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Zoologica Scripta

A phylogeny reconstruction of the Dendrophylliidae (Cnidaria, Scleractinia) based on molecular and micromorphological criteria, and its ecological implications

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Recent molecular phylogenetic studies have shown that most traditional families of zooxanthellate shallow-water scleractinians are polyphyletic, whereas most families mainly composed of deep-sea and azooxanthellate species are monophyletic. In this context, the family Dendrophylliidae (Cnidaria, Scleractinia) has unique features. It shows a remarkable variation of morphological and ecological traits by including species that are either colonial or solitary, zooxanthellate or azooxanthellate, and inhabiting shallow or deep water. Despite this morphological heterogeneity, recent molecular works have confirmed that this family is monophyletic. Nevertheless, what so far is known about the evolutionary relationships within this family, is predominantly based on skeleton macromorphology, while most of its species have remained unstudied from a molecular point of view. Therefore, we analysed 11 dendrophylliid genera, four of which were investigated for the first time, and 30 species at molecular, micromorphological and microstructural levels. We present a robust molecular phylogeny reconstruction based on two mitochondrial markers (COI and the intergenic spacer between COI and 16S) and one nuclear (rDNA), which is used as basis to compare micromorphogical and microstructural character states within the family. The monophyly of the Dendrophylliidae is well supported by molecular data and also by the presence of rapid accretion deposits, which are *ca.* 5 μm in diameter and arranged in irregular clusters, and fibres that thicken the skeleton organized in small patches of a few micrometres in diameter. However, all genera represented by at least two species are not monophyletic, *Tubastraea* excluded. They were defined by traditional macromorphological characters that appear affected by convergence, homoplasy and intraspecific variation. Micromorphogical and microstructural analyses do not support the distinction of clades, with the exception of the organization of thickening deposits for the *Tubastraea* clade.

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Introduction

The family Dendrophylliidae Gray, 1847, comprises 29 genera and 364 species, of which 20 genera and 166 species are extant, ranking third among the Scleractinia in species richness (Cairns *et al.* 1999; Cairns 2001). It is distributed worldwide, with the exception of Antarctica, from shallow water to 2165 m depth (Cairns 2001). The family shows various growth forms, dispersal capabilities and ecologic features (Veron 2000; Cairns 2001) (Figs 1, S2–S6). Its species are either solitary (Fig. 1A,B) or colonial (Fig. 1C–F), and either free-living (Fig. 1B) or attached (Fig. 1A, C–F; Goreau & Yonge 1968; Hoeksema & Best 1991; Cairns 2001; Stolarski & Roniewicz 2001). The majority of genera consist of species that are all azooxanthellate, while those of two shallow-water genera are zooxanthellate (i.e. *Turbinaria* Oken, 1815 and *Duncanopsammia* Wells, 1936), one (*Balanophyllia* Wood, 1844) comprises species that are either typically zooxanthellate (Figs 1A, 9A–C) or azooxanthellate (Fig. 9D–I), and another genus (*Heteropsammia* Milne Edwards & Haime, 1848) is apozooxanthellate, having species with zooxanthellae in shallow water (Fig. 1B) and lacking them in deep water (Cairns 2001, 2007; Cairns & Kitahara 2012), although no clear evidence has been published for the latter.

Cairns (2001) published the most exhaustive phylogeny reconstruction of the Dendrophylliidae hitherto, which was based on an analysis of the skeletal morphology of species from all known 29 genera, using 10 characters and 41 character states and by focusing on the gross morphology of the coralla, the thecal structures, calicular elements, and the presence or absence of zooxanthellae. According to him, the monophyly of the family is reflected by various morphological and traditional microstructural characters, such as synapticulothecal wall with laminar and irregularly perforated septa, composed of a single fan of numerous simple trabeculae (but see discussion); these are united by synapticulae, which corresponds with a smooth axial edge of the septum itself (Vaughan & Wells 1943; Kuzmicheva 1986; Cairns 2001; Stolarski & Roniewicz 2001). Furthermore, the Pourtalès plan (Cairns 1994, 2002; for an illustration and detailed description see http://tolweb.org/Dendrphylliidae/19165), a unique arrangement of the septa, is typical of the Dendrophylliidae, although only corals of some genera display it in adult stage (Wells 1933; Vaughan & Wells 1943; Alloiteau 1952; Cairns 2001). The monophyly of the family was further confirmed by its unique composition of cnidocysts (Picciani *et al.* 2011; Martínez-Baraldés *et al.* 2014).

Recent molecular analyses have challenged the traditional systematics of scleractinian corals showing that the macromorphological classification in suborders and families is unreliable (Romano & Palumbi 1996; Romano & Cairns 2000; Chen *et al.* 2002; Fukami *et al.* 2004, 2008; Le Goff-Vitry *et al.* 2004; Kitahara *et al.* 2010, 2012a,b; Huang *et al.* 2011; Stolarski *et al.* 2011; Arrigoni *et al.* 2012, 2014; Benzoni *et al.* 2012a). Consequently, the majority of traditional scleractinian families have been found to be para- or polyphyletic, whereas the family Dendrophylliidae has retained its status as one of only few monophyletic scleractinian families (Le Goff-Vitry *et al.* 2004; Fukami *et al.* 2008; Kitahara *et al.* 2010). Moreover, it is the only well-supported scleractinian family that includes both shallow and deep-water species (Kitahara *et al.* 2010). Other molecular works have focused on the genetics of single species, such as *Cladopsammia gracilis* (Milne Edwards & Haime, 1848) (Hizi-Degany *et al.* 2007), *Balanophyllia europaea* (Risso, 1826) (Goffredo *et al.* 2004), *Leptopsammia pruvoti* Lacaze-Duthiers, 1897 (Goffredo *et al.* 2009), *Enallopsammia rostrata* (De Pourtalès, 1878) (Miller *et al.* 2010) and *Astroides calycularis* (Pallas, 1766) (Casado-Amezùa *et al.* 2012). Nevertheless, all these studies analysed few genera and species, and most genera have remained largely unstudied from a molecular point of view. Moreover, an exhaustive molecular phylogeny reconstruction of the Dendrophylliidae has never been produced. This would be needed to clarify its evolutionary relationships and would enable a comparison of genetic results with a phylogeny reconstruction based on morphological characters (Cairns 2001), as performed for the Fungiidae, another monophyletic family of scleractinians (Gittenberger *et al.* 2011; Benzoni *et al.* 2012b).

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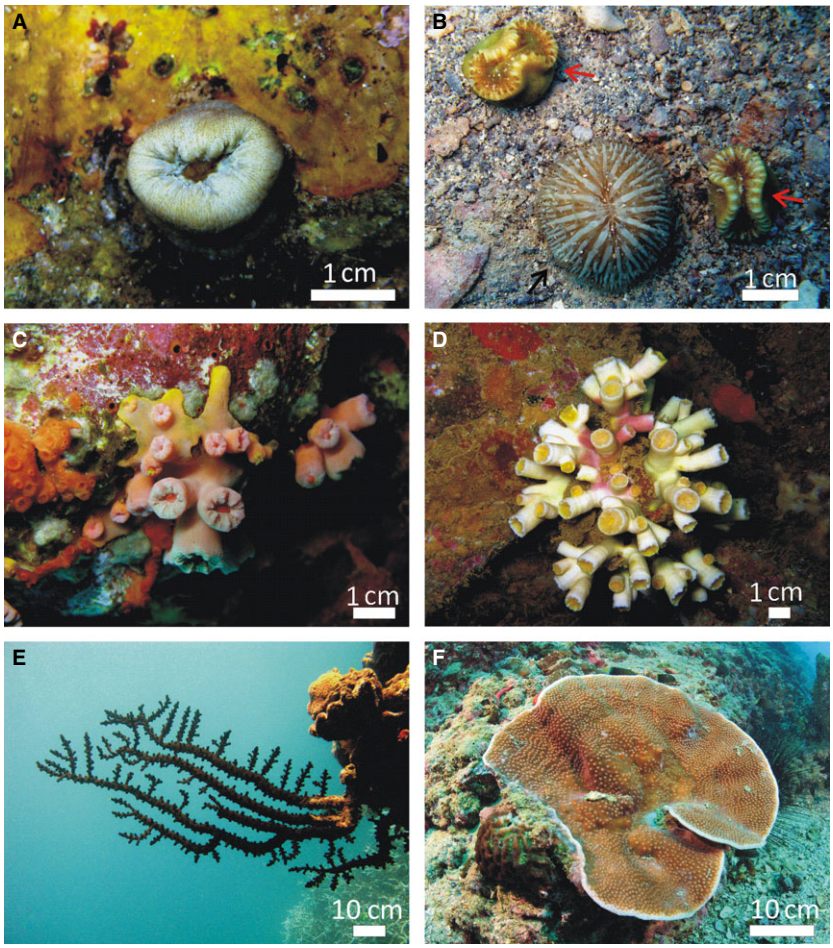

Fig. 1 Some of the Dendrophylliidae species examined in this study having different macromorphology and ecology: —A. *Balanophyllia europaea*, a solitary, zooxanthellate, attached and shallow-water species found in temperate waters (Karistos, Greece, 2 m); —B. two individuals of *Heteropsammia cochlea* (red arrows), a solitary, zooxanthellate, free-living species, living on the sandy seafloor together with a free-living mushroom coral (*Cycloseris cyclolites*, black arrow) in tropical waters (New Caledonia, 10 m); —C. *Rhizopsammia wettsteini*, colonial by budding from stolons, azooxanthellate, attached, a reef-dwelling species found underneath overhangs (Ari Atoll, Maldives, 15 m); —D. *Tubastraea* sp 2, colonial, ramose, azooxanthellate, attached, a reef-dwelling species found in deeper water (Canal Woodin, New Caledonia, 35 m); —E. *T. micranthus*, colonial, ramose, azooxanthellate, attached, a reef-dwelling species found in shallow water (Mayotte Island, 12 m); —F. *Turbinaria mesenterina*, colonial, vase-shaped, zooxanthellate, attached, a reef-dwelling species found in shallow water (Burum, Yemen, 10 m, photograph by E. Dutrieux).

The widespread incongruence between molecular findings and the traditional systematics of Scleractinia has stimulated the search for new micromorphological and microstructural characters that are evolutionary informative. In fact, several studies based on fine-scale morphology of the skeleton, rather than macromorphology, provided support to molecular evidence (Cuif *et al.* 2003; Benzoni *et al.* 2007, 2010, 2011, 2012a,b; Budd & Stolarski 2009, 2011; Gittenberger *et al.* 2011; Janiszewska *et al.* 2011; Stefani *et al.* 2011; Stolarski *et al.* 2011; Budd *et al.* 2012; Kitahara *et al.* 2012a,b; Schmidt-Roach *et al.* 2014), indicating the advantages of an integrated approach for a taxonomic revision of the Scleractinia.

In this study, we have reconstructed a molecular phylogeny for 11 genera and 30 currently recognized extant species of Dendrophylliidae characterized by different corallum morphologies and ecological traits spanning the whole range of variability across this family, including the genera *Astroides* Quoy & Gaimard, 1827, *Duncanopsammia*, *Eguchipsammia* Cairns 1994, and *Rhizopsammia* Verrill, 1870, for the first time in a phylogenetic analysis. One nuclear and two mitochondrial markers were used to infer their phylogenetic relationships. The present examination of the diversity of micromorphological and microstructural characters is also unprecedented, thus providing a complete integrated database for each taxon.

Materials and methods

Sampling

Taxonomic sampling included 68 specimens representing 30 species of Dendrophylliidae (Table S1, Figs 1, 9–13). Coral samples were collected from several localities in the Mediterranean Sea and in the Indian and Pacific Ocean. Per coral a portion of about 2 cm^2 was preserved in 95% ethanol or in CHAOS solution (4 M guanidine thiocyanate, 0.1% N-lauroyl sarcosine sodium, 10 mM Tris pH 8, 0.1 M 2-mercaptoethanol) for molecular analyses. Another fragment was bleached in sodium hypochlorite for 24 hours, rinsed with freshwater and air-dried for morphological analysis, and for later use as voucher specimen.

Corals were identified at species level based on their morphological structures following Zibrowius (1980), Scheer & Pillai (1983), Cairns (1984a, 1991, 1999, 2001, 2004), Hoeksema & Best (1991), Cairns & Zibrowius (1997), Fenner (2005), Tachikawa (2005) and Hickman (2008). Whenever possible, original descriptions and illustrations of dendrophylliid taxa were consulted. Voucher specimens were deposited at the University of Milano-Bicocca (Milano, Italy), the University of Miyazaki (Miyazaki, Japan), Institut de Recherche pour le Développement (Noumea, New Caledonia) and Naturalis Biodiversity Center (Leiden, the Netherlands).

DNA extraction, amplification and sequencing

For samples fixed in 95% ethanol, DNA was extracted using the DNAeasy® Tissue kit (Quiagen Inc., Valencia, CA, USA). For specimens preserved in CHAOS solution, DNA was extracted based on a phenol-chloroform-based method with a phenol extraction buffer (100 mM Tris–Cl pH 8, 10 mM EDTA, 0.1% SDS) (Fukami *et al.* 2004; Huang *et al.* 2011). Sequences from one nuclear and two mitochondrial regions were targeted. The first mitochondrial region covered a portion of cytochrome oxidase 1 (COI) gene, while the second mitochondrial one covered the 3′-end of COI, intergenic spacer (IGR) between COI and trnM, trnM and the 5′-end of large ribosomal subunit (16S), namely IGR in the rest of the text. The nuclear region covered a portion of rDNA including the entire sequences of ITS1, 5.8S and ITS2, and a portion of 18S and 28S.

The partial COI (~750 bp) was amplified using newly designed primers COIDENL (5′- CGCTGGGCGT TTTCTACTAA -3′) and COIDENR (5′- GAAATCATT CCAAAGCCAGGT -3′) or using primer sets ZCO1 and ZCO1R (Forsman *et al.* 2009) in a 50-μL reaction volume containing 1× PCR buffer, 6 mM $MgCl_2$, 0.3 μM for both of each primer, 0.03 mM dNTP, 3 U taq polymerase and 20 ng of DNA. The amplification profile consisted of an initial denaturation step of 94°C for 2 min, followed by 30 cycles of 94°C for 30 sec, 53°C for 1 min, 72°C for 1 min and finally a 7 min extension step at 72°C. The IGR (~500 bp) was amplified using newly designed primers AGAL (5′- CGCATTGAAACACGAGCTTA -3′) and DENF (5′- TTTGCTGGTTGGAATTTGGT -3′) or using primers Cs18F and Cs18R (Lin *et al.* 2011) in a 50-μL PCR mix composed of 1× PCR buffer, 0,5 mM $MgCl_2$, 0.4 μM for both of each primer, 0.02 mM dNTP, 2 U taq polymerase and 20 ng of DNA. Amplification reactions were carried out using the following parameters: 94°C for 4 min, 30 cycles of 94°C for 1 min, 51°C for 1 min, 72°C for 1 min and a final phase at 72°C for 5 min. A portion of rDNA (~750 bp) was amplified using primers A18S (Takabayashi *et al.* 1998) and ITS4 (White *et al.* 1990), and the protocol proposed by Benzoni *et al.* (2012b) or using primers 1S and 2SS (Odorico & Miller 1997). PCR products were purified and sequenced by Macrogen Inc. (Seoul, South Korea), or alternatively, they were treated with shrimp alkaline phosphatase and Exonuclease I at 37°C for 40 min followed by 80°C for 20 min, then sequenced by FASMAC Co., Ltd. (Kanagawa, Atsugi City, Japan), using the same primers that were used for the PCR. All new sequences were deposited in EMBL (accession numbers in Table S1).

Phylogenetic analyses

Sequences were assembled with CodonCode Aligner v 4.2.5 (CodonCode Corporation, Dedham, MA, USA) and manually checked using BioEdit (Hall 1999). Alignments of the four separated data sets were carried out using the E-INS-i option in MAFFT v 7.110 (Katoh *et al.* 2002; Katoh & Standley 2013) under default parameters. *Goniopora columna* was selected as outgroup due the sister relationships of the family Poritidae Gray, 1842, to the family Dendrophylliidae (Cairns 2001; Fukami *et al.* 2008). InDels and parsimony informative sites were detected using DnaSp v 5.10.01 (Librado & Rozas 2009), and InDels were treated as a fifth character in phylogenetic analyses. A chi-square test was used to test for significant deviations from homogeneity of base frequencies across taxa for each gene data set in PAUP v 4.0b.10 (Swofford 2003). Genetic distances and their standard deviation were calculated as uncorrected *p*-distance with MEGA v 5 (Tamura *et al.* 2007).

The three examined loci were concatenated in a single matrix for phylogenetic analyses. The partitioned data set was analysed under Bayesian inference (BI) and maximum parsimony (MP). Bayesian analysis was performed with MrBayes v 3.1.2 (Ronquist & Huelsenbeck 2003) using different nucleotide substitution models for each separate locus as suggested by MrModelTest v 2.3. (Nylander 2004). MrModeltest suggested GTR+I+ Γ for COI, HKY+Γ for IGR and HKY+I+Γ for rDNA. The analyses were run for 1 million generations with sampling every 10 generations, with a burn-in of 25 000. Convergences were assessed by examining average standard deviation of split frequencies and Tracer v 1.5 (Drummond & Rambaut 2007). MP analyses were performed using PAUP v 4.0b.10 (Swofford 2003) with a heuristic search and the tree bisection reconnection (TBR) branch-swapping algorithm. Support values were calculated with 500 bootstrap replicates. MP analyses were also conducted for each separated locus using the same parameters used for concatenated analyses (Figs S1–S3).

Micromorphological/microstructural analyses

Skeletons of the sequenced dendrophylliid taxa were examined for micromorphological and microstructural features.

We analysed also the microstructures of the outgroup, a sample of *Goniopora* sp. collected in the Gulf of Aden (Yemen), in order to compare it with dendrophylliids (Table S1). Specimens were observed intact, as broken and etched samples, or as thin sections (*ca*. 30 μm thick). Transverse broken sections of septa were exposed for *ca*. 20 s of etching in 0.1% formic acid solution, rinsed with distilled water and air-dried following the procedure described by Stolarski (2003). Once dried, the samples were mounted on stubs and sputter-coated with conductive platinum film. Thin sections were observed and photographed with a Nikon Eclipse 80i (Tokyo, Japan) transmitted light microscope, whereas intact and broken/etched skeleton samples were observed with a Philips XL 20 (Amsterdam, the Netherlands) scanning electron microscope (SEM). Thin sections and skeletal fragments attached to microscope stubs are housed at the Institute of Paleobiology (ZPAL, Warsaw). Supplementary micro-CT data were collected with Zeiss XRadia MicroXCT-200 system in the Laboratory of Microtomography, Institute of Paleobiology, Polish Academy of Science, Warsaw.

Phylo-ecological analyses

To study evolutionary trends in the ecology of the Dendrophylliidae, specific morphological characters of ecological importance have been projected on simplified cladograms that only deal with species groups: the development of multiple calices in colonial corals as opposed to single calices in solitary corals, the presence/absence of zooxanthellae, a free mode of life enabling dispersal as opposed to an attached, sessile mode of life, and the maximum diameter of the calices considered relevant for the coral's capacity to shed sediment. The maximum calice diameter of each species was measured in material used for the present research, deposited at University of Milano-Bicocca and University of Miyazaki, and in some specimens already available in the museum coral collection of Naturalis Biodiversity Center, Leiden, with RMNH or ZMA catalogue numbers (Table S3).

Results

Molecular analyses

Complete sequence information was obtained for 64 samples, while for AO100, AO101, AO102 and AO147 specimens PCR amplification of the COI gene failed. The concatenated sequence alignment of 68 samples included 1696 positions. Examining the individual gene data sets, alignments lengths were 577 base pairs (bp) for COI, 450 bp for IGR and 669 bp for rDNA. rDNA was the most variable locus, yielding a good phylogenetic resolution at species level. A total of 188 bp were variable in COI (148 phylogenetically informative), 52 bp were variable in IGR (27 phylogenetically informative), and 421 bp were variable in rDNA (321 phylogenetically informative). No significant deviations from homogeneity of base frequencies were observed across taxa for the individual gene data sets (the *P* values were 1.00 for the three independent loci and for the combined data).

Maximum parsimony topology was consistent with the BI one (Fig. 2). Individual MP analyses of COI, IGR and rDNA revealed general congruence in the phylogenetic signal. No substantial discordances or general patterns of conflicts were detected (Figs S1–S3). Based on COI phylogeny (Fig. S1), the basal clade and the complex clade were resolved and well supported in agreement with Stolarski *et al.* (2011). Within the complex clade, all examined representatives of the Dendrophylliidae cluster together in a well-supported monophyletic group confirming previous findings (Fukami *et al.* 2008; Kitahara *et al.* 2010; Huang 2012).

At genus level, based on the combined tree and the rDNA tree (Figs 2 and S2), *Cladopsammia* is polyphyletic with high intrageneric distance (9.7 $\pm$ 2.1%) and *Rhizopsammia* is paraphyletic (intrageneric distance 2.9 $\pm$ 0.7%). The genus *Balanophyllia* is polyphyletic (intrageneric distance 5.4 $\pm$ 0.4%) based on the combined tree and the partial COI gene (Figs 2 and S1) as previously shown by Kitahara *et al.* (2010). The two species ascribed to the subgenus *Balanophyllia* by Cairns (2001) are monophyletic but not in the same clade as the species assigned by him to the subgenus *Eupsammia* Milne Edwards and Haime, 1848, namely *B.* (*E.*) *imperialis*. The genus *Dendrophyllia* is also polyphyletic (intrageneric distance 5.1 $\pm$ 1.6%) (Fig. 2).

Two major clades are recovered at the basal position of the combined tree (Fig. 2). The first clade comprises representatives of the genera *Cladopsammia*, *Eguchipsammia* and *Heteropsammia*. The second clade is composed of all examined species of *Turbinaria* except *T. peltata* (Esper, 1794). The latter is highly divergent from its congeners and clusters with the monospecific genus *Duncanopsammia* as sister taxon, represented by its type species *D. axifuga* (Milne Edwards & Haime, 1848). The genetic distance of *T. peltata* and *D. axifuga* is very low (1 $\pm$ 0.1%) compared with the average distance between *T. peltata* and the other *Turbinaria* species (7.7 $\pm$ 0.6%). The Mediterranean azooxanthellate species *Leptopsammia pruvoti* (shallow water) and *Dendrophyllia cornigera* (Lamarck, 1816) (deep water) cluster together in a well-supported clade, next to another Mediterranean dendrophylliid, *Astroides calycularis*. The other two Mediterranean species analysed in this study are *Balanophyllia* (*Balanophyllia*) *regia* Gosse, 1853, and *B.* (*B.*) *europaea*, which are closely related to each other and divergent from *Balanophyllia* (*Eupsammia*) *imperialis*. The genus *Tubastraea* has a very low intrageneric distance

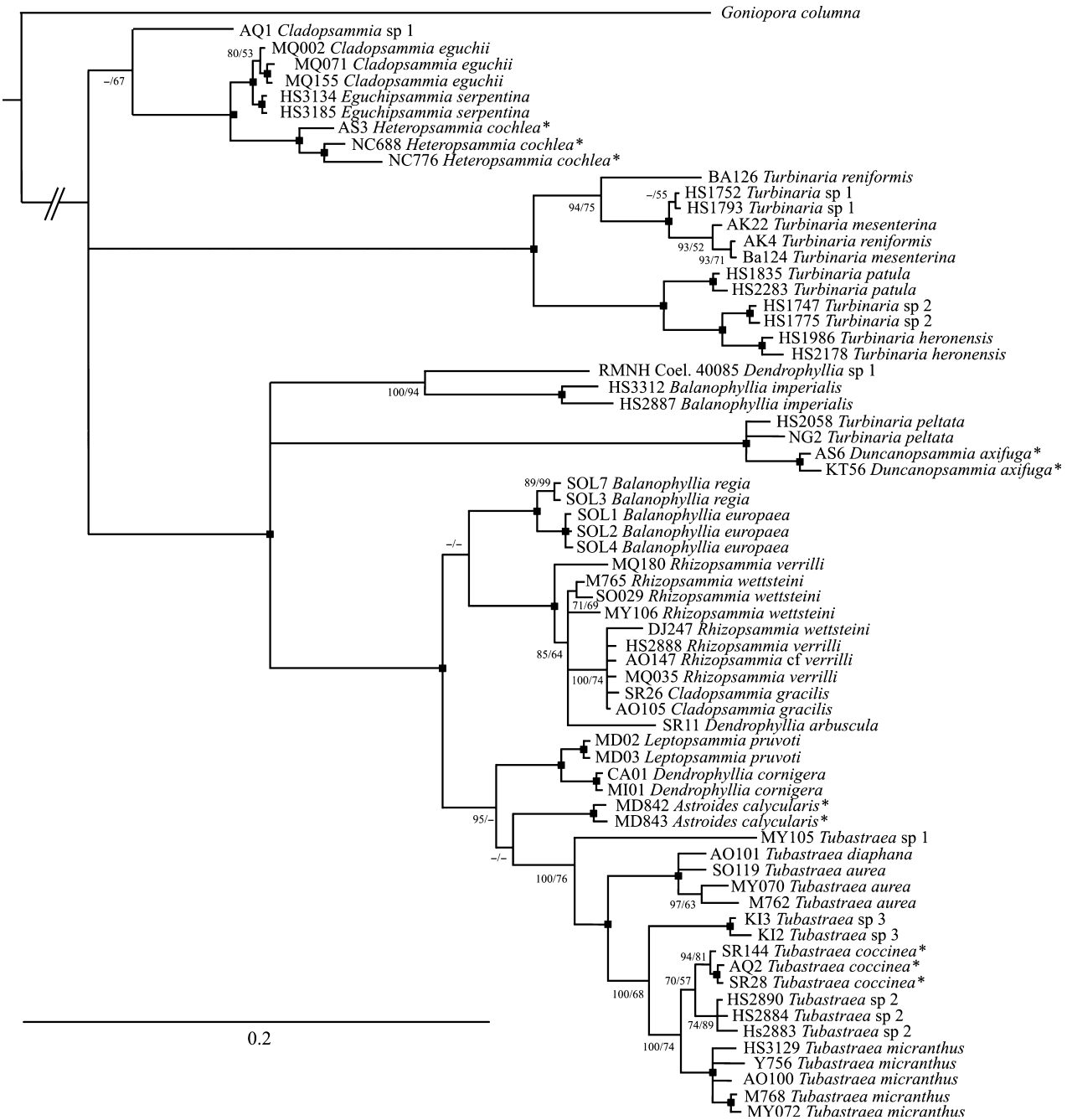

Fig. 2 Combined gene tree for Dendrophylliidae based on three molecular loci (COI, IGR and rDNA), with outgroup *Goniopora*, based on Bayesian inference. Support values are posterior probability and maximum parsimony bootstrap values, respectively. Black squares at the node indicate high-supported clades (BI posterior probability ≥98 and MP bootstrap ≥98). * indicates type species.

(1.5 ± 0.3%), and all the seven species belonging to this genus examined in this study, including the type species *T. coccinea* Lesson, 1829, belong to the same clade. Moreover, within the *Tubastraea* clade, all species represented by more than one sample are monophyletic.

Micromorphology and microstructure

Two main regions of dendrophylliid skeletons were examined to characterize micromorphological/microstructural characters (Table S2). One of them represents the fastest growing part of the skeleton, located at distal edges of

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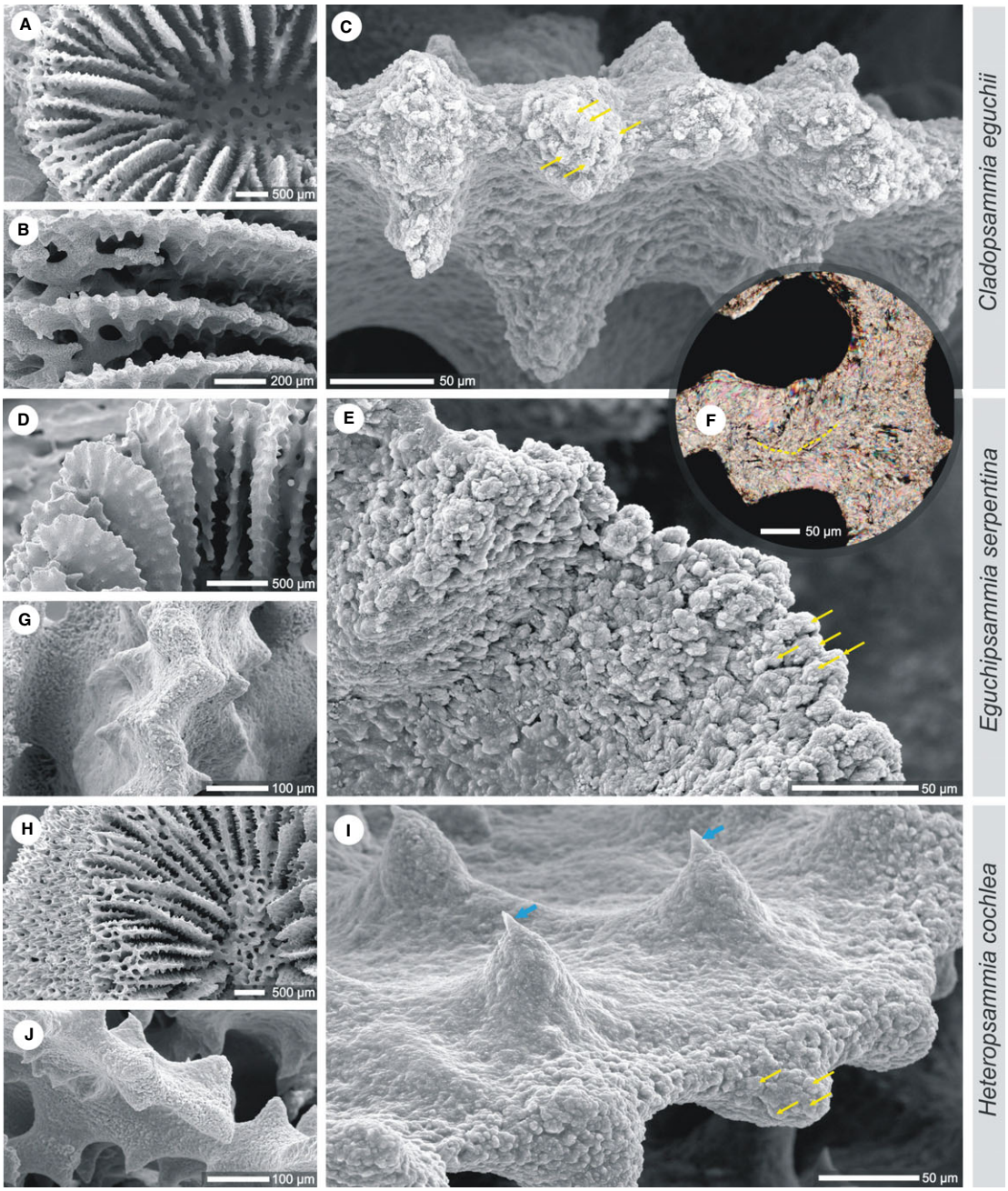

Fig. 3 Micromorphological features of representatives of *Cladopsammia-Eguchipsammia-Heteropsammia* clade. Distal (A, D, H) or distal–lateral (D) views of corallites of *Cladospammia eguchii* (A–C), *Eguchipsammia serpentina* (D–F) and *Heteropsammia cochlea* (H–J). Clusters of nanogranular-fibrous deposits, *ca.* 5 µm in diameter (yellow arrows in C, E and I) that correspond to rapid accretion deposits in sections, group on low septal teeth (if distinct, separated from each other *ca.* 20-30 µm, e.g. C, H). Septal faces covered with granulae that, especially in *Heteropsammia*, can be sharp-pointed (blue arrows in H). Bundles of fibres on septal faces (thickening deposits) form small patches, a few micrometre in diameter (distinct in E). F. Thin section, polarized light, optical microscope (dashed yellow line marks position of RAD; lack of long-ranging light extinction within TD suggests that fibres are differently arranged in superimposing patches. All (except of F) SEM images of natural skeleton surfaces. (A–C) UNIMIB MQ002; (D–F) IRD HS3134; (H–J) IRD NC776.

skeletal elements (e.g. septa). In this region, the skeleton is formed as so-called rapid accretion deposits (RAD, traditionally known as "calcification centres") and is composed of nanogranular-fibrous material (Stolarski 2003; Benzerara *et al.* 2011; Brahmi *et al.* 2012). The other region of interest was located on the lateral faces of

skeletal elements, which represent the slowest growing parts (TD, thickening deposits also known as "fibres"; Stolarski 2003).

Distal edges of skeletal structures. Distal edges of skeletal elements are relatively smooth at low/moderate magnifications (especially in adult septa; Figs 4D, E, P, Q; 5A, 6G, H) or consist of low teeth/spines (especially in ontogenetically younger septa; Figs 3A–C, G–H, 4J–O, 5E, F, 6B, 7D–E, M, N). At higher magnification, clusters of nanogranular-fibrous deposits, which are *ca*. 5 μm in diameter, form a continuous zone along distal septal edges (e.g. Figs 3E, 4B, F, Q–R, 5B) or group on the edges of septal teeth (e.g. Figs 3C, H, 4C, 5F). In etched sections (SEM observations) or thin sections (optical microscope observations) of septa, the microstructural components that correspond to minute-scale morphological structures are visible. Furthermore, hollowed-out areas that form mid-septal zone of closely arranged individual centres correspond to clusters of nanogranular-fibrous deposits on the distal margins (e.g. Figs 4U, V, 5 C, H, 6D, 7C, F). In the thin sections, mid-septal zones consist of darker areas that may form a continuous zone (Fig. 7L) or clusters (Figs 3F, 5G).

Lateral faces of skeletal structures. Lateral faces of most of the examined dendrophylliids are covered with small (few micrometre in diameter) patches of fibres. Fibres within such patches are arranged semiperpendicular to the skeletal surfaces, but because of a slightly different orientation they usually do not form crystallographically continuous units (judged from relatively limited areas of the skeleton with the same light extinction in polarized light, e.g. Fig. 3F). Small fibrous patches are observed on the lateral faces (particularly close to the distal edges) of skeletal elements of all dendrophylliids, although in *Tubastraea* such fibrous bundles form *ca*. 10-μm long shingles, parallel to the skeleton surfaces (Fig. 7K, O). The parallel surface arrangement of fibres within patches is visible in etched sections (Fig. 7I) and in thin sections (Fig. 7L).

Septal faces are covered with granulae that can be sharp-pointed, especially in some taxa (herein illustrated in *Heteropsammia*: Fig. 3I).

Phylo-ecology

Number of mouths (stomata). With regard to the number of mouths 13 of 17 molecular clades (Fig. 8C) show the presence of multiple mouths (polystomatism), which represent so-called colonial forms. Three others show the presence of a single mouth (monostomatism), representing a solitary growth form, and one clade did not display a clearly defined character state (Figs 8C, 9–13). Because there is no single basal clade, it is unclear whether the first dendrophylliids had a single mouth (like in *Balanophyllia*) or more than one. The clade consisting of *Cladopsammia* I, *Cladopsammia* II and *Eguchipsammia* shows a synapomorph development of polystomatism. This character state transformation is less clear in *Heteropsammia* because large specimens of *H. cochlea* usually show a single calice nearly split into two equal parts and occasionally two completely separated calices (Figs 1B, 9M–O), whereas all large specimens of *H. eupsammides* show multiple calices and mouths of various size scattered over their upper surface (Hoeksema & Best 1991). The *Turbinaria* I clade consists of various species that are all polystomatous. In the third major clade, *Turbinaria* II and *Duncanopsammia* are basal and share polystomatism with all other clades, except for the three subclades *Balanophyllia* I, II and *Leptopsammia*, suggesting that the latter reflect three independent reversals from polystomatism to monostomatism.

Symbiosis with zooxanthellae. Most dendrophylliid species are azooxanthellate (Figs 8C, 9D–I). *Heteropsammia* is known to be zooxanthellate although specimens obtained from deeper water have been reported to lack symbiotic algae (Schuhmacher & Zibrowius 1985). Other clades with zooxanthellate species are *Turbinaria* I, *Duncanopsammia*, *Turbinaria* II and *Balanophyllia* II. The latter consists of two species, *B. regia* without zooxanthellae and *B. europeaea* with zooxanthellae (Schumacher & Zibrowius 1985; Goffredo *et al.* 2004, 2007).

Dispersal capacity. Among all 17 clades examined, only *Heteropsammia* consists of free-living, mobile species (Goreau & Yonge 1968; Hoeksema & Best 1991). Branches of *Eguchipsammia* corals have also been reported to break off and to dwell on soft substrate as loose coral fragments

Fig. 4 Micromorphological and microstructural features of representatives of *Turbinaria* I and *Duncanopsammia-Turbinaria* II clades. Distal (A, G, J, P, T) or distal–lateral (D, M) views of corallites of *Turbinaria mesenterina* (A–C), *T. heronensis* (D–F), T. sp. 2 (G–I), *T. reniformis* (J–L), *T. peltata* (M–O), *T. patula* (P–R) and *Duncanopsammia axifuga* (T–V). Clusters of nanogranular-fibrous deposits, *ca*. 5 μm in diameter (yellow arrows in B, C, F, H, L, O, R, V) that correspond to rapid accretion deposits in sections (V), group on septal teeth (H, L) or are homogenously distributed along the distal septal edge (e.g. E–F, Q–R). Septal faces relatively smooth (e.g. E) or covered with low granulae. Bundles of fibres on septal faces (thickening deposits) form small patches, a few micrometre in diameter (e.g. H, N). All SEM images are of natural skeleton surfaces, except in U and V, which are broken-etched surfaces. (A–C) UNIMIB BA124; (D–F) UNIMIB HS3178; (G–I) IRD HS1747; (J–L) UNIMIB BA126; (M–O) IRD HS2058; (P–R) IRD HS2283; (T–V) UNIMIB KT56.

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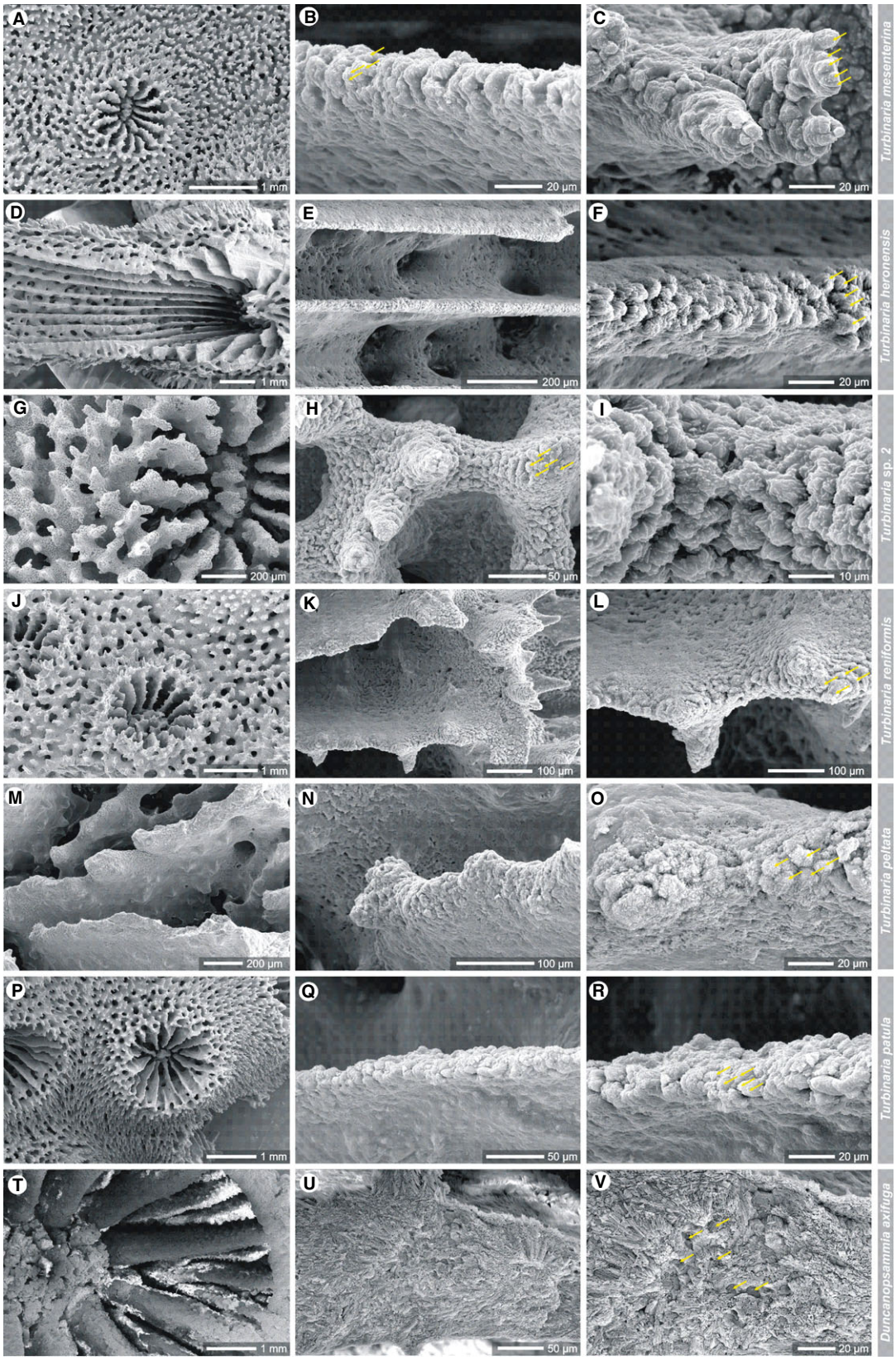
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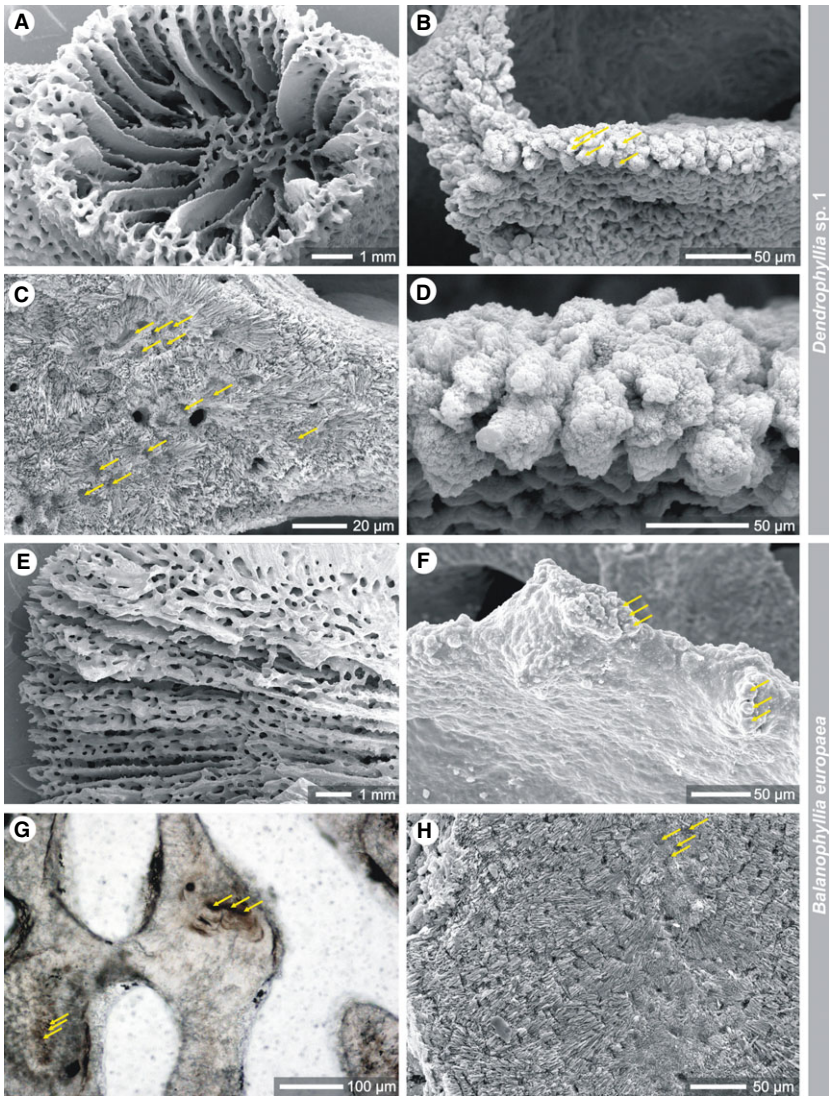

Fig. 5 Micromorphological and microstructural features of representatives of *Dendrophyllia* I and *Balanophyllia* II clades. Distal (A) or distal–lateral (E) views of corallites of *Dendrophyllia* sp 1 (A–D) and *Balanophyllia europaea* (E–H). Clusters of nanogranular-fibrous deposits, *ca.* 5 µm in diameter (yellow arrows in B, F, enlarged in D; natural skeleton surfaces) which correspond to rapid accretion deposits in skeleton sections (yellow arrows in C, G, H) are homogenously distributed along distal septal edge (B, D) or group on small septal teeth (F). Septal faces relatively smooth or covered with low granulae. Bundles of fibres on septal faces (thickening deposits) may form small patches, a few micrometre in diameter (distinct in B). All SEM images of natural skeleton surfaces, except of C, H (broken-etched surfaces) and G (thin section, optical microscope). (A–D) UNIMIB SE02; (E–H) UNIMIB SOL2.

(Cairns 2001), like the specimens used in this study (Fig. 9P–R), whereas they can also form entire deep-water bioherms by themselves (Santodomingo *et al.* 2013; Tempera *et al.* 2014).

Maximum calice diameter. Based on the calice diameter measurements (Table S3, Fig. 8), only two clades were entirely or partly composed of species with calices <5 mm, size class 1: *Turbinaria* I and *Tubastraea* (Fig. 8). Four clades contained species that had the largest (20–30 mm) calices with size class 5: *Cladopsammia* I, *Balanophyllia* I, *Balanophyllia* II and again *Tubastraea*. The remaining 12 clades had species with intermediate sizes.

Discussion

Monophyly of the family Dendrophylliidae: a multidisciplinary confirmation

Molecular phylogenetics has revolutionized traditional systematics of Scleractinia (Romano & Palumbi 1996; Chen *et al.* 2002; Fukami *et al.* 2004, 2008; Kitahara *et al.* 2010,

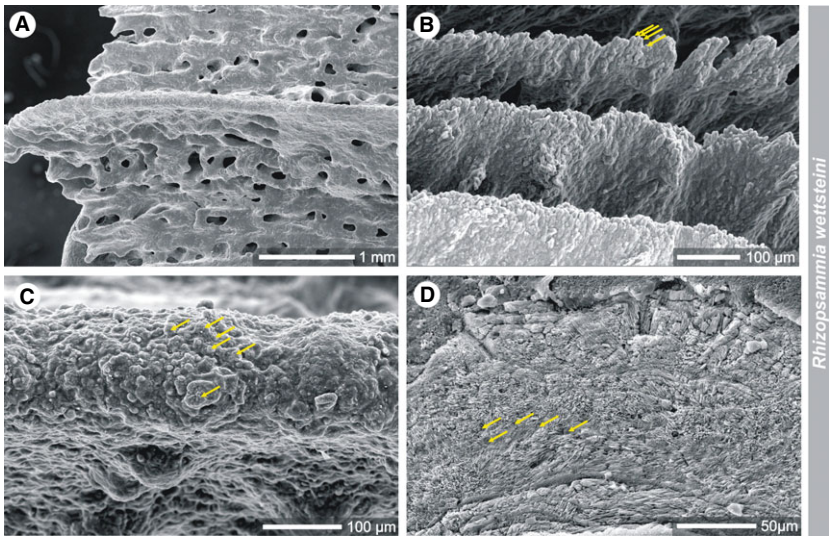

Fig. 6 Micromorphological and microstructural features of representative of *Rhizopsammia* clade (*Rhizopsammia wettsteini)*. Distal–lateral view of corallite (A). Clusters of nanogranular-fibrous deposits, *ca.* 5 µm in diameter (yellow arrows in B, C; natural skeleton surfaces) which correspond to rapid accretion deposits in skeleton sections (yellow arrows in D; broken-etched section) are homogenously distributed along distal septal edge (C) or may group on small septal teeth (B). Septal faces relatively smooth, covered with low granulae. Bundles of fibres on septal faces (thickening deposits) form small patches, a few micrometre in diameter (distinct in B). All SEM images of natural skeleton surfaces, except of D (broken-etched surfaces). (A–D) UNIMIB M765.

2012a,b; Huang *et al.* 2011; Stolarski *et al.* 2011; Kitano *et al.* 2014). A major upheaval was produced by Fukami *et al.* (2008) who showed that 11 of 16 families constituting predominantly, or exclusively, of shallow-water and zooxanthellate taxa were polyphyletic. These results suggest that morphological characters so far rarely used for the reconstruction of phylogenetic relationships among shallow-water scleractinians (Cairns1984b, 1997, 2001; Hoeksema 1989, 1993a; Wallace *et al.* 1991; Wallace 1999) were largely uninformative and prompted the quest for alternatives (Benzoni *et al.* 2007, 2011, 2012a,b; Budd & Stolarski 2009, 2011). However, the inclusion of molecular data from deep-sea and azooxanthellate scleractinians later revealed that the majority of families composed of deep-sea azooxanthellate species were actually monophyletic as traditionally defined (Kitahara *et al.* 2010). The Dendrophylliidae remains the only monophyletic family as traditionally described with representatives from both shallow and deep water, with some, but not all, of the former category having developed the symbiosis with zooxanthellae (Fukami *et al.* 2008; Kitahara *et al.* 2010). In this study, based on three molecular markers and the inclusion of 11 genera, we showed that the monophyly of the dendrophylliids is strongly supported by the use of both mitochondrial and nuclear DNA (Figs 1, S1). In agreement with our molecular findings, micromorphological and microstructural analyses in this study indicate a distinctive arrangement pattern of rapid accretion deposits and organization of thickening deposits for the Dendrophylliidae. This family is characterized by rapid accretion deposits of *ca.* 5 µm in diameter, which are arranged in irregular clusters and fibres that thicken the skeleton in small patches of a few micrometre in diameter. Hence, the results of our multidisciplinary study support previous results obtained by macromorphological approaches (Vaughan & Wells 1943; Kuzmicheva 1986; Cairns 2001, 2007; Cairns & Kitahara 2012) and confirm the monophyly of the family, which includes corals characterized by a synapticulotheca in conjunction with septa composed of only one fan system (Cairns 2001). Furthermore, the monophyly of dendrophylliids seems also to be confirmed by studies on cnidocysts (Picciani *et al.* 2011; Martínez-Baraldés *et al.* 2014). Examination of several species belonging to the genera *Astroides*, *Dendrophyllia*, *Enallopsammia* Sismonda, 1871, *Tubastraea* revealed that the presence of b-rhabdoids in mesenterial filaments is a synapomorphy for these representatives of the family (Picciani *et al.* 2011; Martínez-Baraldés *et al.* 2014). Morphological variation among nematocysts type is less susceptible to changes caused by biotic and abiotic factors than skeletal features (Pires & Pitombo 1992; Terròn-Sigler & Lòpez-Gozàles 2005), and thus, they might be useful for reconstructing evolutionary relationships. However, the evaluation of these structures as potentially informative characters has so far been limited to a restricted number of taxa, and its usefulness for resolving phylogenetic relationships between genera remains to be explored.

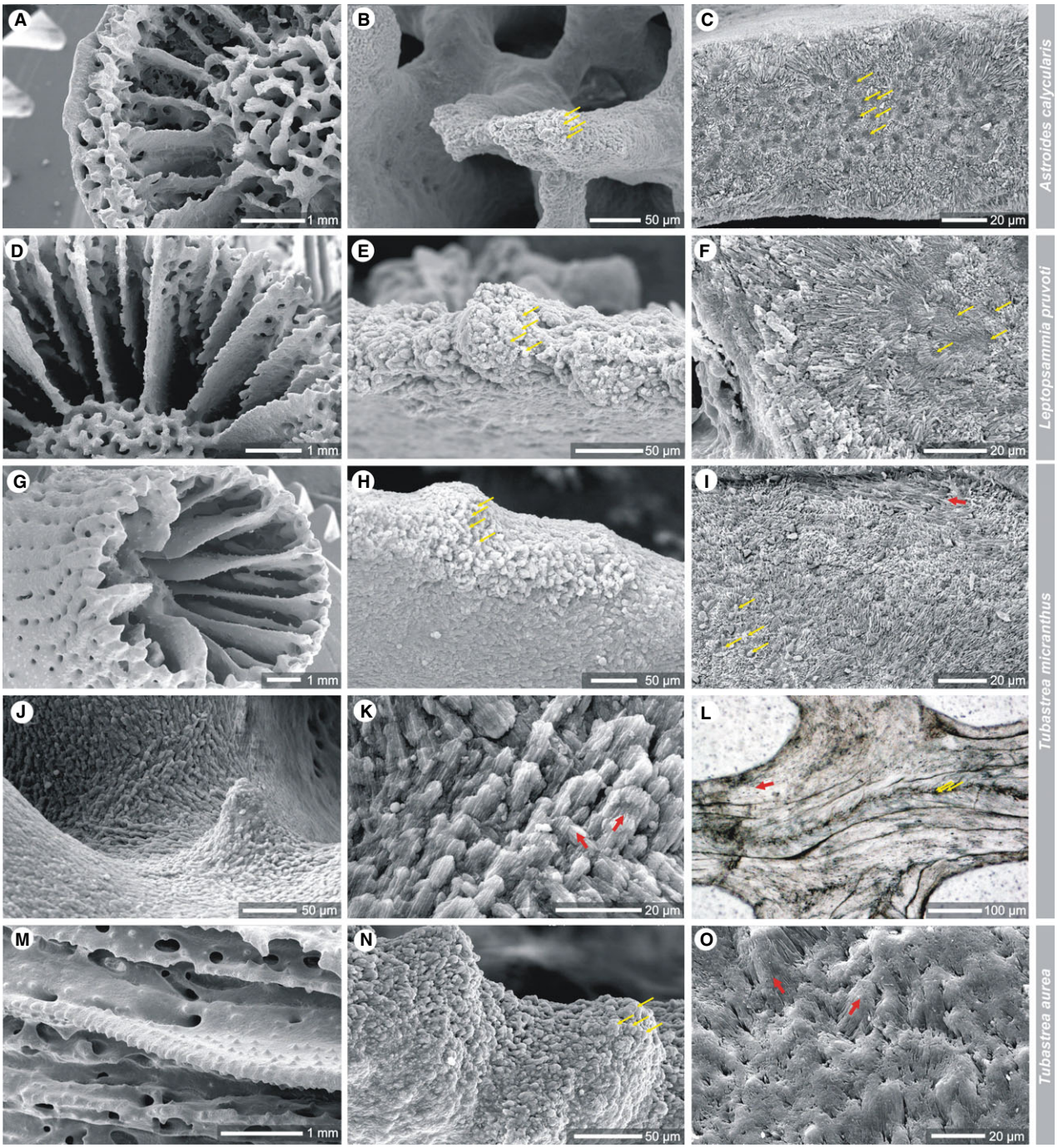

Fig. 7 Micromorphological and microstructural features of representatives of *Astroides*, *Leptopsammia* and *Tubastraea* clades. Distal (A, D, G) or distal–lateral (M) views of corallites of *Astroides calycularis* (A–C), *Leptopsammia pruvoti* (D–F), *Tubastraea micranthus* (G–L) and *Tubastraea aurea* (M–O). Clusters of nanogranular-fibrous deposits, *ca.* 5 µm in diameter (yellow arrows in B, E, H, N; natural skeleton surfaces) which correspond to rapid accretion deposits in skeleton sections (yellow arrows in C, F, L) group on small septal teeth. Septal faces relatively smooth or covered with low granulae. Bundles of fibres on septal faces (thickening deposits) form small patches, a few micrometre in diameter (*Astroides*, *Leptopsammia*) but in *Tubastraea* (J–L, O) form *ca.* 10-µm-thick shingles, parallel to the skeleton surfaces (red arrows in K, L and O). All SEM images of natural skeleton surfaces, except of F, I (broken-etched surfaces) and L (thin section, optical microscope). (A–C) UNIMIB MED843; (D–F) UNIMIB MD03; (G–L) IRD HS3129; (M–O) UNIMIB M762.

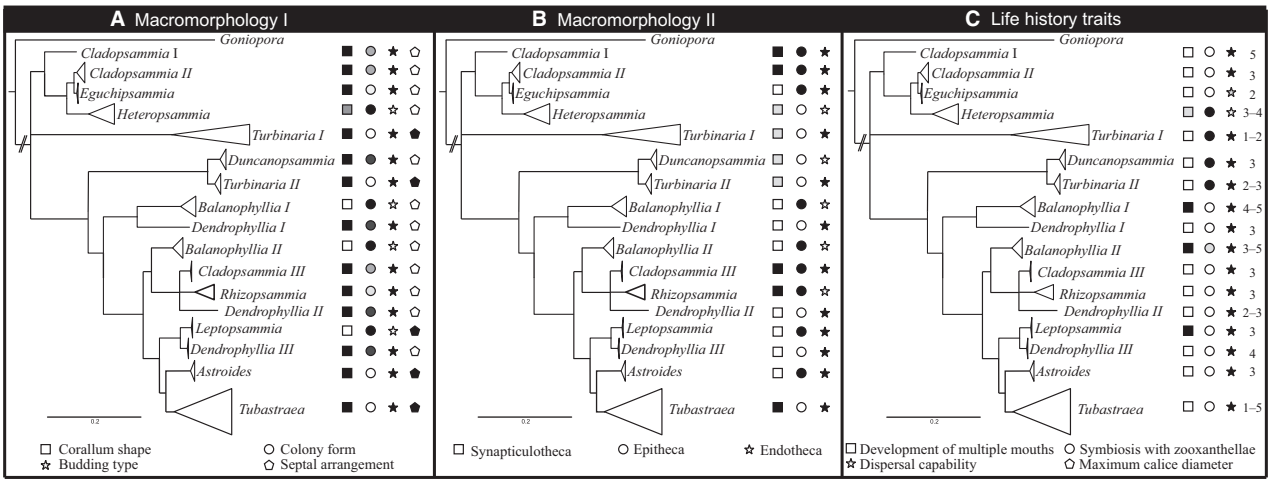

Fig. 8 Comparison between our molecular phylogeny reconstruction based on three markers (COI, IGR and rDNA) and macromorphological characters analysed by Cairns (2001) (A and B), life history traits (C) and micromorphology/microstructure (D). Character states are represented by different colours as: —A. corallum shape (square): globular (grey square), conical (white square), colonial (black square); colony form (circle): plocoid (white circle), detached buds (very light grey circle), stoloniferous-reptoid (light grey circle), budding from common basal coenosteum (middle grey circle), arborescent (dark grey circle), non-solitary (black circle); budding type (star): non-solitary (white star), extratentacular (black star); septal arrangement (pentagon): Pourtalès plan in adult stage (white pentagon), normal (black pentagon). —B. synapticulotheca (square): hispid costae (white square), finely serrate ridges (grey square), granular costae (black square); epitheca (circle): absent (white circle), present (black circle); endotheca (star): absent (white circle), present (black star). —C. development of multiple mouths (square): colonial (white square), colonial or solitary (grey square), solitary (black square); symbiosis with zooxanthellae (circle): azooxanthellate (white circle), apozooxanthellate (grey circle), zooxanthellate (black circle); dispersal capability (star): free (white star), facultative (grey star), attached (black star); maximum calice diameter (number): 0–5 mm (1), 5–10 mm (2), 10–15 mm (3), 15–20 mm (4), 20–30 mm (5).

Unfaithful to the clade: polyphyly of some dendrophylliid genera and taxonomic considerations

Although molecular, micromorphological, macromorphological data and cnidocysts all point to the validity of the family Dendrophylliidae as a monophyletic entity, our molecular phylogeny reconstruction shows for the first time that some of the traditional dendrophylliid genera are polyphyletic in contrast to earlier findings (Kerr 2005: table 2). All the genera analysed with at least two species in our analyses, that is, *Balanophyllia*, *Cladopsammia*, *Dendrophyllia*, *Rhizopsammia* and *Turbinaria*, are not monophyletic (with the possible exception of *Heteropsammia*), and thus, our results suggest that they need taxonomic revision pending the inclusion of type species when possible (see further discussion) (Figs 2 and 8).

The genus *Balanophyllia* is the most speciose in the family Dendrophylliidae. It includes species characterized by solitary coralla which can be firmly attached through a polycyclic base, such as in the subgenus *Balanophyllia*, or they can be free-living with a monocyclic base, such as in the subgenus *Eupsammia* (Cairns 2001). Cairns (2001) gave a detailed review of the genus taxonomy and of the distinction, or lack thereof, by several authors between *Balanophyllia* and *Eupsammia*. He considered both as subgenera of *Balanophyllia* and in his phylogeny reconstruction the two are sister taxa (Cairns 2001; Fig. 2). The holotype of the type species of *Balanophyllia*, *B. calyculus* Wood, 1844, is a fossil specimen from the Pliocene of England, which could not be located and therefore Cairns (2001) designated as neotype a solitary and attached fossil specimen from near the type locality. The holotype of the type species of *Eupsammia*, *Madrepora trochiformis* Pallas, 1766, by subsequent designation (Milne Edwards and Haime, 1850), is a fossil coral from the middle Eocene (Lutetian) of France. In our study, we examined two extant species assigned by Cairns (2001) to the subgenus *Balanophyllia*, that is, *B.* (*B.*) *europaea* (Fig 9A–C) and *B.* (*B.*) *regia* (Fig. 9D–F), and one to *Eupsammia*, that is, *B.* (*E.*) *imperialis* (Fig. 9G–I). The genetic distance between these representatives of the two *Balanophyllia* subgenera is much larger than usually observed between congenerics, and the genus is also polyphyletic. Because the type species of both *Balanophyllia* and *Eupsammia* are extinct, a molecular approach to the resolution of their affinities is therefore formally not applicable. Hence, no taxonomic action can be undertaken unless additional representatives of both subgenera are examined genetically to examine their phylogenetic relationship.

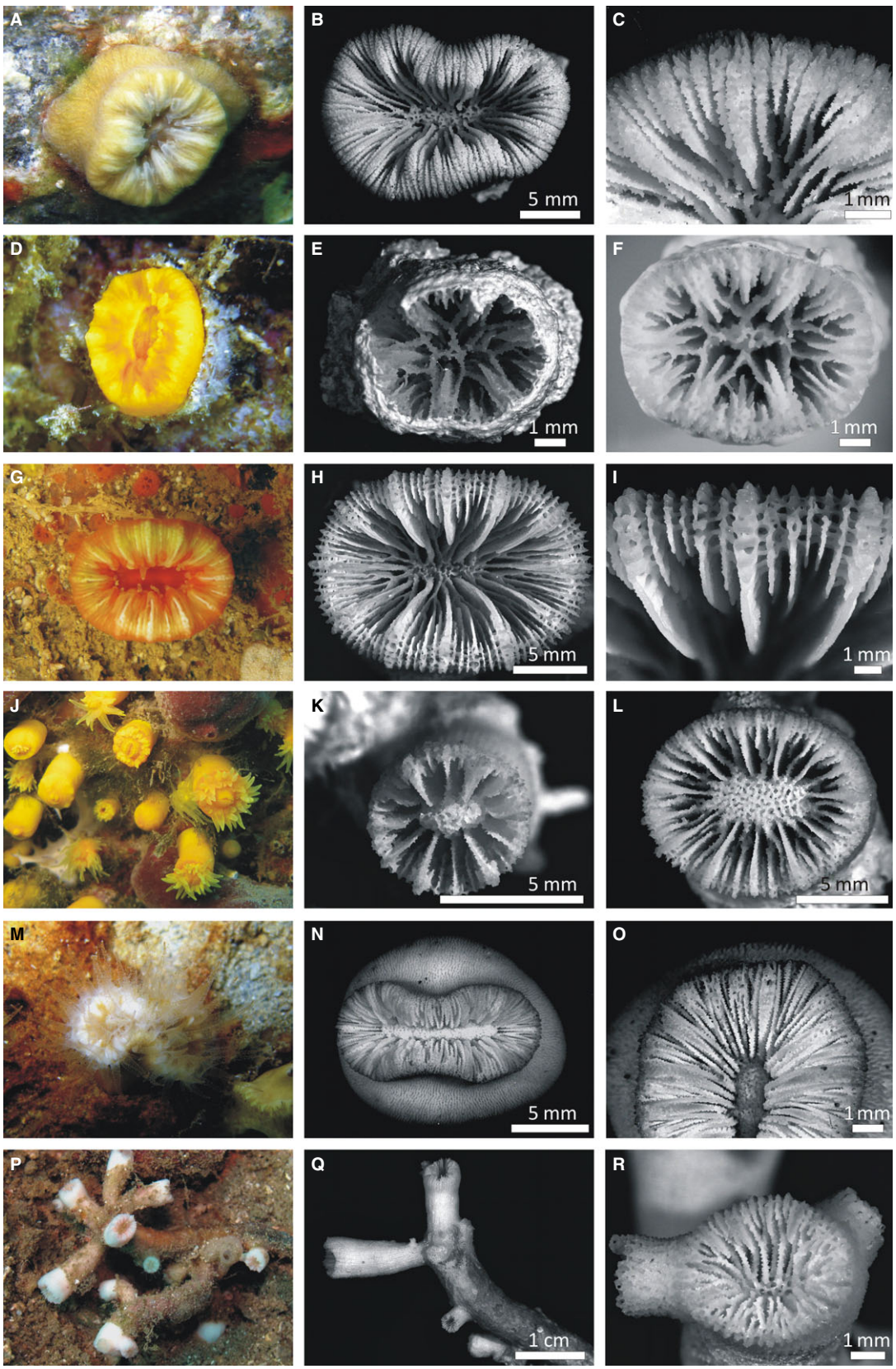
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Fig. 9 *In situ* and skeleton images of the Dendrophylliidae species examined in this study: *Balanophyllia* (*Balanophyllia*) *europaea* (A–C), *B.* (*B.*) *regia* (D–F), *B.* (*Eupsammia*) *imperialis* (G–I), *Leptopsammia pruvoti* (J–L), *Heteropsammia cochlea* (M–O), *Eguchipsammia serpentina* (P–R); —A. UNIMIB SOL4, Karistos, Greece, 2 m; —B. UNIMIB SOL2, top view of the calice; —C. detail of the septa of the same corallum in b; —D. UNIMIB SOL7, Karistos, Greece, 1 m; —E. UNIMIB SOL3; —F. top view of the calice of the same corallum as in d; g) IRD HS3312, Canal Woodin, New Caledonia, 30 m; —H. top view of the calice of the same corallum as in G; —I. detail of the septa of the same corallum as in G–H; —J. Paraggi, Italy, 20 m; —K. UNIMIB MD02, top view of the calice; —L. UNIMIB MD03, top view of the calice; —M. Ilot Brun, New Caledonia, 12 m; —N. UNIMIB NC688, top view of the calice; —O. detail of the septa of the same corallum as in N; —P. IRD HS3185, Cap Bocage, New Caledonia; —Q. IRD HS3134, view of the unattached corallum; —R. top view of a calice of the same specimen as in Q.

One characteristic of the genus *Cladopsammia* is a common basal coenosteum from which corallites bud at random (Cairns 2001) (shown by the white arrows in Fig. 10B, E). According to Cairns (2001), this character state is reached through a filling in of the substrate voids resulting from reptoid budding (shown by the white arrows in Fig. 10J, M), which is typical of the genus *Rhizopsammia*, a supposedly close relative of *Cladopsammia* (Cairns 2001; Fig. 2). Cairns (2001) indicated that "the corallite integration of *Cladopsammia* is intermediate between the stoloniferous/reptoid budding of *Rhizopsammia* [shown by the white arrows in Fig. 10J, M] and the upright branching of *Dendrophyllia*". The type species *Cladopsammia rolandi* Lacaze-Duthiers, 1897, known from the Holocene of Algeria and from the western Mediterranean (Zibrowius 1980), was not included in our analyses. We examined *C. eguchii* (Wells, 1982) from the Marquesas, French Polynesia (Fig. 10A–C), *C.* sp 1 from Japan (Fig. 10D–F) and *C. gracilis* (Milne Edwards and Haime, 1848) from Japan (Fig. 10G–I). While in our molecular analyses, *Cladopsammia* sp 1 and *C. eguchii* belong to the same clade together with the unattached *Eguchipsammia serpentina* (Fig. 9P–R) and the free-living *Heteropsammia cochlea* (Fig. 9M–O), *C. gracilis* is genetically undistinguishable from *Rhizopsammia verrilli* (Fig. 10M–O) and *R. wettsteini* (Fig. 10J–L), which all belong to a distant clade, thus the genus is not monophyletic. It is possible that we identified *R. verrilli* specimens showing a reduced reptoid budding as *C. gracilis*, because "a corallite of *R. verrilli* broken from its base could easily be mistaken for a species of *Balanophyllia* or a *Cladopsammia*" (Van der Horst 1922; Cairns & Zibrowius 1997: 189). It is also possible that the two nominal species have been used to identify specimens of the same species with more or less developed stolons (see *R. verrilli* variability *in situ* in Fenner 2005: 85; and in Hickman 2008: 50; and the morphological similarity with *C. gracilis* in Hickman 2008: 48). In fact, this feature can be very variable as we observed in the field and typically reptoid colonies occurring side by side with colonies devoid of stolons. Moreover, some highly stoloniferous specimens of *R. wettsteini* (Fig. 10J) and colonies of *R. verrilli* with reduced stolons (Fig. 10M) were genetically very closely related in our analyses (Fig. 2). Interestingly, the corallites of *C. gracilis* (Fig. 10I), *R. wettsteini* (Fig. 10K–L) and *R. verrilli* (Fig. 10N–O) are morphologically very similar and have the same septal arrangement and development and the same columella structure despite high intracalicular variability within the same colonies.

Species in the genus *Dendrophyllia* are colonial and grow in various ramose forms via extratentacular budding, while they originate from a single basal stem (Cairns 2001). We examined specimens of the deep-water Mediterranean species *D. cornigera* (Fig. 12D–F) from a canyon system off Spain (Gori *et al.* 2013) and of the shallow-water Indo-West Pacific species *D. arbuscula* Van der Horst 1922 from Japan (Fig. 12G–I), but we did not include the type species *D. ramea* (Linnaeus, 1758). In the present analysis, these two species were not recovered in the same clade. *D. cornigera* is closely related to the shallow-water solitary *Leptopsammia pruvoti* (Fig. 9J–L), also from the Mediterranean, while *D. arbuscula* belongs to the same clade as *Cladopsammia gracilis*, *Rhizopsammia verrilli* and *R. wettsteini* (Fig. 2). In spite of a similar ramose growth form originating from a single basal stem and the presence of a well-developed Pourtalès plan, the corallites of *D. cornigera* (Fig. 12E–F; Zibrowius 1980) and of *D. ramea* (Cairns 1991; Plate 11 h) present a higher number of septa and a more developed columella than the corallites of *D. arbuscula* (Fig. 12H–I) which are indeed similar to those of *C. gracilis*, *R. verrilli* and *R. wettsteini*, by having less septa organized in four cycles with septa of the first two being exsert (Fig. 10J, K–L, N–O) (Cairns & Zibrowius 1997).

The shallow-water, colonial and zooxanthellate genus *Turbinaria* consists of reef-dwelling species occurring in the Indo-Pacific. It can form colonies with growth forms ranging from encrusting to massive, foliose, vase-shaped and ramose (Figs 1F, 12M–S, 13). The species boundaries in this genus have troubled several authors, one of which was Bernard (1896) who attempted to revise the genus and described 58 nominal species, many of which were synonymized by other workers (Veron & Pichon 1980). Of the seven *Turbinaria* species examined in the present study, five have been described, namely *Turbinaria peltata*

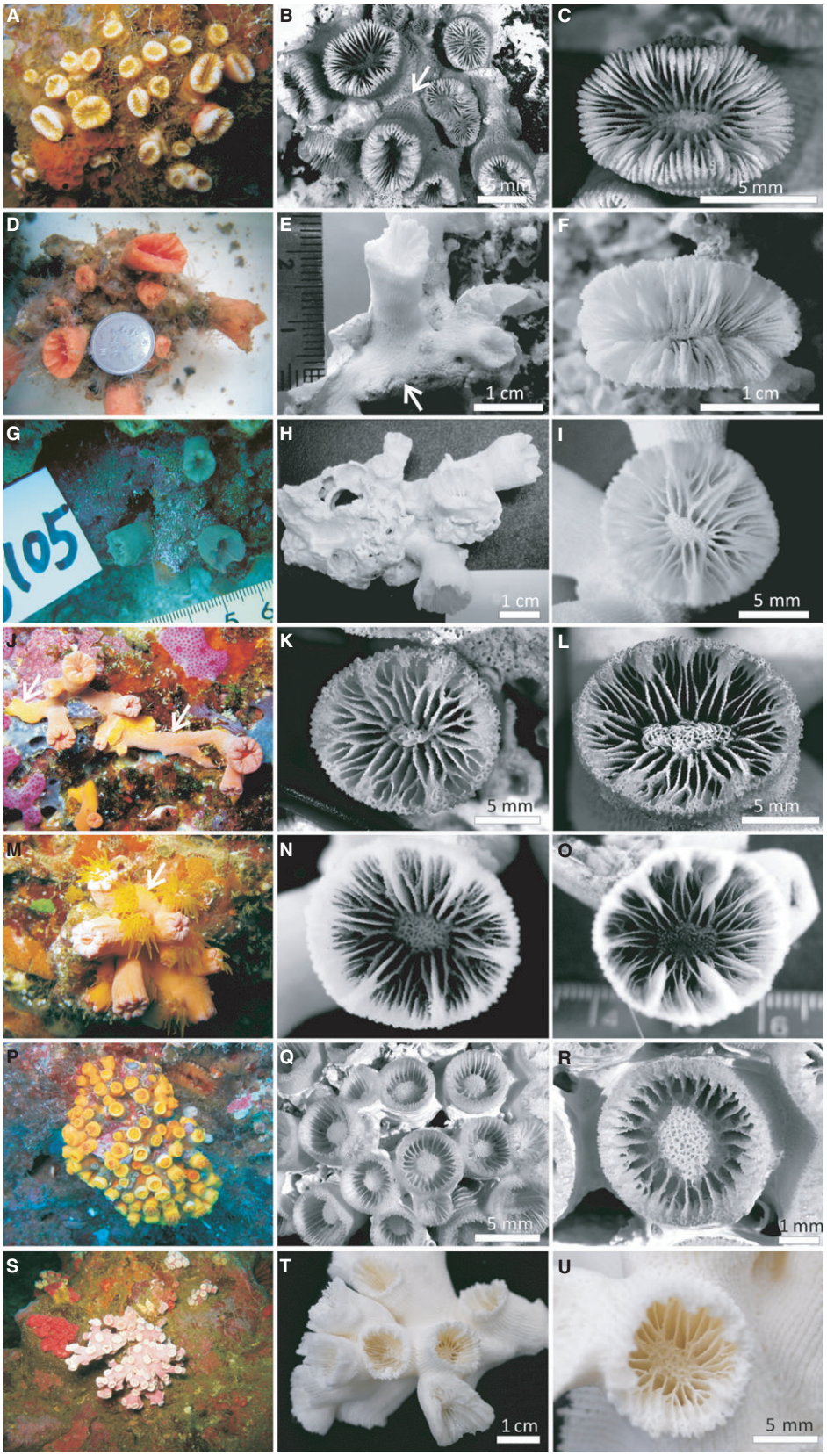
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Fig. 10 *In situ* and skeleton images of the Dendrophylliidae species examined in this study: *Cladopsammia eguchii* (A–C), *C.* sp 1 (D–F), *C. gracilis* (G–I), *Rhizopsammia wettsteini* (J–L), *R. verrilli* (M–O), *Astroides calycularis* (P–R) and *Dendrophyllia* sp 1 (S–U); —A. Eiao Island, Marquesas, French Polynesia, 15 m; —B. UNIMIB MQ155, top view of the corallum; —C. top view of a calice in the same specimen as in B; —D. AQ01, *in vivo* after collection, Japan, Shirahama; —E. corallum of the same specimen as in D; —F. top view of a calice of the same specimen as in D–E; —G. AO105, Japan, Amami-Oshima; —H. corallum of the same specimen as in G; —I. top view of a corallite of specimen SR26; —J. Five Rocks, Ari Atoll, Maldives, 18 m; —K. UNIMIB DJ247, top view of a corallite; —L. top view of a corallite of the same specimen as in K; —M. Nuku Hiva Island, Marquesas, French Polynesia, 25 m; —N. UNIMIB MQ035, top view of a corallite; —O. top view of a corallite of the same specimen as in N; —P. Capo Taormina, Sicily, Italy, 18 m; —Q. UNIMIB MED842, view of the corallum; —R. top view of a corallite of the same specimen as in Q. —S. RMNH Coel. 40085, Ngor Island, Senegal, 40 m (photograph by P. Wirtz); —T. view of the corallum; —U. top view of a corallite of the same specimen as in T. White arrows show coenosarc connecting polyps in *in situ* images and coenosteum connecting calices in skeleton images.

(Fig. 12M–P), *T. reniformis* Bernard 1896 (Fig. 12Q–S), *T. mesenterina* (Lamarck, 1816) (Fig. 12A–C), *T. heronensis* Wells, 1959 (Fig. 12D–G), and *T. patula* (Dana, 1846) (Fig. 13H–J), whereas two are undescribed species from New Caledonia characterized by very small corallites with a lamellar or granular columella, *Turbinaria* sp 1 (Fig. 13K–N) and *Turbinaria* sp 2 (Fig. 13O–R), respectively. While *Turbinaria peltata* is the sister species of *Duncanopsammia axifuga*, all the other *Turbinaria* species were well resolved in a monophyletic and distinctive clade, with the exception *T. mesenterina* and *T. reniformis*. Among these species, *T. peltata* can most easily be distinguished because of its larger corallites (Fig. 12N) and widest columella respective to calice diameter (Fig. 12O). Furthermore, its calices contain the highest number of septa, which are arranged in five cycles (Fig. 12O), the first four-ones being equal or subequal, and the fifth with a length less than ¼ of that of the others (Fig. 12P). Surprisingly, *T. peltata* does not show any partial fusion of its septa as in some of its congenerics (Fig. 13G, J), while its closest relative *D. axifuga* has its septa arranged in a very well-developed Pourtalés plan (Fig. 12L). The holotype of *Turbinaria*'s type species, *Madrepora crater* Pallas, 1766, is lost (Veron & Pichon 1980: 374). Bernard (1896) argued that the first illustration of the holotype was given by Esper (1797) and his opinion must "be taken as representing of the true *T. crater*". Bernard published an illustration of "a specimen" of this species (Plate 1) and of a corallite (Plate XXXIII 1). This specimen, he stated, "compares fairly well with Esper's drawings". The corallite in this drawing has less septa (18) and a smaller columella compared with the calice diameter than any specimen of *T. peltata* we examined or found in published illustrations (e.g. Veron & Pichon 1980; Figs 659–660). Moreover, if Esper (1797) did indeed illustrate the holotype of *T. crater* and after he described *T. peltata* (1794), it is likely that, given the fairly distinctive morphology of the latter, the two species are different. As *T. peltata* is not synomous with the type species of *Turbinaria*, it should be moved to the genus *Duncanopsammia*.

Comparison with previous phylogenies

Macromorphological characters traditionally used in the taxonomy of the Dendrophylliidae (Cairns 1984a, 1991, 1999, 2001, 2004; Hoeksema & Best 1991) are largely incongruent with our molecular data (Figs 2 and 8). Cairns (2001) provided a phylogenetic reconstruction of the Dendrophylliidae including 29 extant and extinct genera using 10 characters and 41 character states. Therefore, it is interesting to compare his comprehensive phylogeny reconstruction based on morphological and ecological characters with our partial one, which was obtained with nuclear and mitochondrial markers through a selection of only extant taxa. Plotting the morphological characters considered by Cairns (2001) on our molecular phylogeny reconstruction in Fig. 8 (only data for columella not shown) allows us to discuss the limitations of macromorphology for phylogenetic reconstructions in this family. In fact, none of the characters used by the Cairns (2001) is uniquely present in a molecularly defined clade (Fig. 2), including those that contributed highly to his phylogeny model, such as corallum shape, colony form, budding type and columella type. For example, species with a solitary corallum, considered an ancestral character state by Cairns (2001), are found in three different clades, and their sister taxa are all colonial. Admittedly, Cairns himself (2001: 9) considered the tree as "a preliminary attempt to assess evolutionary relationships among the genera and the phylogenetic value of various characters". The discrepancies between his reconstruction of phylogenetic relationships between dendrophylliid genera and ours, apart from his inclusion of more taxa, including extinct ones, and the polyphyletic status of most genera examined by us, lie in the clades.

A unique feature of the Dendrophylliidae worth discussing is the presence of the septal arrangement called Pourtalés plan, in which the higher/highest cycle septa (those most recently formed) are the shortest septa and the other cycles are often curved, with axial edges joined in pairs (Cairns 2001). The plan is present in the adult stage in some taxa (e.g. *Balanophyllia regia*: Fig. 9F), or only in early developmental stages in others, and can only

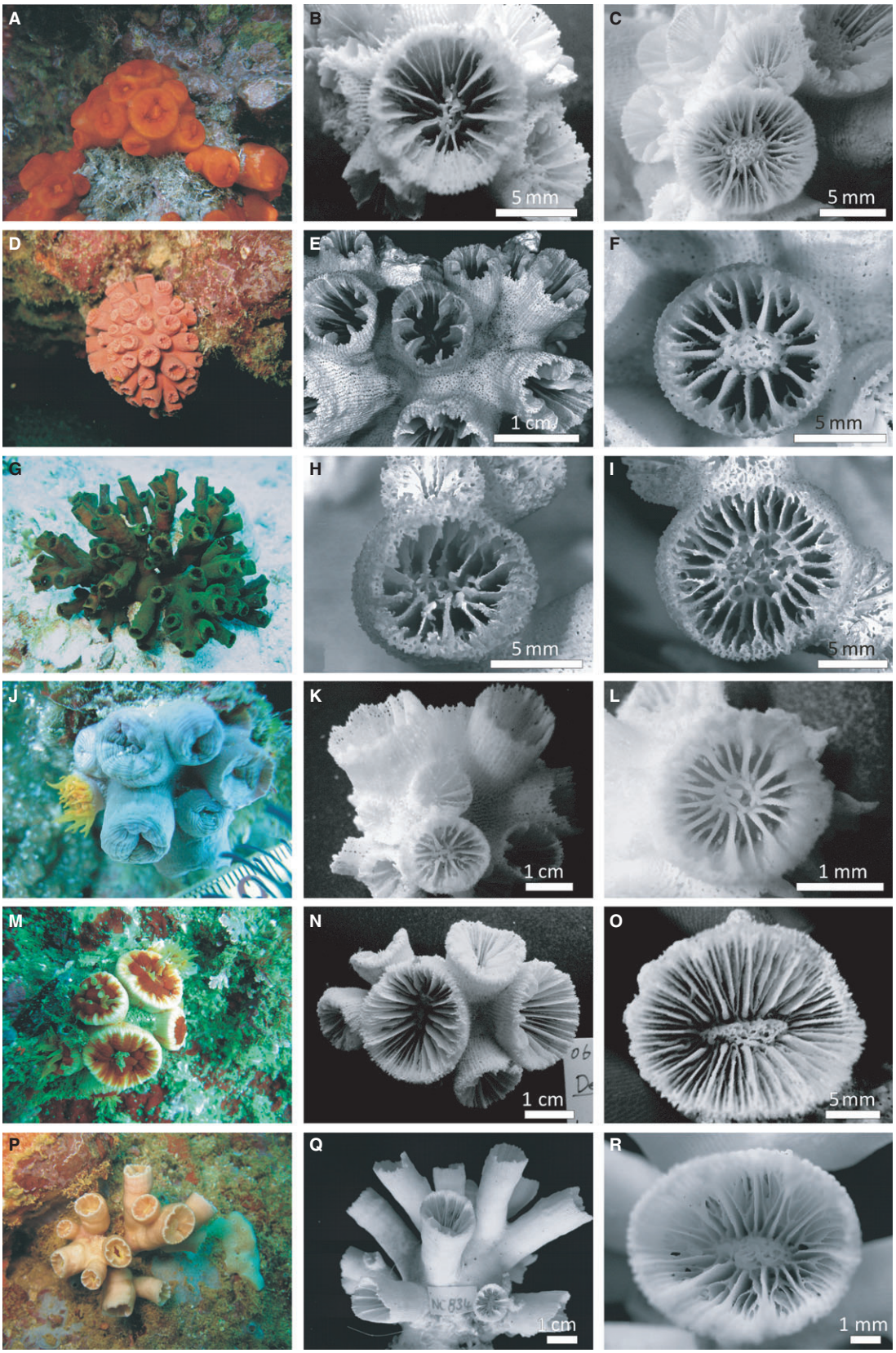
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Fig. 11 *In situ* and skeleton images of the Dendrophylliidae species examined in this study: *Tubastraea coccinea* (A–C), *T. aurea* (D–F), *T. micranthus* (G–I), *T. diaphana* (J–L), *Tubastraea* sp 3 (M–O), *Tubastraea* sp 1 (P–R); —A. SR144, Japan, Shirahama, 1 m; —B. top view of a corallite of the same specimen as in A; —C. top view of a corallite of the same specimen as in A–B showing typical Pourtalés Plan; —D. Bir Ali, Yemen, 10 m; —E. UNIMIB SO119; —F. UNIMIB M762, top view of a corallite; —G. Bir Ali, Yemen, 10 m; —H. UNIMIB Y756, top view of a corallite; —I. UNIMIB Y756, top view of a larger corallite from the same specimen as in h; —J. AO101, Japan, Amami-Oshima; —K. view of the corallum of the same specimen as in J; —L. top view of a corallite of the same specimen as in J–K; —M. KI3, Japan, Kii-Nagashima; —N. view of the corallum of the same specimen as in M; —O. top view of a corallite of the same specimen as in M–N; —P. IRD HS2884, Canal Woodin, New Caledonia, 20 m; —Q. IRD HS2883, side view of the corallum; —R. top view of a corallite of the same specimen as in Q.

partially be visible in others (e.g. *Turbinaria heronensis*: Fig. 13G). Cairns (1991) considered this a derived character state. The monophyletic genus *Tubastraea* is well represented in our analyses, by a total of seven species. All *Tubastraea* species (Fig. 11) group in a well-supported clade of a larger group, including also *Leptopsammia pruvoti*, *Dendrophyllia cornigera* and *Astroides calycularis*. This clade provides a good case for a discussion on the value of the Pourtalés plan as an informative character in the taxonomy and systematics of the Dendrophylliidae. Among the species of this clade, the septa of *D. cornigera* are clearly arranged according to the Pourtalés plan (Fig. 12F), whereas *L. pruvoti* and *A. calycularis* lack such a septal arrangement (Cairns 2001). However, based on the material examined in our study and specimens in the MNHN collected by H. Zibrowius, partial septal fusion is indeed visible in larger corallites of these two species, but without a fully developed Pourtalés plan (Figs 9L and 10R, respectively). This situation is even more remarkable in the genus *Tubastraea*, in which septa according to its diagnosis should be normally arranged with higher-cycle septa having most axial edges fused to lower-cycle septa but without Pourtalés plan (Cairns 2001). The within- and between-species variation of septal arrangement observed in the *Tubastraea* species analysed by us is, however, bewildering. In some species, absence of fusion of septa is indeed observed as expected (e.g. *Tubastraea* sp 1, Fig. 12C), while in others, like *T. micranthus*, partial fusion of septa is obvious in some corallites within the same colony (Fig. 11I) but not in others (Fig. 11H), whereas *Tubastraea* sp 1 has all septa arranged according to the Pourtalés plan (Fig. 11R). In series of virtual micro-CT sections of *T. micranthus* corallite (Fig. S5), one may observe that such partial, not clear fusion of septa can be consistent in whole ontogeny. Although the presence of the Pourtalés plan was used by some authors in the past to separate two subfamilies, this subdivision seems to be lacking any evolutionarily basis as already discussed by others. Therefore, the septal plan itself, although a distinctive character in the family, cannot be used for a reliable taxonomic revision of the genus *Tubastraea* (Fig. 11).

Micromorphological / microstructural support for the molecular clades

Traditionally, the number, size and distribution pattern of "calcification centres" (mineral deposits formed in fastest growing skeletal regions = rapid accretion deposits, RAD) is considered one of the main taxonomic criteria among scleractinian corals (Wells 1956; for review see also Stolarski & Roniewicz 2001). Indeed, several traditional scleractinian clades (families), which are also supported by molecular markers, show a distinct arrangement of septal and wall "calcification centres" (Stolarski 2000; Cuif *et al.* 2003; Benzoni *et al.* 2007; Budd & Stolarski 2009, 2011). Distinct microstructural features of dendrophylliid skeletons were described by Cuif *et al.* (2003) who included some dendrophylliid taxa (four species representing three genera: *Tubastraea micranthus*, *Balanophyllia* (*Balanophyllia*) *regia*, *B.* (*B.*) *europaea* and *Astroides calycularis*) in a combined molecular (28S rRNA) and morphological (microstructural) analysis of Scleractinia. Cuif *et al.* (2003: 465) noted that dendrophylliids (clustered into his clade "G") have calcification centres "less than 4–5 μm in diameter (they reach up to 25–30 μm in other families (...)), and are irregularly grouped in small clusters (...) instead of being simply circular patches as in other families". The same overall microstructural features as described by Cuif *et al.* (2003) were also found in all examined dendrophylliids of the present study: nanogranular-fibrous deposits of rapid accretion deposits (RADs) *ca.* 5 μm in diameter form clusters along the entire distal septal edge (e.g. Figs 3E, 4F, 5B, 6B, 7C, E) or occur on small septal teeth (e.g. Figs 3C, H, 4C, 5F). Consequently, the arrangement pattern of RADs, although distinct for dendrophylliids, does not allow to discriminate their clades (Table S2).

Several recent studies pointed out that the organization of thickening deposits (TD) is a valuable skeletal taxonomic character. For example, TDs in micrabaciids are composed of an irregular meshwork of fibre bundles oriented subparallel to the surface (Janiszewska *et al.* 2011; Stolarski *et al.* 2011), in gardineriids bundles of fibres form small, vesicular units (Stolarski *et al.* 2011), in many traditional caryophylliids the TDs consist of bundles of fibres running perpendicular to the skeletal surface, whereas in flabellids and

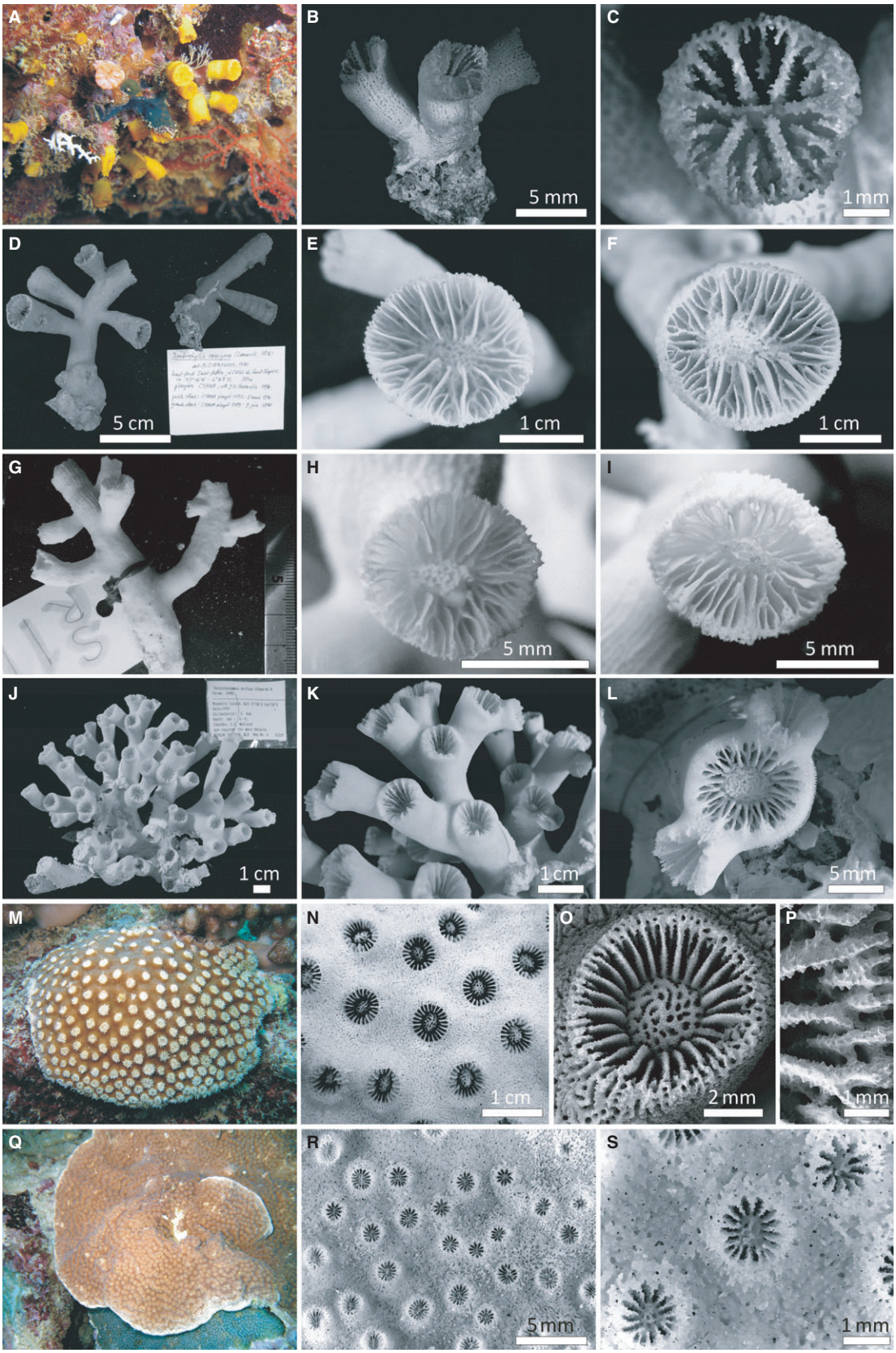
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Fig. 12 *In situ* and skeleton images of the Dendrophylliidae species examined in this study: *Tubastraea* sp 2 (A–C), *Dendrophyllia cornigera* (D–F), *D. arbuscula* (G–I), *Duncanopsammia axifuga* (J–L), *Turbinaria peltata* (M–P), *T. reniformis* (Q–S); —A. UNIMIB MY105, Mayotte Island, 3 m; —B. side view of the corallum of the same specimen as in A; —C. top view of a corallite of the same specimen as in A–B; —D. side view of a specimen identified by H. Zibrowius and donated to the MNHN (unregistered), Saint Julien, France, 90 m (coll. J.G. Harmelin 09/06/1990); —E. top view of a corallite of specimen identified by H. Zibrowius and donated to the MNHN (unregistered), Morocco Atlantic coast, 155 m (07/06/1924); —F. top view of a corallite of the same specimen as in E; —G. SR11, side view of the corallum; H) top view of a corallite of the same specimen as in G; —I. top view of a corallite of the same specimen as in H–G; —J. MTQ G 51519, Magnetic Island, Australia; —K. side view of part of a branch of the same colony as in J; —L. top view of a corallite of the same specimen as in J–K; —M. Socotra Island, Yemen, 14 m; —N. IRD HS2058, top view of the corallum surface; —O. SEM image of the top view of a corallite of the same specimen as in N; —P. SEM image of the top view septa of a corallite of the same specimen as in N–P; —Q. Bir Ali, Yemen, 8 m; —R. UNIMIB BA126, top view of the corallum surface; —S. detail of the corallites of the same specimen as in R.

acroporids, they show a microlaminar organization corresponding to the scale-like microtexture of their skeleton surfaces (Stolarski 2003; Nothdurft & Webb 2007; Kitahara *et al.* 2012a,b). In *Goniopora* (Fig. S4), which was used as outgroup in our analysis, TDs form undulated layers of fibres that correspond to a "Persian lamb" skeleton microtexture, which was not observed in the dendrophylliids of the present study. In dendrophylliids, fibres that thicken the skeleton (TD) form small patches, a few micrometre in diameter. Fibres within such patches are often arranged semiperpendicularly to the surface but never as consistently as in, for example, *Desmophyllum* (Przeniosło *et al.* 2008). Furthermore, in polarized light (see Fig. 3F), only rarely a complete light extinction of larger skeletal regions is visible, which would indicate a similar arrangement of axes of individual crystallographic domains. In *Tubastraea*, TD fibres form *ca.* 10-μm thick shingles, which are parallel to the skeleton surfaces (Fig. 7I, J–L, O). This feature can be a microstructural character potentially supporting the *Tubastraea* clade as a result of future analyses (Table S2).

Phylo-ecology based on life history traits

Phylo-ecological analyses, in which ecological traits are projected on phylogeny reconstructions as tools to compare ecological traits among closely related taxa, are rare, especially among reef corals with the ecologically diverse, monophyletic Fungiidae as example (Gittenberger *et al.* 2011; Hoeksema 2012a; Hoeksema *et al.* 2012). Likewise, the monophyletic Dendrophylliidae are also suitable for such an integrative research approach. Besides including shallow- and deep-water taxa (Fukami *et al.* 2008; Kitahara *et al.* 2010), the Dendrophylliidae are currently occurring in temperate and tropical waters where they display a remarkable variation of growth forms and ecological traits (Figs 1, 9–13). Various life history traits were plotted on the combined phylogenetic tree obtained in the present study, and their occurrence throughout the family is discussed.

Number of mouths (stomata): from solitary to colonial and back. The present phylogeny reconstruction of the Dendrophylliidae shows a character state transformation from solitary to colonial corals and reversals from multiple mouths to a single one. Barbeitos *et al.* (2010) included four solitary dendrophylliids and three colonial species (divided over two clades) in their study on coral coloniality, which also showed evolutionary developments from single mouths to more and vice versa. *Heteropsammia* sp. was considered solitary in their study, although large specimens of *H. cochlea* may actually show two mouths and *H. eupsammides* corals consistently grow multiple mouths (Hoeksema & Best 1991). The present study deals with 30 dendrophylliid species and confirms the conclusion by Barbeitos *et al.* (2010) that coloniality has been acquired and lost among the Dendrophylliidae. This differs from phylogeny reconstructions of the Fungiidae, which show various evolutionary developments from single towards multiple mouths by intra- or extrastomatal budding (10 times based on 52 species) but no reversals towards solitary forms (Hoeksema 1991a; Gittenberger *et al.* 2011; Benzoni *et al.* 2012b). In most other scleractinian families, reversals towards solitary growth forms appear to be uncommon, but those families were represented by less than 11 species and several of these families are polyphyletic (Barbeitos *et al.* 2010). In other anthozoan higher-order taxa, solitary growth forms are even more exceptional than among scleractinians and it is not always clear whether they are apomorph or plesiomorph. For example, *Sphenopus* spp. (Hexacorallia, Zoantharia, Sphenopidae) are anthozoans that feature solitary free-living polyps among other Zoantharia genera and families consisting of attached colonial forms (Reimer *et al.* 2012). As another example, Octocorals are known to be colonial, apart from the solitary species *Taiaroa tauhou* Bayer & Muzik 1976; the only species in the family Taiaroidae (Bayer & Muzik 1976). In comparison with their closest relatives, many of these rather exceptional solitary species have a relatively large polyp size in common.

Maximum calice diameter: does size matter?. The Dendrophylliidae show much variation in maximum calice size with small and large calices scattered over various clades (Table S3, Fig. 8). A possible advantage of many small polyps is unclear, except that in the event of partial damage of colonial corals, their regeneration is easy because the

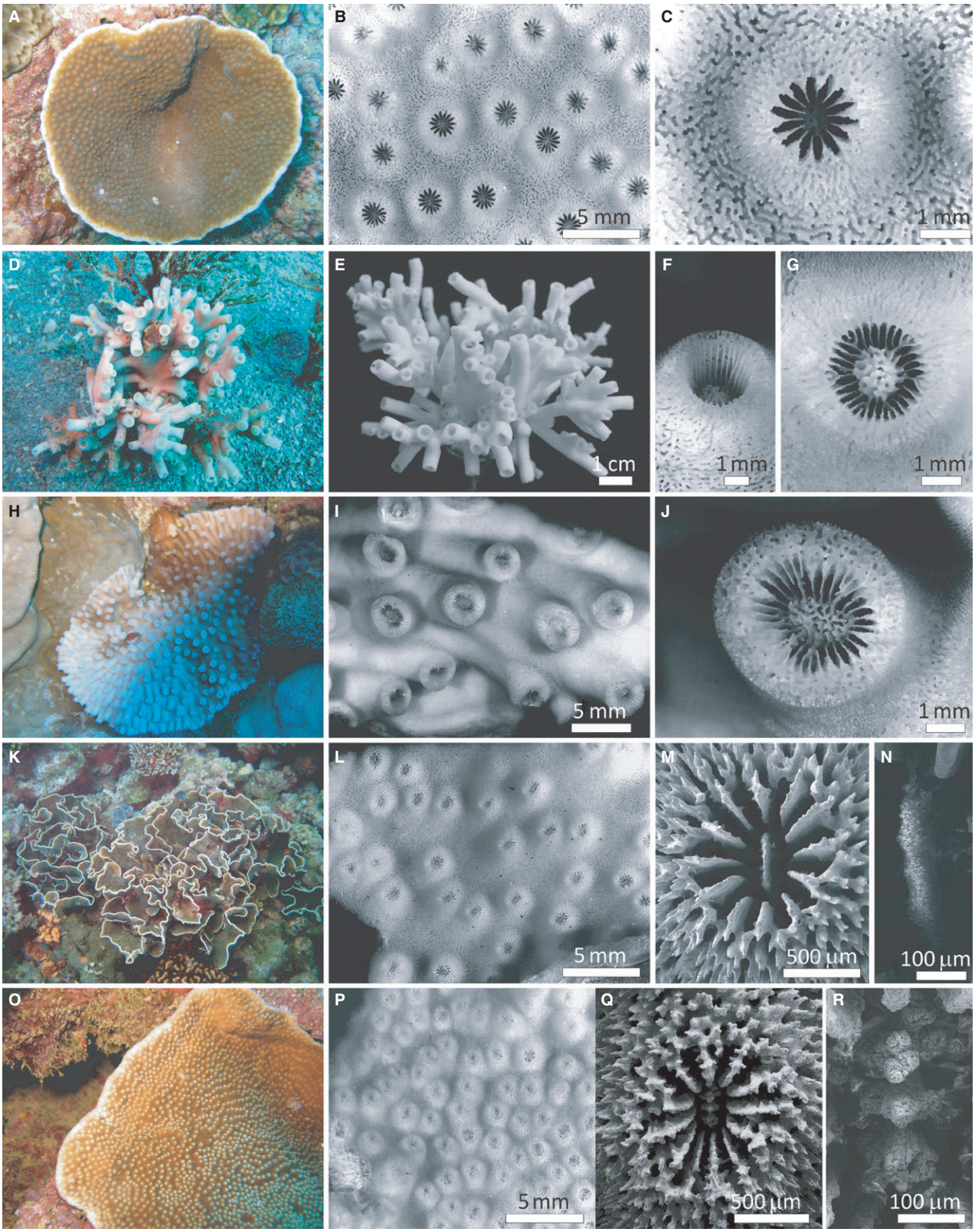
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Fig. 13 *In situ* and skeleton images of the Dendrophylliidae species examined in this study: *Turbinaria mesenterina* (A–C), *T. heronensis* (D–G), *T. patula* (H–J), *T.* sp 1 (K–N), *T.* sp 2 (O–R); —A. Bir Ali, Yemen, 8 m; —B. UNIMIB BA124, top view of the corallum surface; —C. top view of a corallite of the same specimen as in B; —D. IRD HS3024, New Caledonia, 8 m; —E. top view of the corallum of the same specimen as in F; —F. side view of a corallite of the same specimen as in D–E; —G. top view of the same corallite as in F; —H. IRD HS1835, New Caledonia; —I. top view of part of the corallum of the same specimen as in H; —J. top view of a corallite in the same specimen as in I; —K. IRD HS1775, Cap Goulevin, New Caledonia, 18 m; —L. top view of the corallum of the same specimen as in K; —M. SEM image of the top view of a corallite of the same specimen as in K–L; —N. detail of the columella of the same corallite as in M; —O. IRD HS1752, Côte Oubliée, New Caledonia; —P. top view of the corallum of the same specimen as in O; —Q. SEM image of the top view of a corallite of the same specimen as in O–P; —R. detail of the columella of the same corallite as in p.

remaining undisturbed calices may continue to grow and bud (Nugues & Roberts 2003). Among scleractinians in general, there is no clear relation between calice size and resistance to sedimentation (Erftemeijer *et al.* 2012), although a large polyp size in the Fungiidae has been observed to facilitate sediment shedding (Bongaerts *et al.* 2012). The shape of the calice outline may be more important, as oval polyps may shed sediments more easily than circular ones (Hoeksema 1991a; Goffredo *et al.* 2004, 2007, 2011). On the other hand, fungiids with large polyps may be more susceptible to the onset of bleaching than those with small ones because of their larger surface area (Hoeksema 1991b). But large polyps may also offer better opportunities for the capture of large prey, such as jellyfish and salps (Alamaru *et al.* 2009; Hoeksema & Waheed 2012). This may be advantageous for species without zooxanthellae that solely depend on food intake for their nutrition, and such species are common among the Dendrophylliidae (Cairns 2001). Finally, the maximum growth in dendrophylliid calices may also be determined by life history strategy and demography (Goffredo *et al.* 2004, 2010).

Symbiosis with zooxanthellae: dependence on light. Five of 17 dendrophylliid clades contain species that are zooxanthellate (Figs 1, 9–13). This is a distinct minority and in all of them, except *Turbinaria* species, the presence of zooxanthellae is clearly derived from an ancestral state without zooxanthellae. In the clades *Duncanopsammia* and *Turbinaria*, the presence of zooxanthellae is a synapomorphy, implying that the evolution towards becoming zooxanthellate was possible but not common among the Dendrophylliidae. The ancestors of the Dendrophylliidae were probably reef corals that lived in symbiosis with zooxanthellae (Barbeitos *et al.* 2010), like in the present *Turbinaria* clade. This suggests that other dendrophylliids lost this symbiosis and their dependence on sunlight as also shown by a cave-dwelling agariciid coral (Hoeksema 2012b).

Dispersal capacity moving around. One dendrophylliid clade consists of two free-living *Heteropsammia* species, which have obtained the capacity to shed sediments by use of their tentacles, mucus, ciliary tracts and body musculature (Fisk 1981). They can even free themselves from burial and move around on the sea floor with the help of a sipunculid worm living partly inside the corallum (Goreau & Yonge 1968; Fisk 1983; Hoeksema & Best 1991; Hoeksema 1993b). By a combination of derived traits (mobility, algal symbiont and relatively large calices), *Heteropsammia* corals are the most atypical dendrophylliids of all.

Conclusion

In the present paper, we have presented a first phylogeny reconstruction of the Dendrophylliidae, combining molecular and micromorphological analyses for a total of 30 species. The monophyly of the family is strongly supported by each of the two analyses, while most of the analysed genera are not monophyletic based on DNA sequences. Although macromorphological characters are often inconsistent with molecular data, several papers have demonstrated the utility of micromorphogical characters to understand evolutionary patters in scleractinian corals (Hoeksema 1989; Cuif *et al.* 2003; Benzoni *et al.* 2007; Budd & Stolarski 2009, 2011; Gittenberger *et al.* 2011; Stolarski *et al.* 2011; Budd *et al.* 2012; Kitahara *et al.* 2012a; Schmidt-Roach *et al.* 2014), except in *Deltocyathus magnificus* (Kitahara *et al.* 2012b). In the case of the Dendrophylliidae, we showed that microstructures failed to discriminate among the majority of molecular clades, with the notable exception of *Tubastraea*. Nevertheless, we strongly suggest more detailed microstructural and biogeochemical studies and, as top priority, the inclusion of as many as possible extant species within the next molecular phylogeny reconstruction because in our study only 20% of the total number of extant species was phylogenetically analysed. Further comprehensive integrative molecular and morphological phylogenetic analyses will be needed in order to add a broader spectrum of extant species, above all those from deep-water habitats, to a robust morphological tree, which would also help to clarify the phylogenetic position of extinct taxa.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Maximum parsimony tree based on COI data set. Numbers are bootstrap values. Values <50% are not shown.

Fig. S2. Maximum parsimony tree based on rDNA data set. Numbers are bootstrap values. Values <50% are not shown.

Fig. S3. Maximum parsimony tree based on IGR data set. Numbers are bootstrap values. Values <50% are not shown.

Fig. S4. Micromorphological and microstructural features of *Goniopora* sp, used as outgroup for the family Dendrophylliidae. Distal view of corallite (A) and two successive enlargements: (B) peripheral part of the corallite and palus showing "Persian lamb" microtexture and (C) enlargement of tip of the palus showing tubercles (yellow arrows) corresponding to rapid accretion deposits (RAD) in skeleton sections (yellow arrows in D). There is a distinct difference between relatively smooth tips of tubercles and "Persian lamb" texture of regions corresponding to thickening deposits (TD); D) broken and etched section of the skeleton showing RAD (hollowed-out spots marked with yellow arrows) and regularly banded and undulated TD. (A-D) UNIMIB Y698.

Fig. S5. Micro-CT 3D reconstructions (A–C) and virtual sections of the corallite of *Tubastraea micranthus* (D–T). Region from which 16 virtual sections were extracted is marked with arrows in C. Example of partial fusion of septa (arrow) can be consistently observed in ontogeny. (A–T) IRD HS3129.

Table S1. Specimens of Dendrophylliidae used in this study, each with corresponding collection code, identification, sampling locality, EMBL accession numbers and micromorphological/microstructural analysis information. * indicates type species. Museum abbreviations are as follows: UNIMIB University of Milano-Bicocca, Milano, Italy; MUFS University of Miyazaki, Departement of Fisheries Science, Miyazaki, Japan; IRD Institut de Recherche pour le Développement, Noumea, New Caledonia. [1] = CoralCal4 expedition (IRD), 2012; [2] = MLD IRD; [3] = Pakaihi o te Moana expedition (AAMP), 2011; [4] = CoralCal1 expedition (IRD), 2007; [5] = Tara Oceans expedition, Djibouti Leg, 2010; [6] = Tara Oceans expedition, Mayotte Leg, 2010; [6] = Yemen Scleractinia Biodiversity Project (Total E&P - Creocean - University of Milano-Bicocca), 2010; [7] = CoralCap expedition (IRD), 2007; [8] = CoralCal2 expedition (IRD), 2008; [9] = CoralCal3 expedition (IRD), 2009. Dash means no data.

Table S2. Micromorphological and microstructural characteristics of the Dendrophylliidae. Characters that seem distinct to representatives of molecularly distinguished clades are in bold.

Table S3. Size classes of maximum calice diameter measured in dendrophylliid species from clades analysed in the present study (Figs 2, 8): 1 = 0 < 5 mm, 2 = 5 < 10 mm, 3 = 10 < 15 mm, 4 = 15 < 20 mm, 5 = 20 < 30 mm.