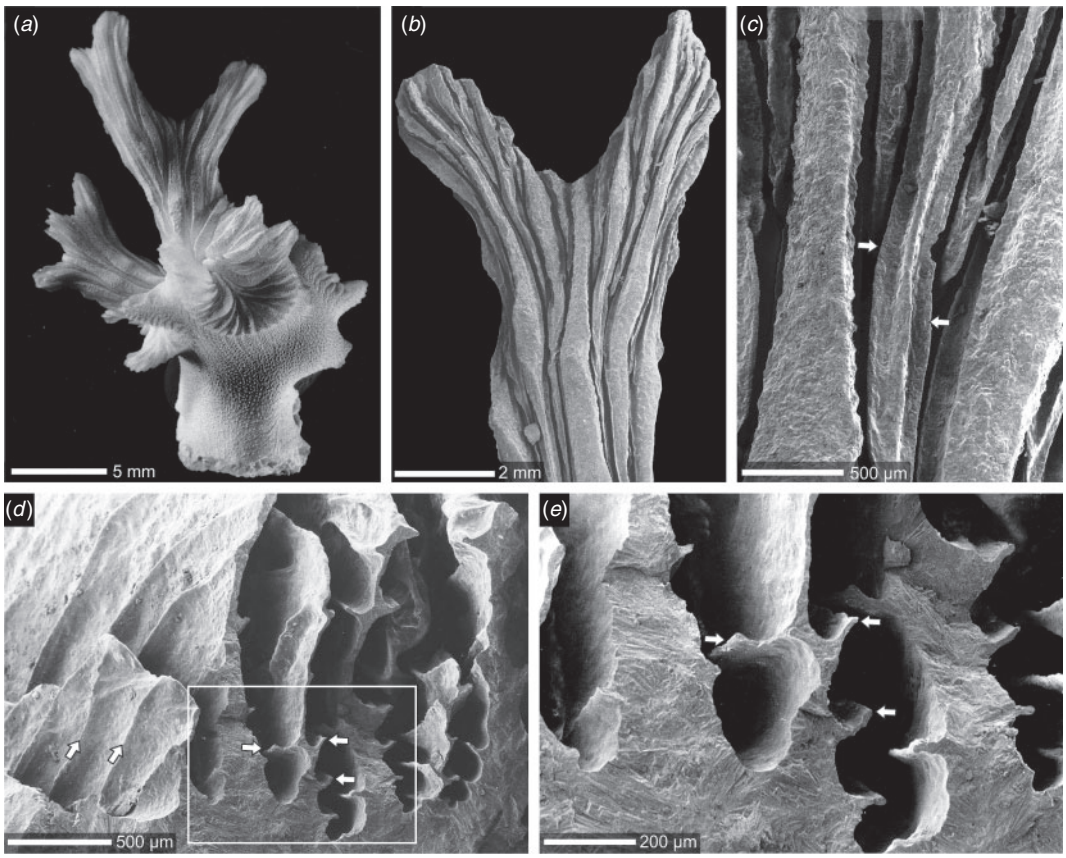

Fig. 2. Macro- and micromorphology of *Dactylotrochus cervicornis* (Moseley, 1881); ZPAL H.25/7-R-SCL251a, Loyalty Islands, 167°55,98′E/21°08,50′S, 380 m (MUSORSTOM 6, station DW 480). (*A*) Lateral view of corallum. (*B*) Bifurcating calicular extension. (*C*) Distal view of septa showing well developed menianes (arrows). (*D*) Broken calicular extension with continuous menianes visible on septal surfaces and their transverse sections (*E*, enlarged). Optical macrophotograph (*A*) and SEM images (*B–E*).

during ontogenetic development become continuous between corallum wall and septa, a pattern described as typical of marginotheca (Fig. 3*J*; see also Stolarski 1995). The outer surface of juvenile coralla is covered with very small scale-like deposits (Fig. 3*F*). In contrast, the inner surface (including septa and inner sides of the wall) is usually smooth. In corallum transverse sections, scale-like organisation of thickening deposits of the outer part of coralla is distinguishable from fibrous organisation of thickening deposits of septa and inner part of the wall (Fig. 3*E*, *G*, *H*). In septal longitudinal sections, centers of RAD form continuous zone (Fig. 4*F*) but some additional centers occur at the meniane bases (Fig. 4*C*, *E*, *F*). In all examined sections, meniane shown only fibrous microstructure (Fig. 4*C*, *E*) that explains their transparency as viewed in stereoscopic microscope (all skeletal parts that contain RAD are semi-transparent).

Discussion

Recognising evolutionary lineages (i.e. monophyletic groups) in a classification changes the emphasis from associating a taxon name with a set of characteristics to associating a name with a lineage (de Queiroz and Gauthier 1992), which should mirror the species genealogy (Hennig 1966; Mayr 1969). Here, the view is adopted that classification should be based on phylogeny, with species grouped on the basis of their evolutionary relationships. This approach requires that only monophyletic groups be recognised as taxonomic entities.

The systematic classification of scleractinian corals based on morphological characters represents a challenge in several ways. The paucity of macro-morphological characters in addition to homology and homoplasy restricts the usefulness of morphological phylogenetics (Cairns 2001; Budd *et al.* 2010). Such challenges pose major limitations to the development of a consistent phylogenetic classification system for the order. Despite this, the morphological characteristics on which classification schemes have traditionally been based (Wells 1956; Chevalier and Beauvais 1987; Veron 1995) are still broadly used.

Recently, however, molecular phylogenetic analyses have been applied to scleractinian evolutionary relationships, resulting in substantially different evolutionary hypotheses when compared with schemes based on morphology. Molecular phylogenetic principles have the potential to guide scleractinian taxonomy to classification schemes that better reflect the evolutionary history of the order. The investigation of clades identified in molecular analyses (e.g. Budd and Smith

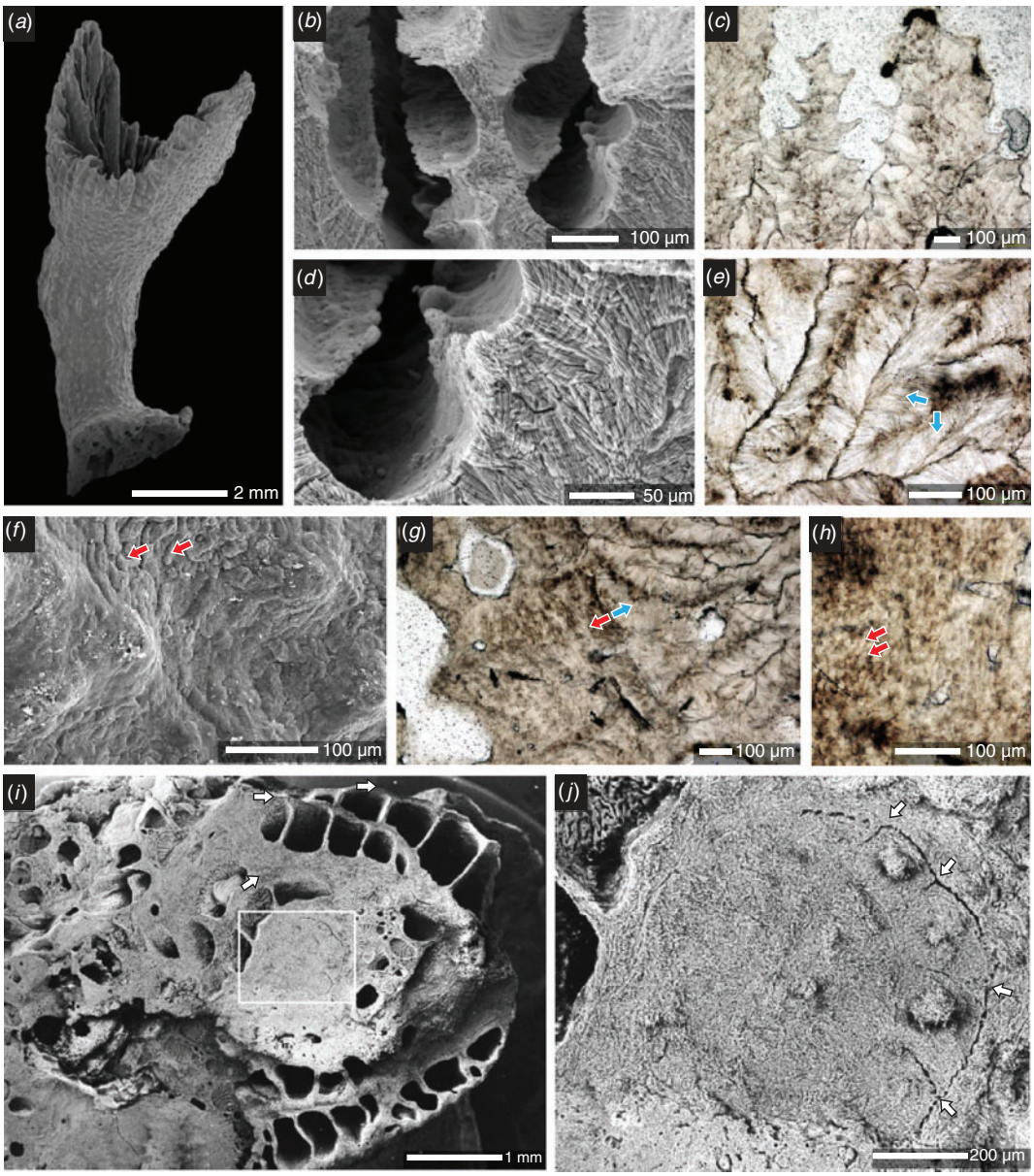

Fig. 3. Early ontogeny and microstructural features of *Dactylotrochus cervicornis* (Moseley, 1881); ZPAL H.25/7-R-SCL251a (*B*–*E*, *G*, *H*), and ZPAL H.25/7-R-SCL251b (*A*, *F*), Loyalty Islands, 167°55,98′E/ 21°08,50′S, 380 m (MUSORSTOM 6, DW 480). (*A*) Juvenile specimen with scale-like (*F*, red arrows) organisation of tectura. Scale-like deposits of tectura are visible in sections of the corallum base (*H*, red arrows) and they contrast with fibrous organisation of thickening deposits of septa (*C*, *D* and *E*, blue arrows). (*G*) Distinct border between scale-like (red arrow) and fibrous deposits (blue arrow) indicates change from intracalicular to extracalicular (tectura) deposits. (*B*) Menianes are formed by fibres of septal thickening deposits that on the growing edge of meniane may form bead-like structures (*D*, enlarged). (*I* and *J*) Polycyclic corallum base (*I*, successive thecal rings marked with arrows) with initial (protothecal) wall formed as marginotheca (*J*, enlarged). Transmitted light images of thin sections (*C*, *E*, *G*, *H*), and SEM images of corallum surface (*A*, *F*) and etched sections (*B*, *D*, *I*, *J*).

2005; Benzoni *et al*. 2007, 2011; Stefani *et al*. 2008; Gittenberger *et al*. 2010; Budd and Stolarski 2011) has led to the identification of key morphological characters that were previously overlooked. These studies point to the potential of integration of both approaches (i.e. molecular and morphological), a procedure that has been called ‘reciprocal illumination’ (Hennig 1957), and the hope is that it will lead to robust hypotheses on the morphological/genetic evolution at all taxonomic ranks and shed light on the intraspecific phenotypic plasticity displayed by many representatives of the order.

Inconsistencies between classifications based on morphology and molecular data are most pronounced in the cases of scleractinian families that are composed mainly of zooxanthellate representatives (Fukami *et al*. 2008). However,

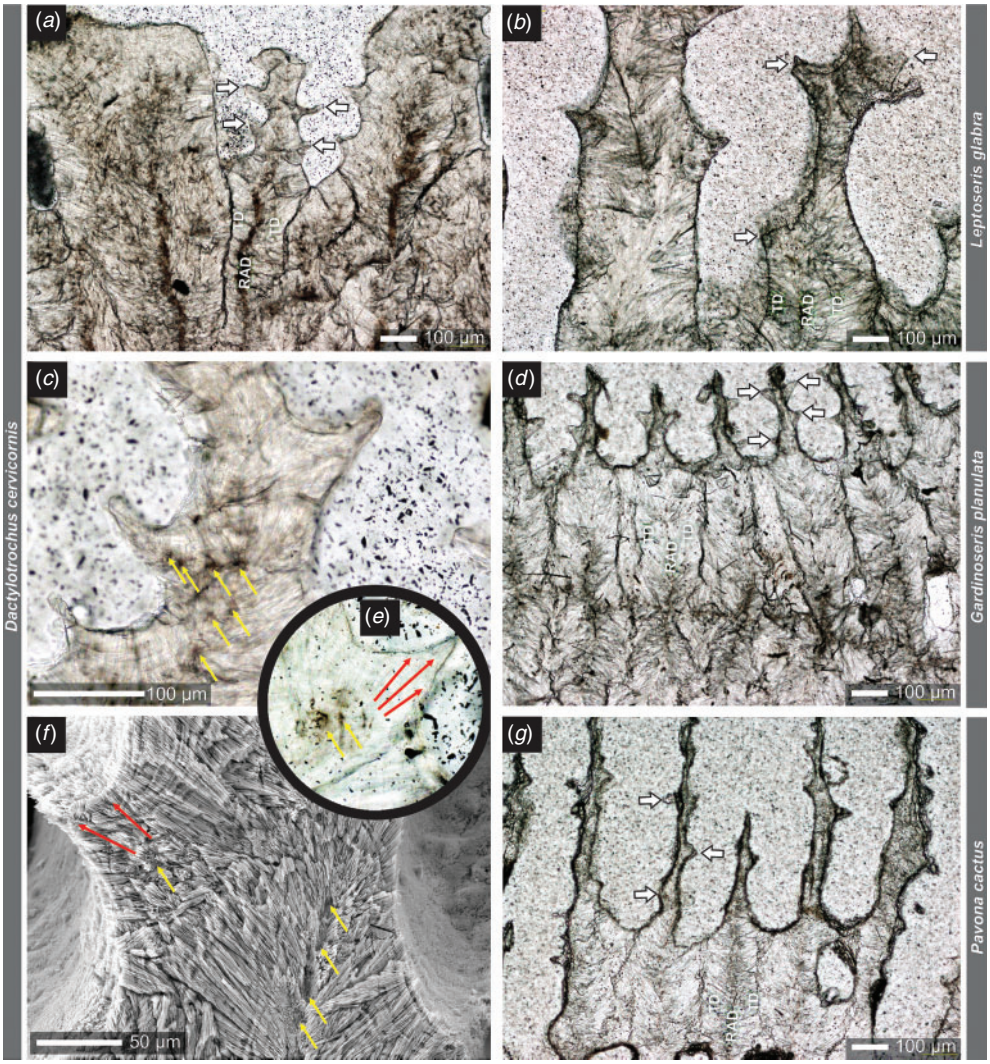

Fig. 4. Microstructural organisation of the skeleton of *Dactylotrochus cervicornis* (*A*, *C*, *E*, *F*) compared with selected representatives of Recent agariciids: *Leptoseris* (*L. glabra*) (*B*), *Pavona* (*P. cactus*) (*D*), and *Gardinoseris* (*G. planulata*) (*G*). In *D. cervicornis* and in all other agariciids, zone of Rapid Accretion Deposits (RAD) is situated in the middle part of septum (*A*, *B*, *D*, *G*) and consists of superimposed (sometimes slightly irregularly, *C*) centers of rapid accretion (yellow arrows in *C*, *E*, *F*). Septal faces in all agariciids and *D. cervicornis* bear regularly distributed, parallel lines of granules (*Pavona*, *Gardineroseris*) or/and meniane (*Dactylotrochus*, *Leptoseris*); white arrows in *A*, *B*, *D*, *G* (see also Fig. 5). In *Dactylotrochus* menianes are exceptionally well developed (among Recent corals) and translucent in optical microscope. This optical feature is explained by microstructural organisation: menianes are formed by fibres of thickening deposits (red arrows in *E*, *F*) and RAD (not transparent) usually occurs only at the base of bundles of fibres. (*A*, *C*, *E*, *F*) ZPAL H.25/8-R-SCL250, off New Caledonia, 23°40.8′S/168°01.1′E, 230–270 m (SMIB 5. St. DW 102); (*B*) ZPAL H.25/9-R-SCL485, Al-Mukalla, Gulf of Aden (03/2008, 096); (*D*) ZPAL H.25/10-R-SCL493, Balhaf, Gulf of Aden, 13°58′0N/48°10′60E, few meters (03/2008) (*G*) ZPAL H.25/11-R-SCL486, Balhaf, Gulf of Aden, 13°58′0N/48°10′60E, few meters (123, 03/2008). Transmitted light images of thin sections (*A–E*, *G*) and SEM images of etched section (*F*).

the Caryophylliidae, which is the second largest scleractinian family and is composed predominantly of azooxanthellate (deep-water) species, appears to be a completely artificial grouping (Kitahara *et al*. 2010*a*, 2010*b*; Stolarski *et al*. 2011). Representatives of this family are scattered in at least eight different clades across both 'Complex' and 'Robust' coral groups. In applying morphological and molecular phylogenetic approaches to confirm the taxonomic position of the genus *Dactylotrochus* in the family Agariciidae, the present study represents a step towards resolving the taxonomic chaos surrounding the Caryophylliidae.

Of the seven extant genera assigned to Agariciidae on the basis of morphology, all (*Agaricia*, *Gardineroseris*, *Helioseris*, *Leptoseris*, *Pachyseris* and *Pavona*) but *Coeloseris* were included in at least one of the three phylogenetic reconstructions presented herein. The CO1 analyses imply that

Pachyseris speciosa (the only representative of this genus examined) may be more closely related to some 'euphylliids' (*Galaxea fascicularis* and *Euphyllia ancora*) than to agariciids, as suggested by previous studies (Fukami *et al*. 2008; Kitahara *et al*. 2010*b*). In accordance to Dai and Horng (2009), *Pachyseris* should remain in the Agariciidae until additional morphological data are available to elucidate its grouping. Interestingly, the phylogeny based on 16S rDNA suggests that the azooxanthellate caryophylliid genus *Thalamophyllia* is also closely related to agariciids, a trait previously found by Romano and Cairns (2000), and more recently by Barbeitos *et al*. (2010), the latter using the first two domains of the 28S rDNA gene concatenated with partial 12S rDNA. Nonetheless, at this stage morphological support for this implied grouping is lacking.

With the qualifications above, *Dactylotrochus* and all of the agariciid genera examined formed a well supported clade irrespective of the genetic marker and method of analysis used, supporting the transfer of this monotypic genus to Agariciidae (Fig. 1). In addition, *Dactylotrochus* shares several unique sequence indels with the agariciids and has similar base composition at the loci examined. The basal position of *Dactylotrochus* in relation to other agariciids implied in the present study (Fig. 1) is of particular interest as it suggests a link between the extant colonial and fossil solitary agariciids, and suggests that predominantly, this coral family, most of whose extant representatives are colonial and zooxanthellate, had a solitary and azooxanthellate ancestor. Although the structural information has not been subjected to formal cladistic analysis, morphological characters provide additional support for grouping *D. cervicornis* with the Agariciidae. Although classified as a caryophylliid based on the constancy of thecal extension development, the lack of prominent septal dentitions, and similarity of young stages to those of the 'typical' caryophylliid *Desmophyllum* (Wells 1954), *Dactylotrochus* is unique among azooxanthellate corals in having long thecal extensions (Cairns 1999), a feature treated by many authors as 'branches' (Moseley 1881; Gardiner 1899). The most striking feature linking *D. cervicornis* to living agariciids are the long menianes, which among modern scleractinians are only otherwise developed in some species of *Leptoseris*. In *Leptoseris* and *Dactylotrochus*, the initial development of meniane involves fusion of a horizontal series of granulations (Fig. 3*D*). Such horizontal series of granulations are typically developed in various agariciids (Cuif *et al*. 2003), and in longitudinal sections of septa they are hardly distinguishable from meniane (Figs 4, 5, 6). Furthermore, the scale-like organisation of tectura (thickening desposits outside the rapid accretion deposits of the wall) and beaded septal margins are characters that *D. cervicornis* shares with many agariciid taxa (Fig. 6). One point of interest is that *Coeloseris* – the only extant agariciid genus for which molecular data are not yet available – lacks the three morphological characters mentioned

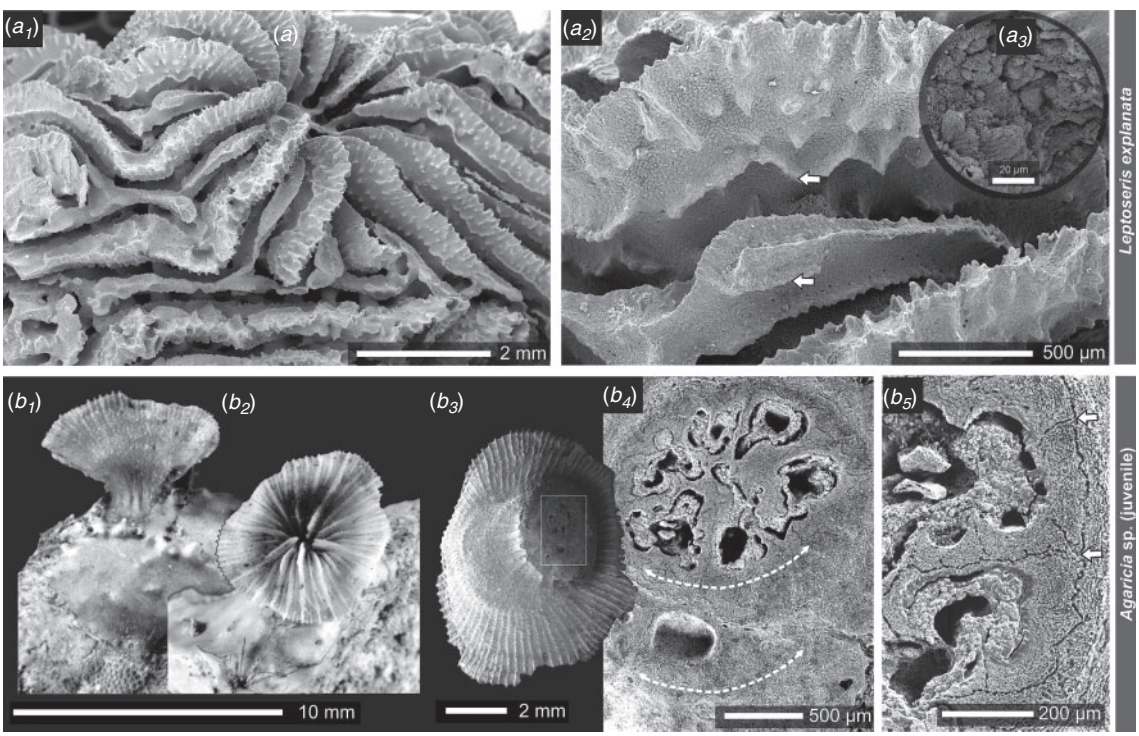

Fig. 5. Agariciid micromorphology. *Leptoseris glabra* (*A*) and *Agaricia* sp. early ontogeny (*B*). Meniane on growing edges may form bead-like structures (a_2, white arrows) whereas the surface of the wall and septa shows scale-like texture (a_2, a_3). Juvenile *Agaricia* sp. (lateral (b_1) and distal (b_2) views) shows polycyclic corallum base (b_3, b_4). Successive thecal rings marked with dashed lines (b_4). Initial (protothecal) wall formed as marginotheca (b_5, arrows indicate junction of wall and septal zones of rapid accretion deposits). (*A*) ZPAL H.25/; (*B*) ZPAL H.25/12-R-SCL704 (USNM 300990), Belize, Carrie Bow Cay, 1.5 m depth. SEM images of corallum surface (a_1–a_3) and etched sections (b_3–b_5), and optical macrophotographs (b_1, b_2).

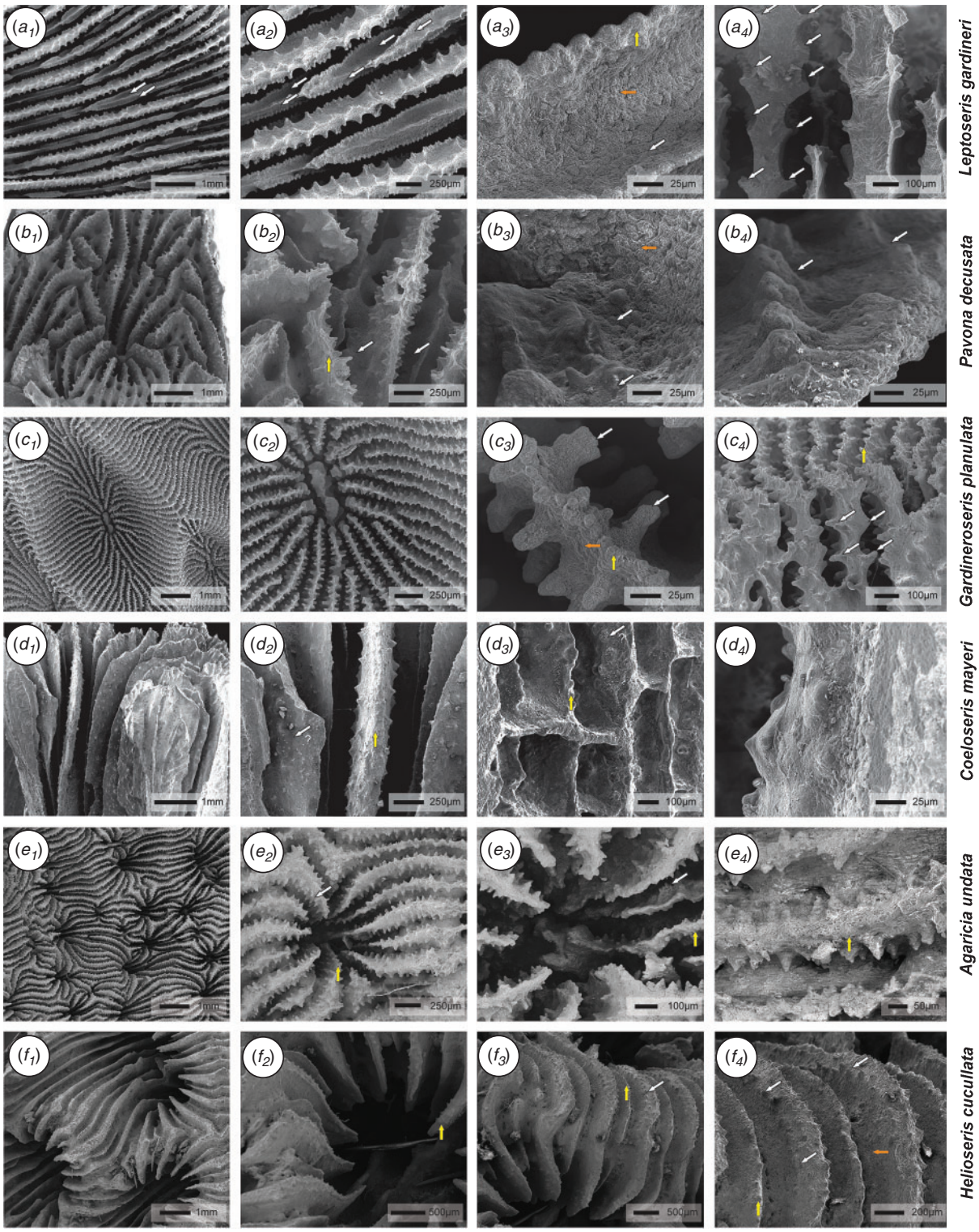

Fig. 6. Macro- and micromorphology of selected representatives of Recent agariciids. (*A*) *Leptoseris gardineri*, (*B*) *Pavona decusata*, (*C*) *Gardineroseris planulata*, (*D*) *Coeloseris mayeri*, (*E*) *Agaricia undata*, and (*F*) *Helioseris cucullata.* Different magnification views showing: large-scale organisation of corallites or septal organisation (subscripted with '1'); calicular view detail (subscripted with '2'); septal menianes or aligned rows of granules (subscripted with '3′ – note the potential absence of the latter in *C. mayeri* (indicated by ?)); and transverse or longitudinal view of septal menianes or granules (subscripted with '4'). Arrows indicate beaded septal edges (yellow arrows); menianes or aligned septal granules (white arrows); and microtexture of septal face (orange arrows). SEM images of corallum surface (*A–F*).

above. *Coeloseris* differs from all other agariciids, as a result of septal face granules arranged perpendicular (not parallel) to septal edge (alternating in position within each septal face), and its septal margin is sinuous and more lacerate. In addition, its tectura appears to be much more smooth than in other agariciids (Fig. 6), and the thin tabular dissepiments between septa (Fig. 6*D* –4, 5) are a unique feature among extant agariciids.

Superficial morphological similarities between the early ontogenetic stages of *Dactylotrochus* and *Desmophyllum* have been regarded as support for *Dactylotrochus* within the Caryophylliidae. Although juvenile stages of *Dactylotrochus* (before the development of thecal extensions) show some similarity to juvenile *Desmophyllum* (i.e. lack of pali and columella), they also share many features with the initial/juvenile coralla of a broad range of corals. Characters such as the occurrence of marginothecal wall at initial stages, polycyclic bases and narrow zone with centers of rapid accretion are common in various scleractinian taxa (e.g. dendrophylliids, astrangiids, various traditional caryophylliids, agariciids; see Durham 1949; Fig. 5*B*).

Whereas these other features are common to juvenile coralla of many corals, in its early stages the *Dactylotrochus* corallum displays several distinct characters that are shared with traditional agariciids and some allied corals. Bead-like structures on the growing edges of meniane most likely reflect their 'modular' foundations. Another striking, non-caryophylliine feature of *Dactylotrochus* is the scale-like deposits developed on the outer wall surface (Fig. 3*F*, *G*, *H*). Similar tiny scale-like structures do occur, however, in agariciids (Fig. 5*A*, 6) and are also common in taxa that are allied with agariciids in molecular analyses (e.g. acroporiids (Nothdurft and Webb 2007), some traditional oculinids (*Galaxea*; see Stolarski 2003)). Taken together, a range of molecular, micromorphological and microstructural features support the affinity of *Dactylotrochus* with the agariciids.

The transfer of *D. cervicornis* to the Agariciidae clarifies some of the uncertainty surrounding the family Caryophylliidae. As our ability to delineate monophyletic groups improves, and as additional morphological and/or genetic data become available, the composition of a group may change, but the name and its underlying evolutionary significance will probably remain stable. Accordingly, we propose the transfer of the genus *Dactylotrochus* and the species *D. cervicornis* to the family Agariciidae.

Taxonomic Summary

Family **AGARICIIDAE** Gray, 1847 emended

Solitary (ahermatypic and azooxanthellate) or colonial (hermatypic and zooxanthellate), attached. Colony shape branching, massive, columnar, encrusting or foliose, all formed mainly by intratentacular or circumoral budding. Wall septothecate or synapticulothecate, the later usually becoming solid or absent. Septa rarely porous, formed by a continuous middle rapid accretion zone flanked by perpendicular to slightly oblique bundles of fibres (thickening deposits). Septal margins usually beaded. Septa from colonial representatives directly confluent between centers, united by compound synapticulae. Septal faces with scale-like microtexture and bear rows of granules or menianes, both composed of RAD. Endothecal dissepiments mostly absent. Columella trabecular or absent.

Extant genera belonging to the family Agariciidae

Agaricia Lamarck, 1801

Type species: *Madrepora undata* Ellis & Solander, 1786.
Species included: *A. agaricites* (Linnaeus, 1758); *A. fragilis* Dana, 1846; *A. grahamae* Wells, 1973; *A. humilis* Verrill, 1901; *A. lamarcki* Milne Edwards & Haime, 1851; *A. tenuifolia* Dana, 1846; *A. undata* (Ellis & Solander, 1786).

(?) ***Coeloseris*** Vaughan, 1918

Type species: *Coeloseris mayeri* Vaughan, 1918.
Species included: *Coeloseris mayeri* Vaughan, 1918.

Dactylotrochus Wells, 1954

Type species: *Tridacophyllia cervicornis* Moseley, 1881.
Species included: *Dactylotrochus cervicornis* (Moseley, 1881).

Gardineroseris Scheer & Pillai, 1974

Type species: *Gardineroseris ponderosa* (Gardiner, 1905).
Species included: *Gardineroseris planulata* (Dana, 1846).

Helioseris Milne Edwards & Haime, 1849

Type species: *Madrepora cucullata* Ellis & Solander, 1786.
Species included: *H. cucullata* (Ellis & Solander, 1786).

Leptoseris Milne Edwards & Haime, 1849

Type species: *Leptoseris fragilis* Milne Edwards & Haime, 1849.
Species included: *L. amitoriensis* Veron, 1990; *L. cailleti* (Duchassaing & Michelotti, 1864); *L. explanata* Yabe & Sugiyama, 1941; *L. foliosa* Dinesen, 1980; *L. gardineri* Van der Horst, 1921; *L. glabra* Dinesen, 1980; *L. hawaiiensis* Vaughan, 1907; *L. incrustans* (Quelch, 1886); *L. kalayaanensis* Licuanan & Aliño, 2009; *L. mycetoseroides* Wells, 1954; *L. papyracea* (Dana, 1846); *L. scabra* Vaughan, 1907; *L. solida* (Quelch, 1886); *L. striata* Fenner & Veron, 2002; *L. tenuis* Van der Horst, 1921; *L. tubulifera* Vaughan, 1907; *L. yabei* (Pillai & Scheer, 1976).

Pavona Lamarck, 1801

Type species: *Madrepora cristata* Ellis and Solander, 1786.
Species included: *P. bipartita* Nemenzo, 1980; *P. cactus* (Forskål, 1775); *P. chiriquiensis* Glyn, Mate & Stemann, 2001; *P. clavus* (Dana, 1846); *P. danai* (Milne Edwards & Haime, 1860); *P. decussata* (Dana, 1846); *P. diffluens* Lamarck, 1816; *P. divaricata* Lamarck, 1816; *P. duerdeni*

Vaughan, 1907; *P. explanulata* (Lamarck, 1816); *P. frondifera* Lamarck, 1816; *P. gigantea* Verrill, 1869; *P. lata* Dana, 1846; *P. maldivensis* (Gardiner, 1905); *P. minuta* Wells, 1954; *P. varians* Verrill, 1864; *P. venosa* (Ehrenberg, 1834); *P. xarifae* Scheer and Pillai, 1974.

(?) ***Pachyseris*** Milne Edwards & Haime, 1849

Type species: *Agaricia rugosa* Lamarck, 1801.

Species included: *P. foliosa* Veron, 1990; *P. gemmae* Nemenzo, 1955; *P. rugosa* (Lamarck, 1801); *P. speciosa* (Dana, 1846).

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