Phylogenetic relationships and revision of the genus Blastomussa (Cnidaria: Anthozoa: Scleractinia) with description of a new species

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Phylogenetic relationships and revision of the genus *Blastomussa* (Cnidaria: Anthozoa: Scleractinia) with description of a new species

Francesca Benzoni[1*], Roberto Arrigoni[1], Zarinah Waheed[2], Fabrizio Stefani[3] & Bert W. Hoeksema[2]

Abstract. The Indo-Pacific coral genus *Blastomussa* (Cnidaria: Anthozoa: Scleractinia) includes three species, i.e., *B. merleti*, *B. wellsi*, and *B. loyae*. Following the re-examination of relevant type material, other museum specimens, and the study of newly sampled corals, the genus is revised and the new species *B. vivida* is described. The new species differs from its congeners by being encrusting, having coralla with a cerioid corallite arrangement and much larger corallites. In vivo, the expanded polyp mantle is fleshy and characterised by bright, vivid colours. Specimens were sampled in New Caledonia, northern Papua New Guinea, Sabah (northern Malaysia), Brunei Darussalam and the east coast of Peninsular Malaysia. Additional records from Southeast Asia and the western Pacific were obtained through the study of museum collections and published illustrations of living animals in situ: Japan, Vietnam, Indonesia, Philippines, and Australia. The new species appears widespread and has so far been misidentified as *B. wellsi*, which has smaller corallites, less septa, and a phaceloid corallite arrangement. The phylogenetic relationships within the genus *Blastomussa* and with other genera were investigated by analyses of their nuclear and mitochondrial DNA. These other genera are *Parasimplastrea*, *Plerogyra*, *Physogyra*, all currently incertae sedis in the Robust clade of Scleractinia as a result of molecular coral systematics, and *Nemenzophyllia*, whose phylogenetic position is examined for the first time. Representatives of all these genera are characterised by fleshy polyps with well-developed and expandable mantles. They are all closely related and form a strongly supported clade. The results of the molecular analyses provide evidence for *Blastomussa*'s monophyly and show that the new *B. vivida* is a distinct species, which is most closely related to *B. wellsi*. Furthermore, the only known extant species of the genus *Parasimplastrea* appears to be embedded within the *Blastomussa* clade, thus prompting its taxonomic revision. Because *Blastomussa* is closely related to the monospecific *Nemenzophyllia*, the affinities of their polyp and corallite morphology are discussed. Although polyp morphology and molecular data suggest that *Blastomussa*, *Plerogyra*, *Physogyra*, and *Nemenzophyllia* could constitute a new scleractinian family, the macro and micromorphology of their skeletons need to be examined before a family diagnosis can be formulated.

Key words. COI, rDNA, *Nemenzophyllia*, *Parasimplastrea*, *Plerogyra*, *Physogyra*

INTRODUCTION

Corals of the Indo-Pacific coral genus *Blastomussa* Wells, 1961 are popular in the aquarium trade because of their brightly coloured fleshy polyp mantle (Veron, 2000) and are therefore increasingly targeted by commercial harvesting (Green & Shirley, 1991; Lilley, 2001; Raymakers, 2001; Wabnitz et al., 2003; Jones, 2011). Three extant nominal *Blastomussa* species have been described so far and are currently considered valid: *B. merleti* (Wells, 1961), *B. wellsi* Wijsman-Best, 1973, both first described from New Caledonia, and *B. loyae* Head, 1978, from the Red Sea. Along with describing *B. loyae*, Head (1978) also revised the genus and placed his new species in the subgenus *Ceriomorpha* Head, 1978, which is characterised by a cerioid corallite arrangement (Head, 1978; Scheer & Pillai, 1983). Although *B. loyae* was synonymised with *B. merleti* (Sheppard & Sheppard, 1991; Veron, 2000), it was recently formally re-established (Kleemann & Baal, 2011).

Wells (1961) originally classified *Blastomussa*'s type species, *B. merleti*, in the genus *Bantamia* Yabe & Eguchi, 1943, which was considered closely related to *Galaxea* Oken, 1815, mainly owing to its smooth septa and fasciculate corallum. Then, based on the examination of new *B. merleti* specimens with strongly "lobulate" septa, he described the genus *Blastomussa* and assigned it to the family Mussidae Ortmann, 1890. Referring to the similarity of its septal dentation with that of *Cynarina* Brüggemann, 1877, he stated that "the mussid affiliation of *Blastomussa merleti* is scarcely to be doubted" (Wells, 1961: 276). Wijsman-Best (1973) realised that this new *Blastomussa* material actually belonged to a different species, which she described as *B. wellsi*. In his description of the genus, Wells (1961) also highlighted the extra-tentacular budding in *Blastomussa* as a distinguishing character from all the other mussid genera. Recent molecular analyses (Fukami et al., 2004, 2008; Arrigoni et al., 2012) and microstructural research (Budd & Stolarski, 2009, 2011)

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have led to the revision of the Mussidae (Budd et al., 2012). Consequently, the family is now only known from the Atlantic, while the once Indo-Pacific mussids now belong to the Lobophylliidae Dai & Horng, 2009. *Blastomussa*, however, is genetically distantly related to the rest of the Lobophylliidae (see Fukami et al., 2008; Arrigoni et al., 2012; Budd et al., 2012). It belongs to a distinct lineage together with *Plerogyra* Milne Edwards & Haime, 1848 and *Physogyra* Quelch, 1884 (see Fukami et al., 2008), and the poorly known genus *Parasimplastrea* Sheppard, 1985 (Arrigoni et al., 2012) and is currently considered to belong to the Plesiastreidae (see Dai & Horng, 2009) or incertae sedis (Budd et al., 2012). While similarities between the fleshy polyps of *Blastomussa* and *Parasimplastrea* were remarked on by various authors (Sheppard & Sheppard, 1991; Veron, 2000; Pichon et al., 2010), affinities of *Blastomussa* with *Plerogyra* and *Physogyra*, which are both characterised by polyps typically presenting "grape like" vesicles during the day and once placed in the Euphylliidae Milne Edwards, 1857, are less obvious. However, *Nemenzophyllia* Hodgson & Ross, 1981, another euphylliid genus that previously never was genetically analysed, has polyps that resemble large, inflated *Blastomussa* polyps (Veron, 2000).

Following the re-examination of the *Blastomussa* type specimens, museum material, and the study of newly sampled material, we observed a number of corals that have common distinctive morphological traits. These corals are here described as belonging to *Blastomussa vivida*, new species. We also revised the genus *Blastomussa*, here considered a senior synonym of *Parasimplastrea*, and discussed the validity of *B. omanensis* (Sheppard & Sheppard, 1991). Finally, we examined for the first time the phylogenetic relationships between *Blastomussa*, *Physogyra*, and *Plerogyra*, and the poorly studied genus *Nemenzophyllia* and compared their polyp and corallite morphologies.

MATERIAL AND METHODS

Sampling. Specimens of *Blastomussa wellsi* and *B. merleti* were collected from their type locality, New Caledonia, *B. loyae* from Djibouti, *B. omanensis* from Yemen, and *B. vivida*, new species, from New Caledonia, Papua New Guinea, Brunei Darussalam, Sabah (northern Borneo, Malaysia), and the east coast of Peninsular Malaysia. Specimens were photographed and collected while SCUBA diving. Digital images of living corals in the field were taken with a Canon Powershot G9 in an Ikelite underwater housing system in New Caledonia, Djibouti, Yemen, and Papua New Guinea, and with a Sea&Sea DX-2 camera system in Brunei and Malaysia. Coral specimens were collected, tagged, and preserved in absolute or 95% ethanol for further molecular analysis. Specimens from Djibouti were fixed in CHAOS solution (Sargent et al., 1986). After the sampling of fixed tissues for DNA extraction, each corallum was immersed in sodium hypochlorite for 48 hours to remove all soft parts, rinsed in freshwater and dried for microscope observation. Images of coral skeletons were taken with a Canon G5 digital camera and through a Leica M80 microscope equipped with a Leica IC80HD camera.

Abbreviations.

AIMS	Australian Institute of Marine Science, Townsville, Australia
BMNH	The Natural History Museum (formerly known as British Museum of Natural History), London, UK
CC1	IRD CoralCal1 Expedition, Côte Oubliée, New Caledonia, 2007
CC2	IRD CoralCal2 Expedition, Chesterfield-Bellona, 2008
CC4	IRD CoralCal4 Expedition, New Caledonia, 2012
ICZN	International Commission on Zoological Nomenclature
IRD	Institut de Recherche pour le Développement, Nouméa, New Caledonia
KAUST	King Abdullah University of Science and Technology, Thuwal, Saudi Arabia
MTQ	Museum of Tropical Queensland, Townsville, Australia
ORSTOM	Office de la Recherche Scientifique et Technique d'Outre-Mer, former name of the present IRD, Nouméa, New Caledonia
RMNH	Rijksmuseum van Natuurlijke Historie collection, Naturalis Biodiversity Center, Leiden, the Netherlands
TMPE	Tun Mustapha Park Expedition, 2012
TOE	Tara Ocean Expedition, 2009-2012
UBDM	Universiti Brunei Darussalam (Biology Department) Museum
UNIMIB	Università di Milano-Bicocca, Milan, Italy
USNM	Smithsonian Institution, National Museum of Natural History (formerly known as United States National Museum of Natural History, Washington, USA
WAM	Western Australian Museum, Perth, Australia
ZMA	Zoölogisch Museum Amsterdam collection Naturalis Biodiversity Center, Leiden, the Netherlands

In the list of examined material for IRD specimens the station number (ST) is provided, when available, after the sampling locality. Station numbers can be searched in the IRD online database LagPlon (http://lagplon.ird.nc/consultv2_5/rechSimple.faces) where additional details on the reef habitat, GPS coordinates, and a map of each station can be found.

DNA extraction and molecular analyses. Total DNA was extracted and purified from specimens fixed in ethanol using the DNAeasy® Tissue kit (QIAGEN, Qiagen Inc., Valencia, California, USA) reagents. For specimens fixed in CHAOS, DNA extraction was conducted using a phenol-chloroform based method with a phenol extraction buffer (100 mM Tris HCl pH 8, 10 mM EDTA, 0.1% SDS) (Sargent et al., 1986; Fukami et al., 2004). Two independent molecular markers, the mitochondrial cytochrome *c* oxidase subunit 1 gene and a portion of rDNA (including the complete sequences of ITS1, 5.8S, and ITS2, and a part of 18S and 28S), were sequenced to investigate evolutionary relationships of the genus *Blastomussa*. COI locus was amplified using MCOIF

Table 1. List of the collected specimens examined in this study for molecular analyses. For each specimen collection code, identification, COI and rDNA GenBank accession numbers, locality, and collector are indicated. B.W.H. = B.W. Hoeksema; F.B. = F. Benzoni; Z.W. = Z. Waheed.

Code	Genus and species	COI	rDNA	Locality	Coll.
UNIMIB BLA01	*Blastomussa vivida*	HF954183	HF954269	Brunei Darussalam	B.W.H.
UBDM.6.00003	*Blastomussa vivida*	HF954184	HF954270	Brunei Darussalam	B.W.H.
RMNH Coel. 40091	*Blastomussa vivida*	HF954185	HF954271	Brunei Darussalam	B.W.H.
TMP18	*Blastomussa vivida*	HF954186	HF954272	Northern Sabah, Malaysia	B.W.H.
LEM32	*Blastomussa vivida*	HF954187	HF954273	North Sulawesi	B.W.H.
PFB193	*Blastomussa vivida*	HF954188	HF954274	Papua New Guinea	F.B.
PFB241	*Blastomussa vivida*		HF954275	Papua New Guinea	F.B.
IRD HS3011	*Blastomussa wellsi*	HF954189	HF954276	New Caledonia	F.B.
IRD HS3250	*Blastomussa wellsi*	HF954190	HF954277	New Caledonia	F.B.
DJ050	*Blastomussa loyae*	HF954191	HF954278	Djibouti	F.B.
DJ150	*Blastomussa loyae*	HF954192	HF954279	Djibouti	F.B.
NT	*Nemenzophyllia turbida*	HF954193	HF954280	Eastern Sabah, Malaysia	Z.W.
LEM30	*Nemenzophyllia turbida*	HF954194	HF954281	North Sulawesi	B.W.H.
MY007	*Physogyra lichtensteini*	HF954195	HF954282	Mayotte	F.B.
MY006	*Plerogyra sinuosa*	HF954196	HF954283	Mayotte	F.B.
DJ273	*Plerogyra sinuosa*	HF954197	HF954284	Djibouti	F.B.

and MCOIR primers and the protocol proposed by Fukami et al. (2004). A fragment of rDNA was obtained using ITS4 (White et al., 1990) and A18S (Takabayashi et al., 1998) primers, following the protocol published by Benzoni et al. (2011). PCR products were purified and directly sequenced using an automated 3730xl DNA Analyzer (Applied Biosystem, Foster City, CA, USA). Sequences produced in this study have been deposited in EMBL, and accession numbers are listed in Table 1.

Nucleotide sequences were used to construct Maximum Parsimony (MP) and Bayesian Inference (BI) trees using PAUP* 4.0b10 (Swofford, 2003) and MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001), respectively. MP analysis was performed using heuristic search and TBR branch swapping algorithm. Support for nodes was assessed with the bootstrap confidence levels using 1000 replicates. The Akaike Information Criterion approach was used to select the model of DNA evolution that best fitted the data, as implemented in MrModeltest 2.3 (Nylander, 2004). The appropriate model of nucleotide substitution was HKY + G for COI gene and HKY + I + G for rDNA. BI trees were obtained with 1.5 million generations for COI (1 million for rDNA), saving a tree every 10 generations for both loci and discarding the first 37500 trees as burn-in for COI (25000 for rDNA).Tracer 1.5 (Drummond & Rambaut, 2007) was used to estimate the convergence of the runs.

For COI, the corallimorpharian *Ricordea florida* was selected as outgroup and it was aligned with newly obtained sequences of *Blastomussa*, *Nemenzophyllia*, *Physogyra*, and *Plerogyra* and sequences of the Euphylliidae (Complex clade) and other families from the Robust clade. For rDNA, *Pavona cactus* (Forskål, 1775), a representative of Complex clade (Fukami et al., 2008), was selected as outgroup and it was aligned with representatives of families from the Robust clade and with newly obtained sequences of *Blastomussa*, *Nemenzophyllia*, *Physogyra*, and *Plerogyra*.

TAXONOMY

Genus *Blastomussa* Wells, 1968

Blastomussa Wells, 1968; Chevalier, 1975; Veron & Pichon, 1980; Head, 1978; Veron, 2000
Ceriomorpha Head, 1978

Diagnosis. [adapted from Wells (1968) and Head (1978)] Solitary or colonial, colony formation by extra-tentacular budding from the periphery of the corallite. Colonies phaceloid, pseudo-cerioid, or cerioid and encrusting. Corallite wall septothecal, costate, epitheca well developed and extended until a few mm below the wall margin in phaceloid coralla. Septa composed of one or more fan systems each forming a lobate tooth, septal sides ornamented by fine granulations. Columella present, trabecular, from pronounced and showing bilateral arrangement of fused processes reduced to few granulate papillae. Endothecal dissepiments vesicular, inclined downward from the corallite wall. Polyps fleshy and brightly coloured, oral disc can have different colour from the rest of the animal, tentacles and/or mantle are extended at day time, often fluorescent. Mantle vesicles are present in daytime. In phaceloid colonies, polyps lack organic connection in adult stage.

Type species. *Bantamia merleti* Wells, 1961

Blastomussa merleti (Wells, 1961)
(Figs. 1A–C, 7A, 8A, 9A)

Bantamia merleti Wells, 1961, figs. 1–5
Not *Blastomussa merleti* sensu Wells, 1968, figs. 4–5
Blastomussa merleti — Chevalier, 1975: Pl. XXIX, fig. 6, pl. XXX, figs. 5–7; Head, 1978: fig. 1a; Veron & Pichon, 1980: figs. 392–394, 767; Scheer & Pillai: 1983, pl. 35 figs. 5–6, 10–11; Veron, 1986: figs. 1–3; Sheppard & Sheppard, 1991: figs. 113a–b;Veron, 2000 *partim*: Volume 3, pp. 4–5, figs. 2–4; Pichon et al.: 2010, p 222 figs. 1–3, p 223 figs. 4–5; Turak & DeVantier: 2011: 163; Kleemann & Baal, 2011: fig. 5
Blastomussa merletti — Claereboudt, 2006: p.209 fig. 1, p. 210, figs. 1–4, p. 211, figs. 1–4

Type material. Holotype (USNM 45390), Banc Gail, New Caledonia, coll. Y. Merlet, 30–40 m (Fig. 7A).

Other material. New Caledonia (USNM 83336), Banc Gail, coll. M. Best, 35 m; (IRD HS235), Banc Gail, ST0114, coll. P. Laboute, 30 July 1986, 26 m; (IRD HS1686), Ouinné, Côte Oubliée, ST1083, CC1, coll. F. Benzoni & G. Lasne, 26 March 2007, 15–35m; (IRD HS1850), Banc Gail, ST0114, CC1, coll. F. Benzoni & G. Lasne, 7 November 2007, 35m; (IRD HS2676), Prony Bay, Creek of the North Bay, ST0032, coll. G. Lasne, 9 June 2009, 12m; (RMNH Coel. 14035) South New Caledonia, unspecified locality, coll. ORSTOM, Nouméa. **Australia** (MTQ G 42930), Lizard Island, (14°40'S; 145°27'E), coll. J.E.N. Veron, 12–22 m; (MTQ G 70483), coll. J.E.N. Veron; (MTQ G AIMS 107:4, WAM 254–85), Houtman Abrolhos, coll. J. Veron.

Description. *Blastomussa merleti* forms phaceloid colonies by extra-tentacular budding (Fig. 1A). Corallites are regularly spaced. Corallites are round to oval and 5–7 mm in largest diameter (Figs. 1A, C, 7A). Three cycles of septa are present, the first two reach the columella and are equal or sub-equal as the first can be slightly thicker and more exsert (Figs. 1B, C). The third is reduced to less than $^1/_2$ to $^1/_3$ of the length of the first two (Fig. 1C). Septa are composed of one to three fan systems thus attaining smooth to dentate margins (Fig. 1B) (Chevalier, 1975: Fig. 204). Septal margins and sides finely granulated. Columella formed by trabecular processes from the inner margins of septa and by round papillae in the center. The papillae can be separated or fused to form a sub-lamellar structure in the middle of the columella (Figs. 1A, C, 7A) which gives it a quasi-bilateral symmetry (see also Chevalier, 1975, Fig. 211). Epitheca forms few millimeters below the margin of the corallite wall which bears costae (Fig. 1A).

Polyp tentacles retracted towards the oral disc during the day (Fig. 8A, 9A). Mantle vesicles smooth (Fig. 9A), polyp colours varying from light brown, or orange to bright red.

This species lives in semi-protected to protected environments and strives well in low light and high turbidity conditions.

Geographic distribution. This species has been recorded from the Red Sea, the Indian and western Pacific Ocean (see above mentioned references).

Blastomussa wellsi Wijsman-Best, 1973
(Figs. 1D–F, 7D, 8D, 9D)

Blastomussa merleti sensu Wells, 1968: figs. 4–5; Veron, 2000 partim: Vol. 3, pp. 4–5, fig. 2; Dai & Horng, 2009, p. 151
Blastomussa wellsi — Wijsman-Best, 1973: figs. 1–2; Chevalier: 1975, pl. XXIX, fig. 5, pl. XXXI, figs. 3–5; Head, 1978: fig. 1b; Veron & Pichon, 1980: figs. 395 and 769; Scheer & Pillai, 1983: pl. 35 figs. 7–8, 10–11; Veron, 1986: figs. 1, 3, 4; Veron, 2000: Volume 3, pp. 6–7, figs. 1–3, 6; Hoeksema & van Ofwegen, 2004; Dai & Horng, 2009: p. 152; Wallace et al., 2009: fig. 60

Type material. Holotype (ZMA Coel 6905), Grotte Merlet, Passe Kouaré, New Caledonia, coll. M. Wijsman-Best, 1968, 30–35 m (Fig. 7D). Paratypes (ZMA Coel 6906, 6907, 6908), Banc Gail, New Caledonia, coll. Y. Merlet, 30–35 m.

Other material. New Caledonia (USNM 83337), Nouméa, outer reef slope, coll. R. Catala Mar.1973, 50 m; (USNM 83338), Banc Gail, coll. R. Catala, 1962, 35 m; (USNM 83339), Banc Gail, coll. R. Catala, 35 m; (MTQ G 48384), coll. P Joannot, 17 November 1991; (IRD HS382), Ilôt N'Do, coll. J.L. Menou, 11 February 1987, 12 m; (IRD HS557), Canal Woodin, coll. P. Laboute, 5 October 1987, 4 m; (IRD HS569), Dumbéa, coll. P. Laboute, 23 October 1987, 40 m; (IRD HS646), Grotte Merlet, coll. P. Laboute, 23 September 1988, 22 m; (IRD HS647), Grotte Merlet, coll. P. Laboute, 23 September 1988, 20 m; (IRD HS899), Ile des Pins, coll. P. Laboute, 11 March 1989, 4 m; (IRD HS1307), Kouakoué, ST1062, CC1, coll. G. Lasne & F. Benzoni, 16 March 2007, 24 m; (IRD HS1368), Kouakoué, ST1063, CC1, coll. G. Lasne & F. Benzoni, 16 March 2007, 22 m; (IRD HS1661), N'Goé, Port Comboui, ST1079, CC1, coll. G. Lasne & F. Benzoni, 23 March 2007, 20 m; (IRD HS2111), Ilot Avon, Chesterfields, ST1161, CC2, coll. G. Lasne, J. Butscher & A. Gerbault, 13 July 2008, 25 m; (IRD HS2130), Bampton Reef, Chesterfields, ST1163, CC2, coll. G. Lasne, J. Butscher & A. Gerbault, 14 July 2008, 12 m; (IRD HS2630), Dumbéa, ST0041, coll. G. Lasne & F. Benzoni, 19 May 2009, 23 m; (RMNH Coel. 14041, 14042) South New Caledonia, unspecified locality, coll. ORSTOM, Nouméa. **Australia** (MTQ G 42934), Newcastle, (32°56'S; 151°46'E); (MTQ G 42949), Dewar Island, Murray Islands, (09°55'S; 144°05'E), 2–27 m; (MTQ G 42950), Fantome Island, Palm Islands, (18°41'S; 146°31'E), 15–20 m.

Description. *Blastomussa wellsi* forms phaceloid colonies by extra-tentacular budding (Figs. 1D, 7D). Although corallites are normally regularly spaced, recently budded ones can still have connections and coralla may be partially cerioid. Corallites are round to oval and 8–13 mm in largest diameter (Figs. 1D, 7D). Four cycles of septa are present, the first three reach the columella and are equal or sub-equal as the first can be slightly thicker, the third is reduced or incomplete (Figs. 1D, E, 7D). Septa are composed of multiple fan systems thus margins are lobed (Fig. 1E) (Chevalier, 1975, Fig. 213). Septal margins and sides finely granulated (Figs. 1E, F). Columella formed by trabecular processes from the inner margins of septa and by papillae in the center. The papillae are often fused to form a lamellar structure in the middle of the corallite, which gives the columella a bilateral symmetry (Figs. 1F, 7D). Epitheca forms a few mm below the margin of the corallite wall, which bears costae.

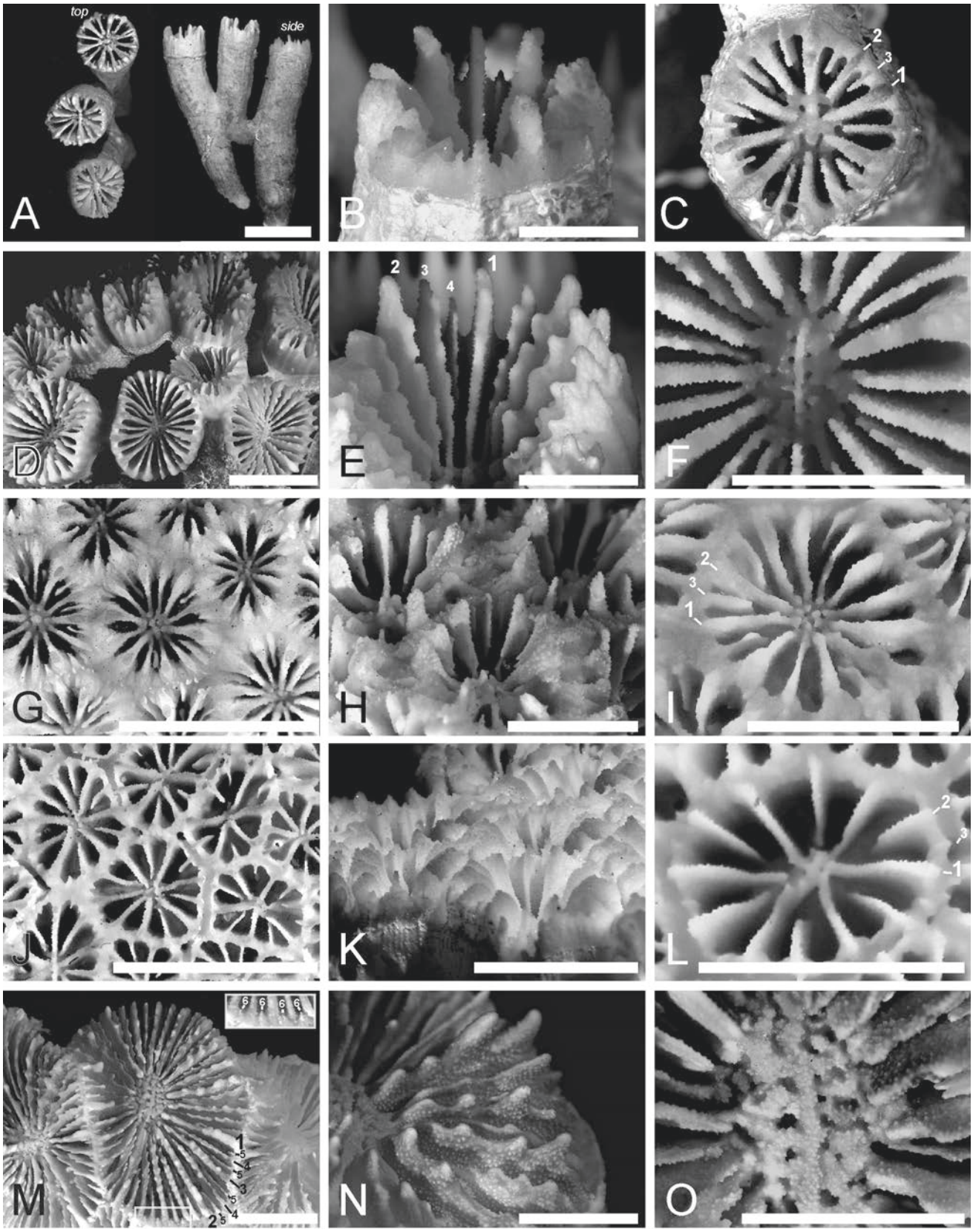

Fig. 1. Morphology of examined specimens, *Blastomussa merleti*: A, top and lateral view of typically phaceloid corallites (IRD HS3264); B, side view of a corallite of the same specimen; C, detail of a corallite (IRD HS1686). *B. wellsi*: D, corallite arrangement (IRD HS3011); E, side view of a corallite; F, columella of the same specimen. Morphology of examined specimens, *B. loyae*: G, cerioid corallites (UNIMIB DJ050); H, lateral view of the colony surface showing exsert septa devoid of dentation in the same specimen as in G; I, detail of a corallite *B. omanensis*: J, polygonal corallites showing the typical "groove and tubercule" appearance (UNIMIB MU094); K, side view of the same specimen as in J; L, detail of a corallite. Morphology of examined specimens, *B. vivida*, new species: M) ceriod corallites of a paratype (RMNH Coel. 40091; same specimen as in Fig. 2D); N, side view of septa of specimen IRD HS3000; O, columella of the same specimen. Scale bars A, D, G, J, M = 1 cm; B, C, E, F, H, I, K, L, N, O = 5 mm. Numbers 1–6 in front of the septa in C, E, I, L, and M indicate their cycle number.

Polyp tentacles retracted towards the oral disc during the day (Figs. 8D, 9D). Mantle vesicles rugged and sometimes of lighter colour (Fig. 9D), polyp colours ranging from light brown, or orange to bright red, and sometimes with green orals discs (Fig. 8D).

This species lives in wave-exposed environments. In New Caledonia it was only observed below 15 m deph in well-lit outer slopes.

Geographic distribution. This species has been recorded from the Red Sea, the Indian and western Pacific Ocean (see references mentioned above).

Blastomussa loyae Head, 1978
(Figs. 1G–I, 6C–F, 7B, 8B, 9B)

Blastomussa sp. Loya & Slobodkin, 1971
Blastomussa (Ceriomorpha) loyae Head, 1978: fig. 1 c–d
Blastomussa loyae — Scheer & Pillai, 1983: Pl. 35 figs. 9–11; Kleemann & Baal, 2011: figs. 1–4
Blastomussa merleti sensu Sheppard & Sheppard, 1991, fig. 113c
Parasimplastrea sheppardi Veron 2002 partim: Figs. 308 and 310
Not *Parasimplastrea sheppardi* Veron, 2000: Volume 3 p. 239; Veron 2002: figs. 309, 311

Type material. Holotype (BMNH 1977.5.5.1), Sudan, coll. S. Head, 5 m. Paratypes (BMNH 1977.5.5.2, 1977.5.5.3), Sudan, coll. S. Head; (ZMA Coel. 8322), Port Sudan, Sudan, coll. S. Head (Figs. 6E, F).

Other material. Egypt (MTQ G 55860), Sharm el Sheikh, 15 m (neotype of *Parasimplastrea sheppardi* Veron, 2000 designated herein (Figs. 6C, D); (MTQ G 70484), Sinai, coll. J.E.N. Veron; (MTQ G 70484), Sinai, coll. J.E.N. Veron; **Saudi Arabia** (BMNH unregistered), Jeddah, coll. C. Sheppard, October 1984; (KAUST SA005), Al Lith, Whale Shark Reef, (20°07.690'N; 40°12.513'E), coll. F. Benzoni, 2 March 2012, 20 m; (KAUST SA009), Al Lith, Shi'b Ammar, (19°34.242'N; 40°00.527'E) coll. F. Benzoni, 3 March 2013; (KAUST SA197), Farasan Banks, Marka Island, (18°12.534'N; 41°20.073'E) coll. F. Benzoni, 7 March 2013; (KAUST SA237), Farasan Banks, Shi'b Radib, (18°04.385'N; 40°53.154'E), coll. F. Benzoni, 8 March 2013; **Djibouti** TOE, coll. F. Benzoni (UNIMIB DJ018), North Gulf of Tadjoura, Ras Ali, (11°46.354'N; 42°57.286'E), 28 January 2010, 10 m; (UNIMIB DJ050), North Gulf of Tadjoura, Oblal, (11°51.680'N; 43°6.480'E), 28 January 2010, 8 m; (UNIMIB DJ150), Maskali Island, (11°42.349'N; 43°9.177'E), 31 January 2010, 12 m; (UNIMIB DJ197), Ankali, (11°43.590'N; 43 19.590'E), 2 February 2010, 18 m; (UNIMIB DJ242), North Gulf of Tadjoura, Obock, (11°57.517'N; 43°18.787'E), 3 February 2010.

Description. *Blastomussa loyae* forms encrusting coralla. Budding extra-tentacular, corallites attain a cerioid or sub-cerioid arrangement (Figs. 1G–I, 6C–F, 7B) by lack of separation of calices following the budding process, and, by secondary fusion, respectively, as described in detail by Head (1978). Corallites are round to oval and 5–8 mm in largest diameter (Figs. 1G–I, 6C–F). Three cycles of septa are present, the first two reach the columella and are equal or sub-equal as the first can be slightly thicker, the third is reduced or incomplete (Figs. 1G, I, 6D, F). Septa are composed of one fan system thus margins are smooth (Figs. 1H–I, 6D) (Kleemann & Baal, 2011). Occasionally, in larger calices more than one fan system can develop (Head, 1978). Septa typically exsert from the colony surface (Figs. 1H, 6D). Septal margins and sides finely granulated (Figs. 1H, I). Columella formed by trabecular processes, often fused at the base (Figs. 6F, 7B), with papillae visible at the centre and variably developed with the same corallum. In several of the examined specimens septa of the first and second cycle appear to be hollow (Fig. 7B).

Polyp tentacles retracted towards the oral disc during the day when the mantle is expanded (Figs. 8B, 9B). Because the cerioid corallites are close together, the mantle of adjacent polyps touch and become polygonal, giving the coral an overall plocoid appearance, which disappears as mantles retract (Fig. 8B). Vesicles smooth to slightly rugged (Fig. 9B). Colour varying from light to dark green, with vesicles often of a different colour, ranging from beige to brown.

This species lives in protected environments and strives well in low light and high-turbidity conditions.

Taxonomic remarks. Veron (2002) designated a coral from Egypt (Red Sea) (MTQ G 55860) as "holotype" for *Parasimplastrea sheppardi* (Fig. 6C, D). This designation is invalid because a holotype should have been introduced with the original description (ICZN, 2011). Therefore, this specimen is presently designated neotype of *P. sheppardi*, but because it belongs to *Blastomussa loyae* Head, 1978, *P. sheppardi* is a subjective junior synonym of the species.

Geographic distribution. *Blastomussa loyae* has been recorded in the Red Sea. Based on the material examined in the present study, the know range has been extended to the Gulf of Tadjoura.

Blastomussa omanensis (Sheppard & Sheppard, 1991)
(Figs. 1J–L, 6A–B, 7C, 8C, 9C)

Parasimplastrea omanensis — Sheppard, 1985 (nomen nudum)
Parasimplastrea omanensis Sheppard & Sheppard: 1991, fig. 147 (in synonymy of *Parasimplastrea simplicitexta*); Pichon et al.: 2010, figs. 1–4
Parasimplastrea simplicitexta Sheppard & Sheppard, 1991, fig. 147; not: Veron & Kelley, 1988 (partim): 49, fig. 16D. Not: *Goniastrea simplicitexta* Umbgrove, 1942; 35, pl. 12 fig. 5, pl. 13, Fig. 5
Parasimplastrea sheppardi Veron, 2000: Volume 3, p. 239, figs. 7–10; Moothien Pillai et al.: 2002, figs. 1–3; Veron, 2002 partim: figs. 309, 311; Claereboudt, 2006: figs. 1–6

Type material. Holotype of *B. omanensis* (BMNH 1991.6.4.150), Oman, Dhofar region, coll. C. Sheppard, 7 m (specimen illustrated in Sheppard & Sheppard, 1991, Fig. 147) (Figs. 6A, B), designation by monotypy.

Other material. Oman (USNM 81272), Muscat, coll. C. Sheppard; **Yemen** (UNIMIB BAL037), Gulf of Aden, Balhaf, (13°58.163'N; 48°10.928'E), coll. F. Benzoni, 6 March 2007, 14 m; (UNIMIB BAL212), Gulf of Aden, Balhaf, (13°58.402'N; 48°12.410'E), coll. F. Benzoni, 23 September 2007; (UNIMIB BAL230), Gulf of Aden, Balhaf, (13°50.4167'N; 48°10.5167'E), 23 September

2007; (UNIMIB Y571), Gulf of Aden, Balhaf, (13°58.163'N; 48°10.928'E), coll. F. Benzoni, 6 March 2007; (UNIMIB Y748), Gulf of Aden, Balhaf, (13°50.4167'N; 48°10.5167'E), coll. F. Benzoni, 13 March 2008; (UNIMIB MU094), Gulf of Aden, Al Mukallah, (14°31.067'N; 49°10.335'E), coll. F. Benzoni, M. Pichon & C. Riva, 18 March 2007; (UNIMIB MU160), Gulf of Aden, Al Mukallah, (14°30.793'N; 49°10.339'E), coll. F. Benzoni, M. Pichon & C. Riva, 20 March 2007; (UNIMIB MU205), Gulf of Aden, Al Mukallah, (14°31.477'N; 49°07.855'E), coll. F. Benzoni, M. Pichon & C. Riva, 21 March 2007; (UNIMIB BU016), Gulf of Aden, Burum, (14°19.710'N; 48°59.903'E), coll. F. Benzoni, M. Pichon & C. Riva, 22 March 2007; (UNIMIB SO010), Arabian Sea, Socotra Island, Deubhil, (12°36.279'N; 54°21.053'E), coll. F. Benzoni & A. Caragnano, 11 March 2010; (UNIMIB SO037), Arabian Sea, Socotra Island, Ras Adho, (12°38.638'N; 54°16.147'E) coll. F. Benzoni & A. Caragnano, 13 March 2010; (UNIMIB SO052), Arabian Sea, Socotra Island, Ras Adho, (12°38.672'N; 54°16.043'E), coll. F. Benzoni & A. Caragnano, 13 March 2010.

Description. *Blastomussa omanensis* forms encrusting subcerioid to cerioid coralla (Figs. 1J, L, 6A, B, 7C). Budding extra-tentacular, corallites are joined by secondary fusions, as described by Head (1978) for *B. loyae*, and the spaces between the partial fusions give the inter-corallite area a typical "groove and tubercule" appearance (Sheppard & Sheppard, 1991). In specimens with tightly packed corallites these are not visible and corallite walls appear fused. Corallites are irregularly polygonal and 4–7 mm in largest diameter (Figs. 1J, L, 6A, B, 7C). Three cycles of septa are present, the first is generally complete and reaches the columella, the second can be incomplete and of variable length, the third reduced or incomplete (Figs. 1J, L, 6A, B, 7C). Septa are composed of one fan system thus margins are smooth (Fig. 1L). Septa are only slightly and equally exsert from the colony surface (Fig. 1K). Septal margins and sides finely granulated (Figs. 1L). Columella formed by loose trabecular processes and few papillae, seldom fused at the base (Figs. 1L, 6B, 7C).

Polyp tentacles and mantle vesicles expanded during the day until the polyps are mechanically disturbed and become retracted (Fig. 8C). Mantle vesicles smooth but forming lobes (Fig. 9C). Tentacles and vesicles uniformly brown, tentacle tips round and white, oral disc green. In contrast to its congenerics, this species shows a remarkably consistent colouration among colonies

This species is found in the same protected habitats as *B. merleti* with which it can co-occur.

Taxonomic remark. *Blastomussa omanensis* (Sheppard & Sheppard, 1991) was originally presented as a nomen nudum in an unpublished report by Sheppard (1985). The species was formally redescribed by Sheppard & Sheppard (1991), who renamed it "*Parasimplastrea simplicitexta* (Umbgrove, 1939)" because they erroneously assumed *P. omanensis* to be a synonym of *Goniastrea simplicitexta* Umbgrove, 1942, based on remarks from J.E.N. Veron and J.W. Wells. Sheppard & Sheppard (1991) referred to *Parasimplastrea omanensis* in their synonymy of *P. simplicitexta* and they presented a photograph of a single coral (BMNH 1991.6.4.150) from Oman, which therefore became the holotype of *P. omanensis* by monotypy. *Goniastrea simplicitexta* was not described by Umbgrove in 1939, as mentioned by various authors (Sheppard & Sheppard, 1991; Veron 2000). However, in that year Umbgrove described *Simplastrea vesicularis* Umbgrove, 1939, which might have caused the confusion in the years. *P. simplicitexta* (Umbgrove, 1942) is a valid species, which differs from *P. omanensis* (see Veron, 2000, 2002) and is only known from fossil corals found in Indonesia and Papua New Guinea (Veron & Kelley, 1988). According to Budd et al. (2012: Table 1), *P. omanensis* is a synonym of *G. simplicitexta* but they do not give an explanation and do not mention the different view given by others (Veron & Kelley, 1988; Sheppard & Sheppard, 1991: Veron 2000, 2002). We maintain the name *Blastomussa omanensis* instead of *B. simplicitexta* because no arguments are given to support their synonymy.

Veron (2000: Volume 3, p. 239) gave a new name, *Parasimplastrea sheppardi*, to Sheppard & Sheppard's (1991) species and presented an unnumbered figure containing a black and white photograph of a coral skeleton without locality data and four colour photographs that were taken by others at Oman and Socotra Island. Hence, *P. sheppardi* Veron, 2000, became an objective junior synonym of *P. omanensis*. Veron (2000) did not designate a holotype, but the black and white photograph distinctly shows a specimen of *P. omanensis*, which could serve as lectotype but its whereabouts are unknown. In a subsequent publication, Veron (2002) explained why a new name was given: "The name *Parasimplastrea omanensis* cannot be used because there is no holotype associated with it". Instead of designating a neotype for *P. omanensis*, Veron (2002) designated a coral from Egypt (Red Sea) as "holotype" (= MTQ G 55860) for *Parasimplastrea sheppardi*. This designation is invalid because a holotype should have been introduced with the original description (ICZN, 2011). Therefore, this coral should be considered neotype of *P. sheppardi*. Because this specimen actually belongs to *Blastomussa loyae* Head, 1978, *P. sheppardi* is a subjective junior synonym of another species than intended by Veron. New names should only be given to species that have the same names as other species and when this homonymy would cause confusion (Hoeksema, 1993).

Geographic distribution. *Blastomussa omanensis* has been recorded in the northern Gulf of Aden, the Arabian Sea, and Mauritius (see references mentioned above).

***Blastomussa vivida*, new species,** Benzoni, Arrigoni & Hoeksema 2013
(Figs. 1M–O, 2, 3, 7E, 8E, 9E)

Blastomussa wellsi Veron & Pichon, 1980: fig. 768; Veron, 1986: Fig. 2; Veron, 2000: Vol. 3, pp. 6–7, Figs. 4–5; Hoeksema & van Ofwegen, 2004 *partim*; Wallace et al., 2009: Fig. 60A–B; Dai & Horng, 2009: 152; Turak & DeVantier, 2011: 163

Genus et Species nov.? Yabe et al., 1936, Pl. LII Fig. 2

Holotype. (MNHN IK 2012 14226), New Caledonia, Canal Woodin, ST332, coll. F. Benzoni & B.W. Hoeksema, 25 April 2012. IRD collection code HS3289 (Figs. 2A, C; 3A).

The holotype consists of 2 corallites unequal in size growing on a fragment of biogenic rock encrusted with crustose coralline algae and bored by bivalves. The larger corallite (c1 in Figs. 2A and 3A) measures 1.5 cm in diameter. Septa are arranged in 5 cycles (Fig. 2B). The first three are complete and reach the columella, those of the fourth are less developed and those of the fifth cycle are less than ½ of the others in length. First two cycle septa are thicker than the remainder (Figs. 2A–B). Septa composed of multiple fan systems, and margins are dentated (Figs. 2A–C) (Chevalier, 1975, Fig. 213). Septal margins and sides finely granulated (Figs. 2C). Part of the septa was broken when tissue was sampled for genetic analysis (Fig. 2B at the bottom of the corallite). Columella well-developed and formed by trabecular processes from the inner margins of septa and papillae (Fig. 2B). The smaller corallite (c2 in Figs. 2A, 3A), still in the process of budding, is oriented 45° in relation to the calice surface plane of c1. At the time of collection the polyps were reddish- brown (Fig. 3A).

Paratypes. (IRD HS3100), Banc de Touho, ST1466, CC4, coll. F. Benzoni & B.W. Hoeksema, 15 April 2012 (Fig. 2E); (RMNH Coel 40091), Brunei, Porter Patch, (04°53.55'N; 114°24.14'E), coll. B.W. Hoeksema, 28 April 2011 (Figs. 1M, 2D); (UBDM.6.00002), E Littledale Shoal, (05°06.11'N; 114°46.00'E), coll. B.W. Hoeksema, 27 April 2011 (Fig. 2F); (UBDM.6.00003), Hornet rock, (05°01.23'N; 114°43.90'E), coll. B.W. Hoeksema, 25 April 2011 (Fig. 2H).

Paratypes RMNH Coel 40091 and UBDM.6.00003 are made of more than one corallite (Figs. 2D and H, respectively), while IRD HS3100 and UBDM.6.00002 are made of one corallite (Figs. 2E and F, respectively). Both colonial coralla clearly show the extra-tentacular budding process. In all paratypes at least 6 cycles of dentated septa with finely granulated margins, and well-developed columella. Paratype RMNH Coel 40091 is made of 7 corallites, rather irregular in outline and 2–2.5 cm in diameter (Fig. 2D). The columella is well-developed and with the typical fusion of trabecular processes and papillae forming a lamellar structure giving the columella a bilateral fashion. The columella is finely granulated like the septal sides. Paratype UBDM.6.00003 is the fragment of a larger colony, and includes two complete corallites irregular in outline. In this specimen, septa of the first cycle are thicker than the remainder (Fig. 2H). Paratype IRD HS3100 is the largest corallite known in the type specimens for this species which is 2.8 cm in diameter (Fig. 2E). There are 7 cycles of septa with those of the first two cycles slightly thicker than the others. Part of the specimen broken when tissue was sampled for genetic analysis. The single corallite of paratype RMNH Coel 40092 was part of a corallum comprising at least two more corallites small parts of which are visible at the bottom of the specimen (Fig. 2F). Septa in this specimen are thinner septa than in any other examined specimen. These are arranged in 6 cycles with those of the first two cycles slightly thicker than the others.

Other material. New Caledonia (IRD HS3000), Canal Woodin, ST332, CC4, coll. F. Benzoni & B.W. Hoeksema, 25 April 2012 (Fig. 8E); (IRD HS3263) ST1481, CC4, coll. B. Hoeksema, 23 April 2012 (Fig. 3B); **Papua New Guinea** (UNIMIB PFB193), Sinub Island, (05°7.776'S; 145°48.804'E), coll. F. Benzoni, 15 November 2012; (UNIMIB PFB241), Wonad Island, (05°8.16'S; 145°49.194'E), coll. F. Benzoni, 17 November 2012; **Indonesia** (RMNH Coel. 33351), Bone Tambung, Spermonde Archipelago, South Sulawesi, (05°02'S; 119°16'E), coll. B.W. Hoeksema, 18 June 1997; (MTQ G 60836), Selat Namatote, West Papua, (03°48.9'S; 133°55.6'E), coll. E. Turak, 21 April 2006, 22–29 m; **Australia** (MTQ G 42939), Bullumbooroo Bay, Great Palm Islands, (18°46'S; 146°34'E), 2–15 m; **Japan** (MTQ AIMS Collection unregistered), Kushimoto, coll. J.E.N. Veron; (MTQ AIMS Collection unregistered), Tosashimizu, coll. J.E.N. Veron; **Philippines** (MTQ AIMS Collection unregistered), coll. J.E.N. Veron; **Vietnam** (MTQ AIMS Collection unregistered), coll. J.E.N. Veron; **Brunei** (UNIMIB BLA01), Abana Rock (05°06.48'N; 115°04.22'E), coll. B.W. Hoeksema, 23 April 2011; (RMNH Coel 40092), Hornet Rock (05°01.23'N; 114°43.90'E), coll. B.W. Hoeksema, 25 April 2011; **Malaysia: North Sabah, Banggi Islands**, TMPE, coll. B.W. Hoeksema (RMNH Coel. 40108), Sta. TMP36, Patanunan Island, (07°05.995'N; 117°05.3517'E), 19 September 2012, 8–29 m; (RMNH Coel. 40109), Sta. TMP41, Kalang, (06°59.8017'N; 117°03.2233'E), 18 September 2012, 10 m; (RMNH Coel. 40110), Sta. TMP16, SE Banggi Dangers, N Sibaliu, (07°11.5567'N; 117°23.6333'E), 11 September 2012, 15–16 m; (RMNH Coel. 40112), Sta. TMP37, Molleangan Besar Is., (07°05.12'N; 117°03.5633'E), 19 September 2012, 8 m; (RMNH Coel. 40113), Sta. TMP15, SE Banggi Dangers, N Sibaliu, (07°12.6917'N; 117°28.2283'E), 12 September 2012, 15 m; (RMNH Coel. 40114), Sta. TMP13, NW Tanjung Island, (07°05.6183'N; 117°16.13'E), 11 September 2012, 16 m; (RMNH Coel. 40115), Sta. TMP27, SW Mangsee Great Reef, (07°27.4133'N; 117°13.36'E), 22 September 2012, 15 m; (RMNH Coel. 40116), Sta. TMP38, W Carrington Reef, (07°07.8233'N; 117°13.6983'E), 20 September 2012, 23 m; (RMNH Coel. 40117), Sta. TMP37, Molleangan Besar Island, (07°05.12'N; 117°03.5633'E), 19 September 2012, 8 m; (RMNH Coel. 40118), Sta. TMP18, SW Bankanwan Reef, (07°11.3633'N; 117°17.6567'E), 12 September 2012, 14 m; **Malaysia: Peninsular Malaysia**, east coast, Tioman Island, coll. B.W. Hoeksema (RMNH Coel. 41517, 2 specimens) Sta. TIO-7, North Point (02°53'36"N; 104°09'26"E), 18 June 2013, 27–30 m: (RMNH Coel. 41518, colony 10 cm wide, largest calice 30 mm wide) Sta. TIO-12, east side, Tanjung Semanjin (02°48'41"N; 104°12'36"E), 19 June 2013, 18 m; (RMNH Coel. 41519, 2 specimens), Sta. TIO-16, southeast point, Tanjung Asah (02°43'13"N; 104°12'53″E), 22 June 2013, 20–25 m.

Skeletal variation. Overall, all examined coralla of *B. vivida*, new species, are formed by a variable though small number of corallites ranging between 1.5 and 2.8 mm (largest diameter). In some specimens, corallites, especially if newly formed, have septa of different cycles with the same thickness (Fig. 2E, F). However, in other specimens the first cycle can be visibly thicker and more exsert (Figs. 2A–C, G, H). Budding is mostly observed to happen sequentially (Figs. 2D, G). In some cases it can occur simultaneously around the first, and largest, corallite (Fig. 3D). Although the described bilateral fashion of the columella is very frequently observed, in some corallites only the trabecular processes can be observed (Figs. 2B, E, H). A number of colonial specimens have rounder and more regular corallites than the ones showed in Figure 2 (e.g., RMNH Coel. 33351).

Field characteristics. *Blastomussa vivida*, new species, can be solitary or form small colonies up to 10 cm long. The most striking characteristics in the field are the fleshy polyps and their colouration, which is usually bright orange to red (Fig. 3C–E), but can also be green to brown with contrasting oral discs (Fig. 3F), or nearly black (Fig. 3B). Mantle vesicles are well developed and rugged. This species lives in semi-protected to protected environments and it was often observed to grow on hard substrate covered in sediment.

Etymology. This species is named *vivida* (Latin, *vividus* = lively) after the typically flashy bright-coloured polyps.

Affinities. *Blastomussa vivida*, new species, is morphologically distinct from any other described species in the genus based on the combination of different characters including the primarily ceriod corallite organisation, large corallite size and high number of septa (the largest in the genus), and the development of a columella with a lamellar structure (Table 2). This species has so far been confused with *B. wellsi* (Veron & Pichon, 1980; Hoeksema & van Ofwegen, 2004; Wallace et al., 2009; Turak & DeVantier, 2011). The two species share the strongly dentated septa and a well-developed columella often attaining the above described bilateral structure. However, *B. vivida* can easily be told apart from *B. wellsi*, which has smaller corallites, a lower number of septa cycles, and a phaceloid corallite arrangement (Table 2).

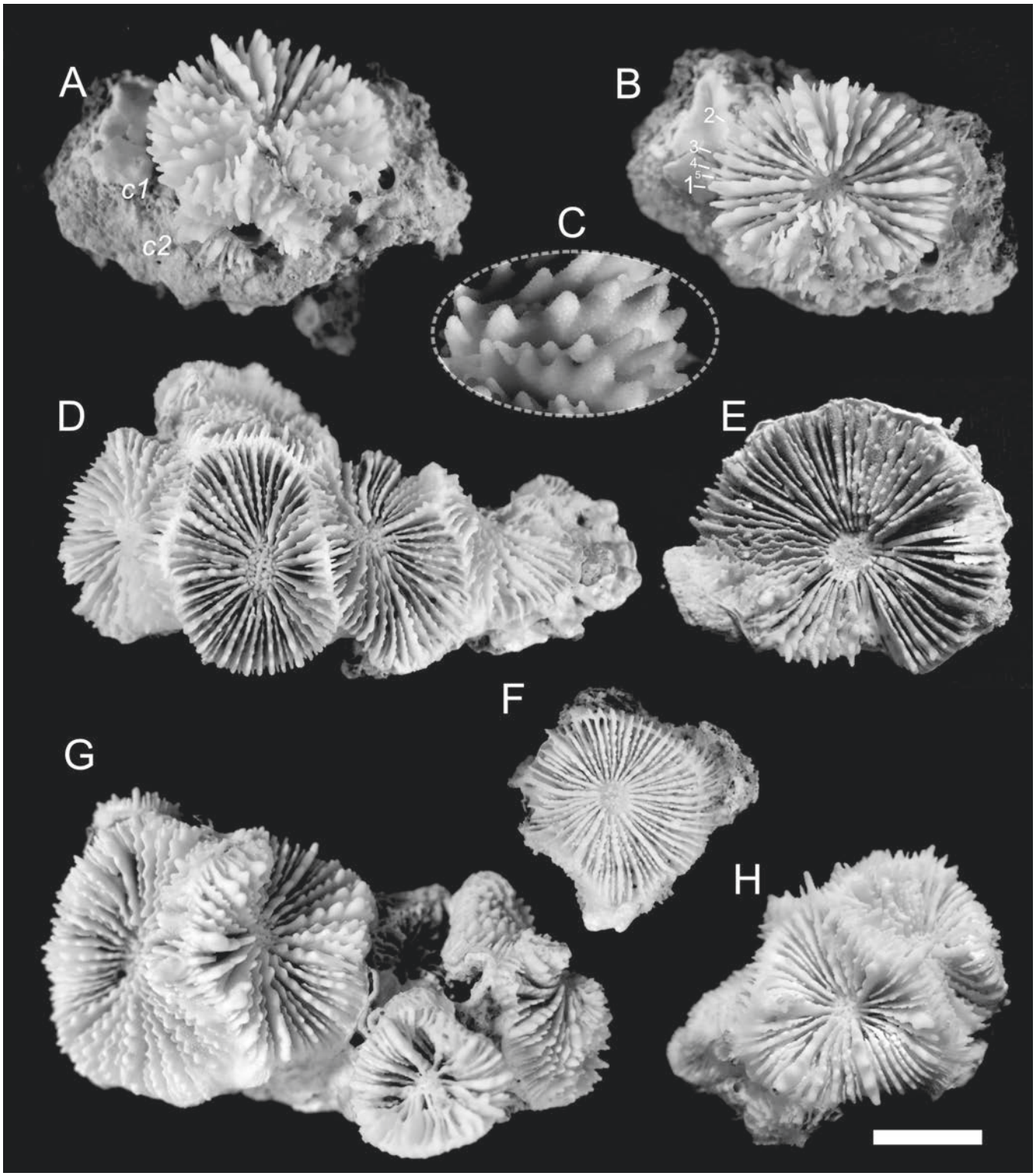

Fig. 2. *Blastomussa vivida*, new species: A, the holotype (MNHN IK 2012 14226) (c1 and c2 are the larger and the smaller corallite, respectively); B, top view of corallite c1 of the same specimen, numbers 1–5 in front of the septa their cycle number; C, detail of the same corallite as in A and B showing the dentation and granulation of the septa; D, paratype (RMNH Coel. 40091); E, paratype (IRD HS3100); F, UBDM 6.0003; G, RMNH Coel. 40092; H, UBDM 6.0002. Scale bar = 1 cm

Geographic distribution. The material listed in this study represents the known distribution of *Blastomussa vivida*, new species, which spans from New Caledonia and Australia in the south, Peninsular Malaysia in the west, and Japan in the north, including various localities in the Coral Triangle (for definition see Hoeksema, 2007; Veron et al. 2009).

MOLECULAR RESULTS

COI phylogeny. The alignment of COI sequences consisted of 609 bp, containing 281 invariable, 178 polymorphic and 158 parsimony informative sites. No indel sites were found.

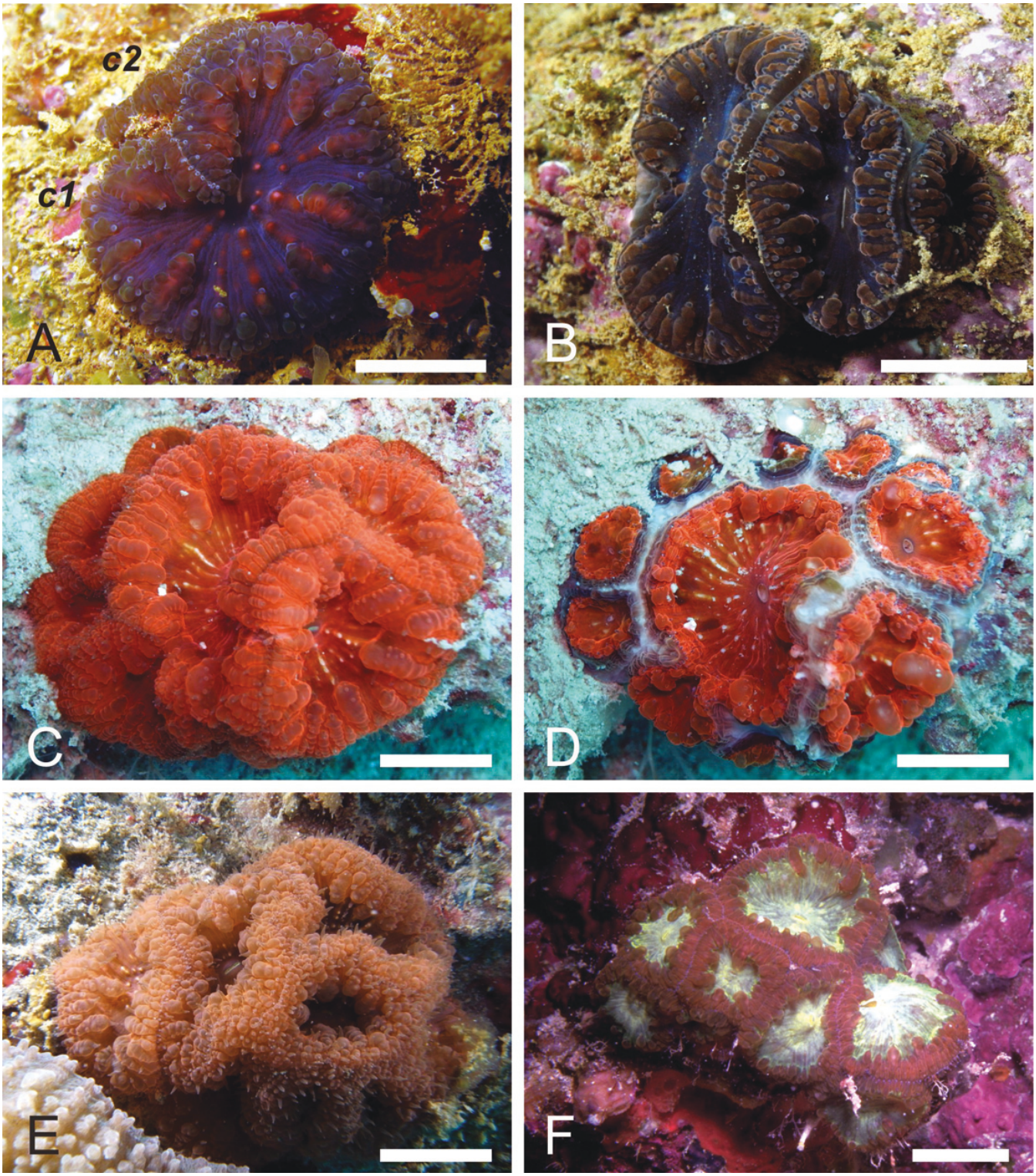

Fig. 3. *Blastomussa vivida*, new species in situ: A, holotype (MNHN IK 2012 14226) from New Caledonia (same specimen as in Figs. 2A–C); B, specimen IRD HS3100 from New Caledonia; C, colony from Kota Kinabalu, Malaysia showing the typically fleshy and bright coloured polyps; D, the same colony as in C with partially retracted polyps showing cerioid arrangement; E, specimen RMNH Coel. 40092 from Brunei (same specimen as in Fig. 2G); F, from Cebu, the Philippines. Scale bars = 1 cm

Table 2. Morphologic characters of *Blastomussa* spp.

	Corallite Diameter (mm)	Number of Cycles of Septa	Septal Margin	Columella	Corallite Arrangement	Corallite Outline
B. merleti	5–7	3	Variably dentated	Radial to bilateral	Phaceloid	Circular to oval
B. wellsi	9–13	4	Strongly dentated	Bilateral	Phaceloid	Circular to oval
B. loyae	4–8	3	Predominantly smooth	Radial to bilateral	Pseudo-cerioid and cerioid	Circular to oval
B. omanensis	4–7	3	Smooth	Poorly developed	Pseudo-cerioid with visible pits	Irregularly polygonal
B. vivida	10–25	5–6	Strongly dentated	Bilateral	Solitary or cerioid	Circular to irregular

MP and BI analyses yielded trees with very similar topologies, thus we reported BI phylogeny with Bayesian posterior probability scores (Pp) and MP bootstrap support (Bs) in figure 4. *Euphyllia* Dana, 1846, the type genus of the Euphylliidae (Complex clade), clusters together with *Ctenella* Matthai, 1928 and *Galaxea* Milne Edwards, 1857 (Fukami et al., 2008; Budd et al., 2012) and these are highly divergent from *Nemenzophyllia*, *Plerogyra*, and *Physogyra*. Within the robust corals, several families are well resolved, such as the Mussidae in which *Blastomussa* was firstly described. Nevertheless, *Blastomussa* is highly divergent from the Mussidae and also from the Lobophylliidae (Fukami et al., 2008; Arrigoni et al., 2012). The five *Blastomussa* species, i.e., *B. vivida*, *B. wellsi*, *B. merleti*, *B. loyae*, and *B. omanensis* form a strongly supported group (Pp = 100, Bs = 100). Two main subclades are evidenced in this clade, one contains *B. vivida* and *B. wellsi*, while the second one includes *B. merleti*, *B. loyae*, and *B. omanensis* (Fig. 4). Despite a low evolution rate of COI in scleractinian corals (Huang et al., 2008), *B. vivida* forms a monophyletic group (Pp = 99, Bs = 65), separated from *B. wellsi* which is instead unresolved. Nevertheless, *B. merleti*, *B. loyae*, and *B. omanensis* share the same haplotype and thus they are unresolved within a well-supported clade (Pp = 100, Bs = 100). The sister group of the *Blastomussa* clade includes *Nemenzophyllia turbida*, which is highly divergent from the Euphylliidae and closely related to *Plerogyra* and *Physogyra*. As shown in Fukami et al. (2008), Benzoni et al. (2011), Arrigoni et al. (2012), Huang (2012), and Huang & Roy (2013), *Plesiastrea versipora* (Lamarck, 1816), *Cyathelia axillaris* (Ellis & Solander, 1786), and *Trochocyathus efateensis* Cairns, 1999 cluster together in a well-supported clade (Pp = 77, Bs = 100) and represent the sister group of *Blastomussa*, *Parasimplastrea*, *Nemenzophyllia*, *Plerogyra*, and *Physogyra* (Fig. 4).

rDNA phylogeny. The alignment of rDNA sequences consisted of 826 bp, containing 289 invariable, 145 polymorphic and 117 parsimony informative sites. 345 indel sites were found and they were treated as a fifth character in phylogenetic analyses.

MP and BI analyses produced congruent trees (Fig. 5) concordant with the COI phylogeny (Fig. 4). All specimens of *B. vivida* cluster together in a well-supported group (Pp = 100, Bs = 100) and they are closely related to, but clearly separated from, *B. wellsi*, in congruence with the COI phylogeny (Fig. 4). This is also highlighted by the genetic distance between the two species, 3.2% ± 0.9 s.d. (uncorrected *p*-distances). The monophyly of *B. vivida* and *B. wellsi* is highly supported (Pp = 100, Bs = 100 for both *B. vivida* and *B. wellsi*), while the species boundaries between *B. loyae*, and *P. omanensis*, closely related to *B. merleti*, remain unclear on the basis of the examined rDNA locus. These three species are very closely related showing low interspecific DNA distances, i.e., 0.6% ± 0.3 s.d. between *B. merleti* and *B. loyae,* 0.7% ± 0.3 s.d. between *B. merleti* and *P. omanensis*, 0.5% ± 0.2 s.d. between *B. loyae* and *P. omanensis*. The sister taxon of these five species is *Nemenzophyllia turbida*, which is more divergent with a mean genetic distance from the *Blastomussa* clade of 13.8% ± 1.7 s.d. (varying from a minimum value of 12.3% ± 1.9 s.d. with *B. wellsi* and 16.1% ± 2.2 s.d. with *B. loyae*). *Plerogyra sinuosa* and *Physogyra lichtensteini* are basal to *Blastomussa* and *Nemenzophyllia*, as also shown in the mitochondrial phylogeny (Fig. 4).

DISCUSSION

Concordant morphologic and genetic data indicate that *Blastomussa vivida* is a distinct species on the basis of the size and arrangement of corallites, the number of septa, and its rDNA and COI phylogeny. The species is currently known from New Caledonia, eastern Australia, Japan, Brunei, Peninsular Malaysia, and from various localities in the Coral Triangle (see Hoeksema, 2007; Veron et al. 2009), and has been represented in museum collections but has thus far been confused with the similar-looking and genetically closely related *B. wellsi*. The latter seldom shows fusion of the corallite walls and forms phaceloid colonies, whereas walls in examined *B. vivida* specimens are fused between adjacent corallites (cerioid arrangement), in some colonies only partially and in others completely. However, so far any *Blastomussa* specimen with larger corallites than *B. merleti* was identified as *B. wellsi* despite these differences.

A search hit in Google images for *B. wellsi* (4 February 2014) provided many pages actually showing *B. vivida* as an aquarists' pet, thus suggesting that while the former species is less common in the aquarium trade, *B. vivida*

could be subjected to harvesting pressure (Jones, 2011). The morphologic and molecular investigations provided several novel results on the phylogenetic relationships among various *Blastomussa* species and between this genus and the genera *Parasimplastrea*, *Nemenzophyllia*, *Plerogyra*, and *Physogyra*, which have led us to undertake taxonomic actions that are discussed in detail hereafter.

Phylogenetic relationships between *Blastomussa* species and their taxonomy. Arrigoni et al. (2012) showed that *B. omanensis* and *B. merleti* are genetically indistinguishable using rDNA and COI. Despite a cerioid vs. phaceloid arrangement, they are otherwise morphologically similar, though well distinct, both in terms of polyp (Fig. 8) and corallite (Fig. 7) morphology (Sheppard & Sheppard, 1991;

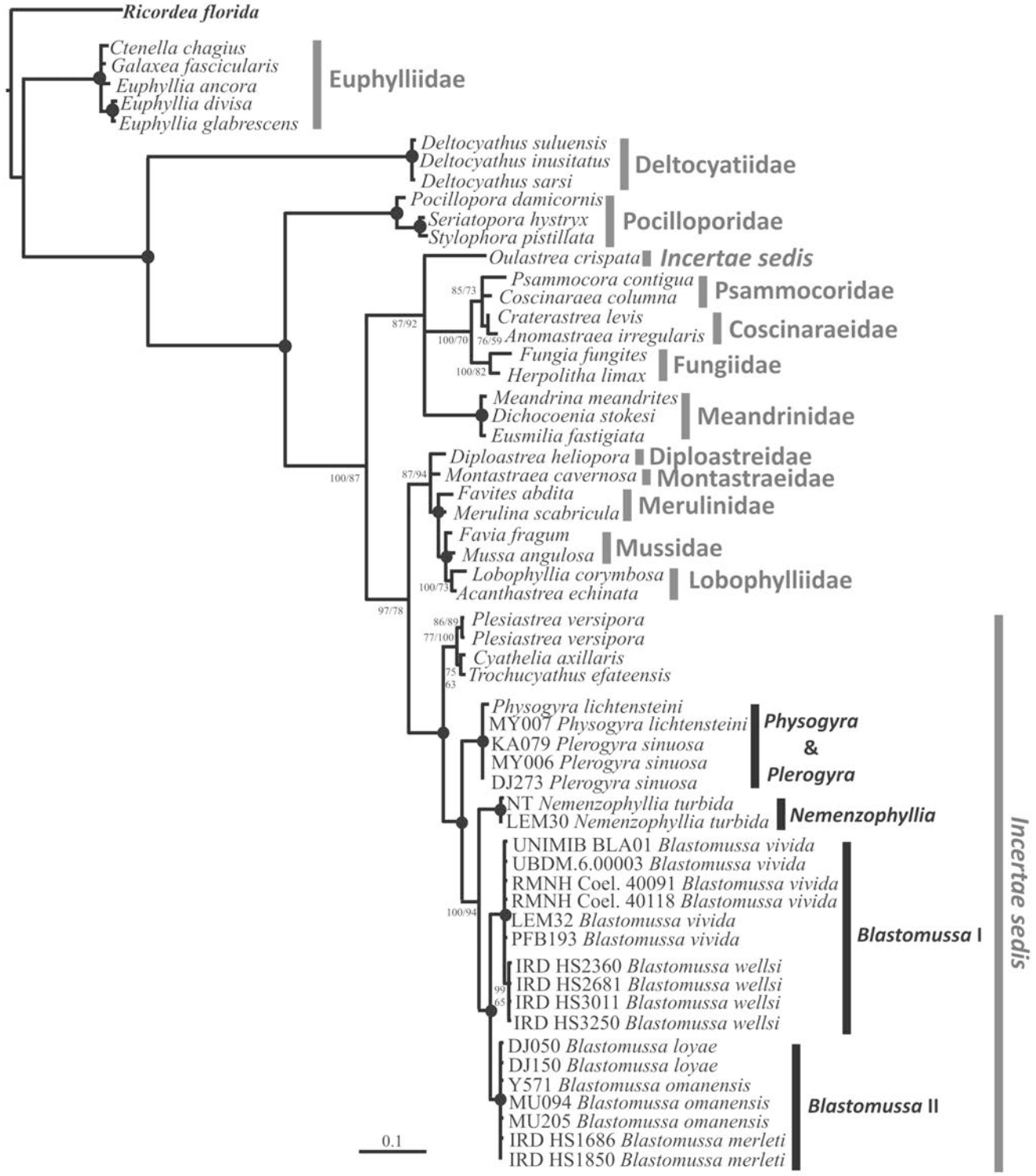

Fig. 4. Phylogenetic tree of mitochondrial gene COI reconstructed with Bayesian Inference. Numbers at each node show percentages of Bayesian posterior probability (>70%) and MP bootstrap (>50%); – = no support. Filled circles indicate well-supported clades (bootstrap values ≥99 and posterior probability of 100).

Veron, 2000; Pichon et al., 2010). *B. omanensis* was hitherto recorded from the Yemen coast of the Gulf of Aden (Pichon et al., 2010), Oman (Claereboudt, 2006), Socotra Island (DeVantier et al., 2004), and Mauritius (Moothien Pillay et al., 2002). Its distribution was restricted to infrequently studied reefs, and a certain similarity between its polyps in vivo (Fig. 8C) to those of *B. merleti* (Fig. 8A) and *B. loyae* (Fig. 8B) have likely played a role in the confusion in the taxonomic literature. The genus *Parasimplastrea* was established by Sheppard (1985), and later re-described by Sheppard & Sheppard (1991), to accommodate *P. omanensis*, which he first described in a report (Sheppard, 1985). The species was then synonymised with *P. simplicitexta* (Umbgrove, 1942) known from the fossil record of Java, southeast Sulawesi, and Papua New Guinea (Veron & Kelley, 1988). Sheppard (1985) apparently did not designate a holotype, thus leaving the nominal species as a nomen nudum. Subsequently, Veron (2000, 2002) moved it from the Oculinidae to the Faviidae Gregory, 1900, and selected a specimen from Egypt of what he believed to be a typical representative of

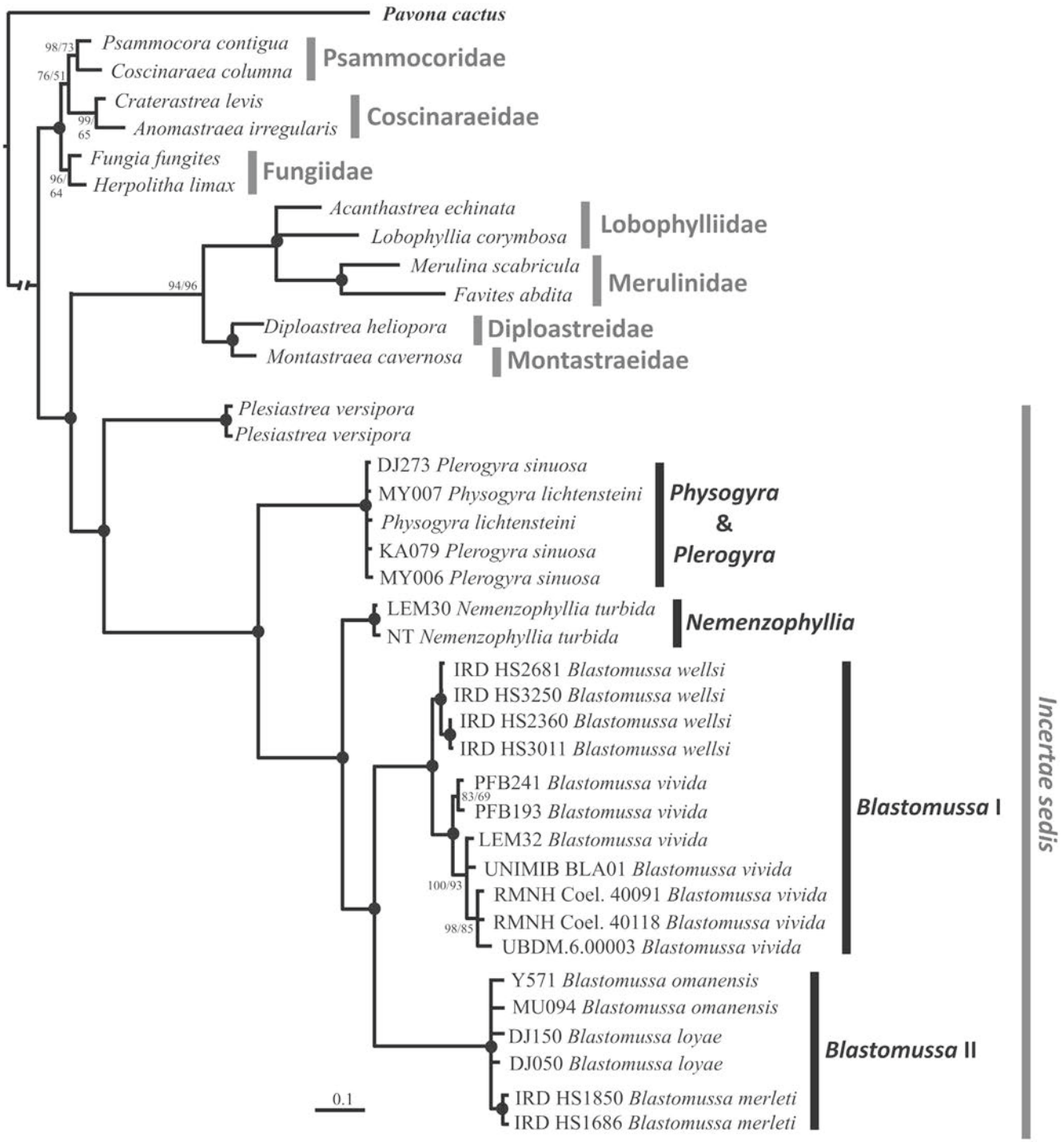

Fig. 5. Phylogenetic tree of rDNA (spanning the entire ITS1, 5.8S, ITS2 and a portion of 28S and 18S) reconstructed with Bayesian Inference. Numbers at each node show percentages of Bayesian posterior probability (>70%) and MP bootstrap (>50%); – = no support. Filled circles indicate well-supported clades (bootstrap values ≥99 and posterior probability of 100).

the species described by Sheppard from Oman, and named it *P. sheppardi*. Hence, Veron (2002) designated a ”type” for a species already known while questionably changing its specific name (Veron, 2000, 2002). The examination of the neotype of *P. sheppardi* revealed that this is actually a specimen of *B. loyae* as shown by the morphologic similarities between the type material of the former (Fig. 6C, D) and of the latter (Fig. 6E, F) (see *Taxonomic remarks* for *B. omanensis*). In more detail, such similarities concern the corallite size and the ceriod arrangement, the absence of pits, the rounded shape of corallites, the unequal thickness of the exsert septa, and the structure of the columella. Consequently, we designated a lectotype for *P. omanensis* (Fig. 6A, B) in the BMNH collection from Oman (type locality) that was

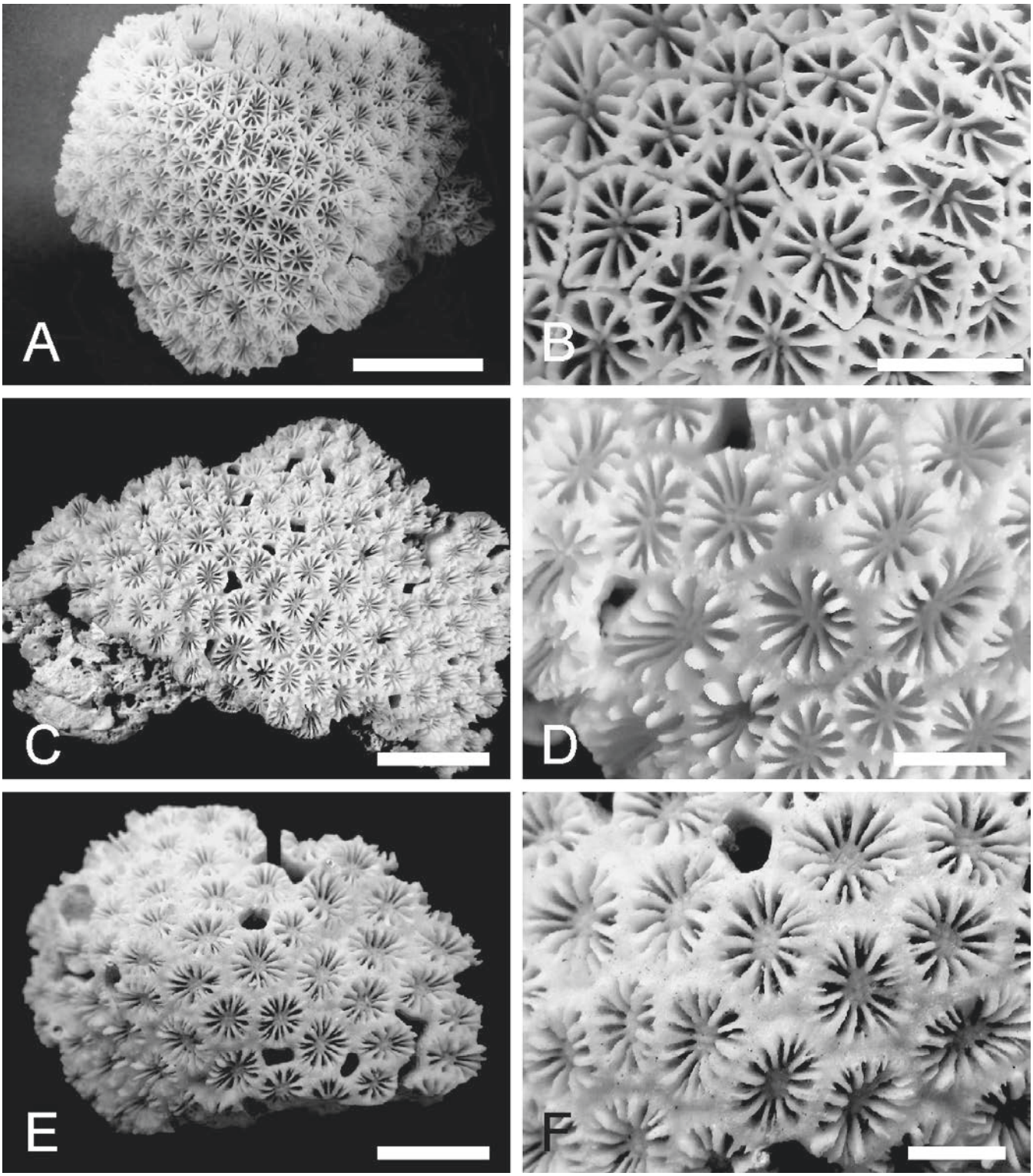

Fig. 6. A, Corallum; and B, detail of corallites of the holotype of *Blastomussa omanensis* (BMNH 1991.6.4.150) collected by C. Sheppard in Oman (Sheppard & Sheppard, 1991: Fig. 147); C, neotype of *Parasimplastrea sheppardi* (MTQ G 55860); and D, close up of corallites; E, paratype of *Blastomussa loyae* (ZMA 8322); and F, close up of its corallites. Scale bars A, C, E = 1 cm; B, D, F = 5 mm.

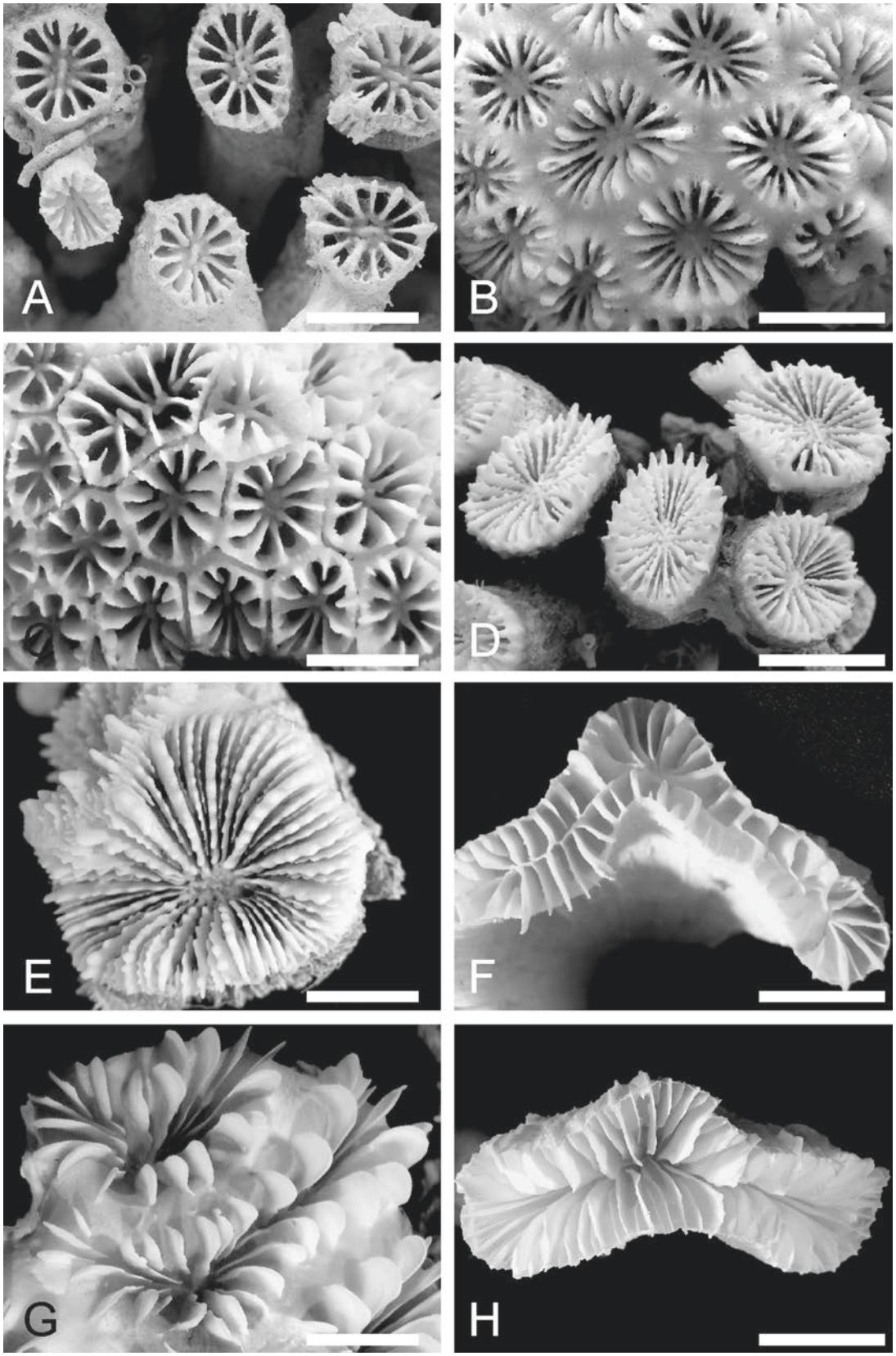

Fig. 7. Skeleton macro-morphology of the examined taxa: A, *Blastomussa merleti*, holotype (USNM 45390); B, *B. loyae*, holotype (BMNH 1977.5.5.1); C, *B. omanensis*, specimen collected by C. Sheppard in Oman (USNM 81272); D, *B. wellsi*, holotype (ZMA 6905); E, *B. vivida*, new species, (RMNH Coel. 40092); F, *Nemenzophyllia turbida*, Philippines (RMNH Coel. 24246); G, *Physogyra lichtensteini* (UNIMIB MY007), Mayotte Island; H, *Plerogyra sinuosa* (UNIMIB MY006), Mayotte Island. Scale bars A, B, C = 5 mm; D–H = 1 cm.

collected by Sheppard himself and illustrated in Sheppard & Sheppard (1991). Furthermore, we moved the species to the genus *Blastomussa*.

The monophyly of the five *Blastomussa* species examined in this study is strongly supported (Figs. 4–5). Two species, *B. wellsi* and *B. vivida*, have larger corallites, a higher number of strongly dentated septa (Fig. 7D, E), and fleshier polyps (Fig. 8D, E). They are closely related though well distinct and their monophyly is highly supported (Figs. 4–5). The other three species, *B. merleti*, *B. loyae*, and *B. omanensis*, have smaller corallites and smooth septa (Fig. 7A–C), and cluster together in another subclade with less resolved species boundaries (Figs. 4, 5), especially between *B. loyae*, and *B. omanensis* despite distinctively different morphologies of their skeletons (Figs. 1, 6, 7) and polyps (Fig. 8). The arrangement of corallites (e.g., cerioid vs plocoid) has traditionally been used in scleractinian corals as a distinguishing character at genus level (e.g., Veron & Pichon, 1980). Hence, it is not surprising that Head (1978) described a new subgenus to accommodate *B. loyae* as a typically cerioid species. However, as recently shown (Arrigoni et al., 2012) this can be rather misleading. In fact, three out of five *Blastomussa* species, i.e., *B. vivida*, *B. loyae*, and *B. omanensis*, are characterised by a primarily or secondarily cerioid arrangement of corallites (Figs. 1, 6, 7).

Phylogenetic relationships between *Blastomussa*, *Nemenzophyllia*, *Plerogyra*, and *Physogyra*. Wells (1956) classified the genera *Plerogyra* and *Physogyra* within the subfamily Eusmiliinae Milne Edwards, 1857, in the large family Caryophylliidae Gray, 1847, together with *Euphyllia*, *Gyrosmilia* Milne Edwards & Haime, 1851 and *Eusmilia* Milne Edwards & Haime, 1848. Chevalier & Baeuvais (1987) recognised all of the above in the emended family Eusmilidae Milne Edwards, 1857, including *Catalophyllia* (=*Catalaphyllia*) Wells, 1971. Veron (1986) first moved all these genera back into in the Caryophylliidae into which he also recognised *Nemenzophyllia*, and then erected the "Euphyllidae" Veron, 2000 (=Euphylliidae Milne Edwards, 1857; see ICZN, 2011) to accommodate *Euphyllia*, *Catalaphyllia*, *Nemenzophyllia*, *Plerogyra*, and *Physogyra* while moving *Gyrosmilia* and *Eusmilia* to the Meandrinidae. The common features of the Euphylliidae sensu Veron (2000) are the solid and smooth septa and the fleshy polyps with expanded tentacles or mantles at daytime. However, molecular analyses (Fukami et al., 2008) have revealed that *Euphyllia* belongs to the complex clade of Scleractinia and that it is closely related to *Galaxea* and *Ctenella*, which according to Veron (2000) are an oculinid and a meandrinid genus, respectively. Instead, *Physogyra* and *Plerogyra* belong to the robust clade and are related to *Blastomussa* (Fukami et al., 2008). A close relationship between *Plerogyra*, *Physogyra*, and *Nemenzophyllia* is not unexpected per se. However, based on skeleton morphology their evolutionary distance from *Euphyllia* and their monophyly together with *Blastomussa* were never hypothesized before in Scleractinia systematics. However, the genera *Blastomussa* and *Plerogyra* were previously assigned to the Plesiastreidae as a new family within the robust group (Dai & Horng, 2009) based on the tree of Fukami et al. (2008). In fact, among *Blastomussa* spp. (Fig. 7A–E), particularly in *B. wellsi* and *B. vivida* new species, septal dentation and columella are markedly more developed than in *Plerogyra* (Fig. 7H), *Physogyra* (Fig. 7G), and *Nemenzophyllia* (Fig. 7F). The latter ones de facto have smooth compact septa and a poorly developed columella like *Euphyllia* (Veron & Pichon, 1980). However, looking at the polyp in vivo, and at the development of the mantle and of the vesicles in living animals, similarities between the examined taxa and differences with *Euphyllia* are evident. It is out of the scope of this paper to discuss morphologic affinities among *Galaxea*, *Euphyllia*, and *Ctenella*, which together constitute the present monophyletic group representing the Euphylliidae in the complex clade (Figs. 5, 6). However, it can be remarked that although the first two share similarly extended tentacles in daytime, none of them forms mantle vesicles. Conversely, *Plerogyra*, *Physogyra*, *Nemenzophyllia*, and *Blastomussa* are characterised by mantle vesicles that are diurnally visible when the tentacles are partially retracted (Fig. 9). In *B. omanensis* only vesicles and tentacles are visible simultaneously during the day (Fig. 9C). In *Nemenzophyllia*, polyps have fleshy mantles with smooth elongated vesicles (Fig. 9F), each positioned above a septum while the tentacles are retracted (Veron, 2000; Hoeksema & van Ofwegen, 2004). Similarity in vivo between *B. wellsi* and *N. turbida* was already indicated by Veron (2000). *P. lichtensteini* and *P. sinuosa* are during the day covered by round to irregularly bifurcating vesicles (Fig. 8G, H) while polyps are nocturnally active and open (Veron, 2000). When vesicles are fully expanded, a homology with the vesicles in *Blastomussa* and *Nemenzophyllia* is not obvious. However, once vesicles are partially retracted (Fig. 9G, H), this becomes more appreciable (arrows in Fig. 9). The poorly known *Plerogyra discus* Veron, 2000 is actually remarkably similar to *N. turbida* by having an extended fleshy mantle and variably inflated elongated and smooth vesicles (Veron, 2000, 2002). In *Euphyllia*, a bewildering variety of different tentacle morphologies are observed, which can be used as diagnostic characters at species level. In this genus, however, tentacles are extended during the day, and mantle vesicles are absent. The phylogenetic position of *Catalaphyllia* still remains to be fully elucidated by molecular and morphologic analyses, however corals of this genus do not form mantle vesicles. Hence, based on our observations, it is unlikely that it would belong to the same evolutionary lineage as the corals examined in the present study. Moreover, Barbeitos et al. (2010) included one sequence of *C. jardinei* in their phylogenetic analyses based on 28S, and this species was found within a clade also including representatives of the Merulinidae (as currently defined). Hence *Catalaphyllia* is not closely related to the Euphylliidae nor to the clade examined in the present study, which needs further study.

Although the strongly supported clade of *Blastomussa*, *Nemenzophyllia*, *Plerogyra*, and *Physogyra* and the typical and exclusive presence of mantle vesicles in all these genera would suggest the need for the erection of a new family level taxon, the actual differences in skeleton morphology between *Blastomussa* spp. and the other genera suggest that additional micromorphological data are needed for the diagnosis of a new family.

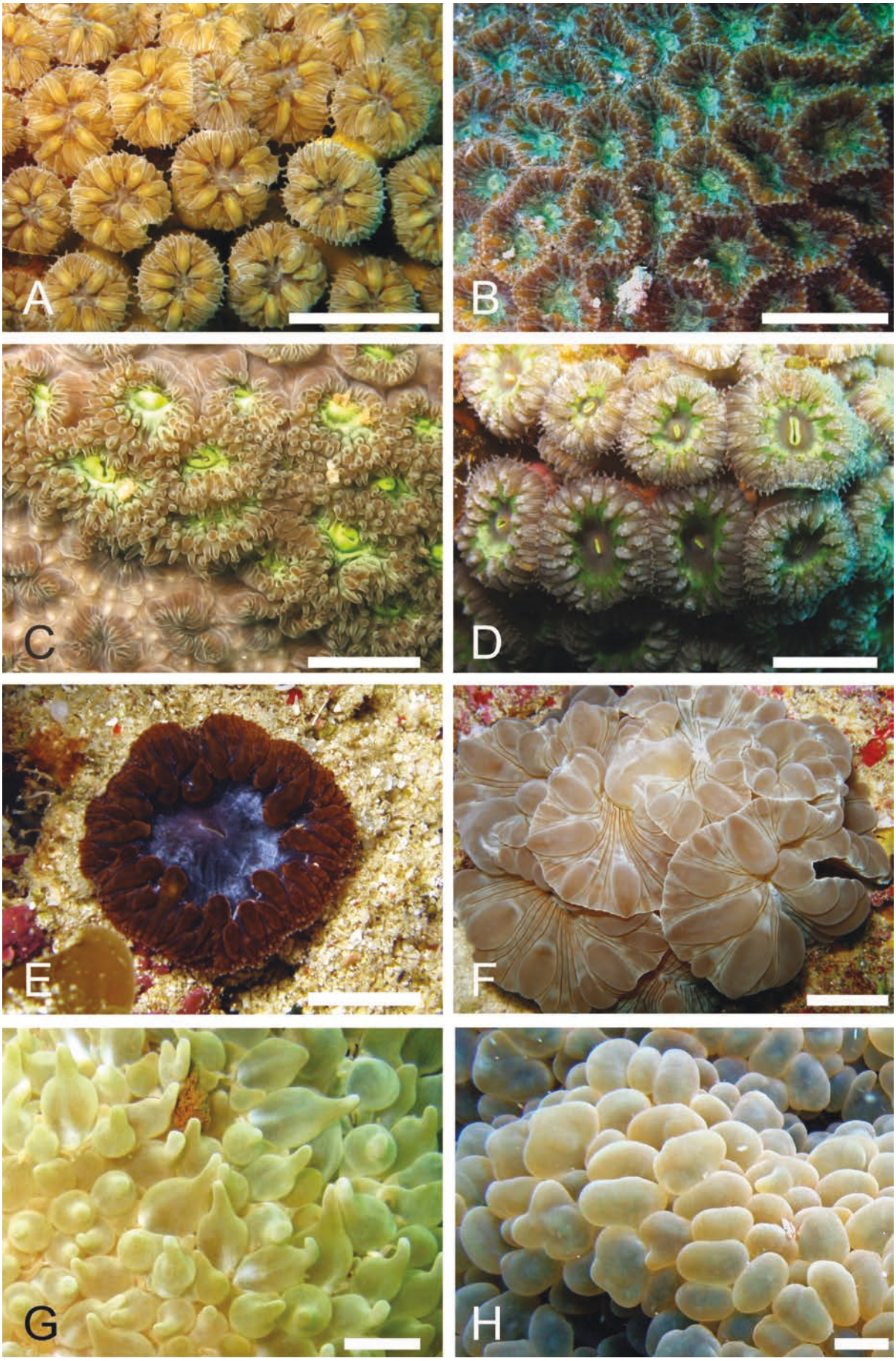

Fig. 8. In situ images of the examined taxa: A, *Blastomussa merleti*, New Caledonia, ST117; B, *B. loyae*, Djibouti; C, *B. omanensis*, Yemen; D, *B. wellsi*, New Caledonia, ST1084; E, *B. vivida*, new species, New Caledonia (IRD HS3000), ST332; F, *Nemenzophyllia turbida*, Semporna, Malaysia; G, *Physogyra lichtensteini*, New Caledonia, ST1477; H, *Plerogyra sinuosa*, New Caledonia, ST1461. Scale bars = 1 cm

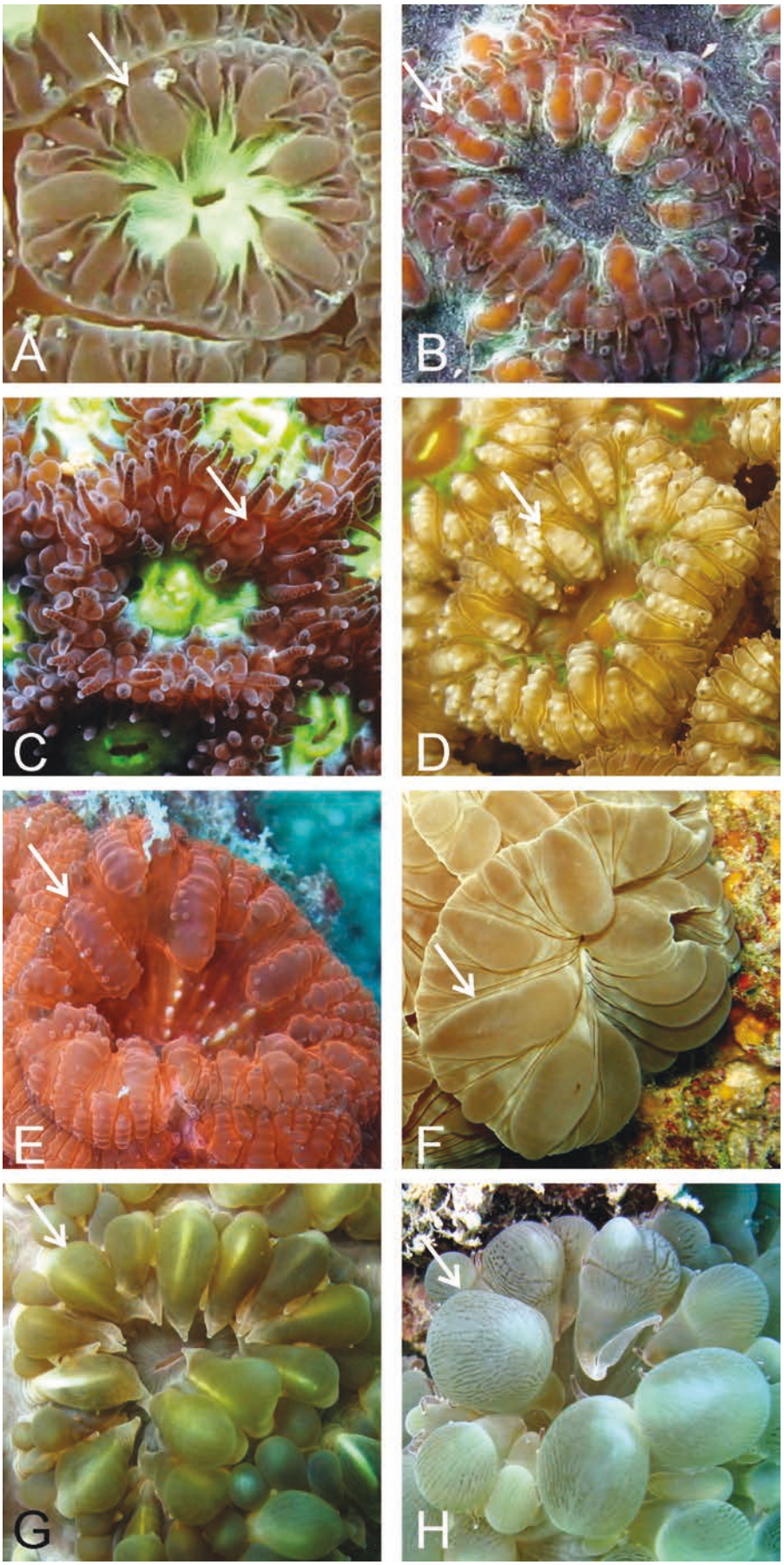

Fig. 9. Close up of the polyps showing mantle vesicles in the examined taxa: A, *Blastomussa merleti*, New Caledonia, ST117; B, *B. loyae*, Djibouti; C, *B. omanensis*, Yemen; D, *B. wellsi*, New Caledonia, ST1084; E, *B. vivida* new species, New Caledonia, ST332; F, *Nemenzophyllia turbida*, Semporna, Malaysia; G, *Physogyra lichtensteini*, New Caledonia, ST1477; H, *Plerogyra sinuosa*, New Caledonia, ST1461. White arrows indicate mantle vesicle.

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