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With eyes wide open: a revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics

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Molecular studies have been instrumental for refining species boundaries in the coral genus *Pocillopora* and revealing hidden species diversity within the extensively studied global species *Pocillopora damicornis*. Here we formally revise the taxonomic status of species closely related to and within the *P. damicornis* species complex, taking into account both genetic evidence and new data on morphometrics, including fine-scale corallite and coenosteum structure. We found that mitochondrial molecular phylogenies are congruent with groups based on gross-morphology, therefore reflecting species-level differentiation. However, high levels of gross morphological plasticity and shared morphological characteristics mask clear separation for some groups. Fine-scale morphological variation, particularly the shape and type of columella, was useful for differentiating between clades and provides an excellent signature of the evolutionary relationships among genetic lineages. As introgressive hybridization and incomplete lineage sorting complicate the delineation of species within the genus on the basis of a single species concept, the Unified Species Concept may represent a suitable approach in revising *Pocillopora* taxonomy. Eight species are herein described (*P. damicornis*, *P. acuta*, *P. aliciae*, *P. verrucosa*, *P. meandrina*, *P. eydouxi*, *P.* cf. *brevicornis*), including a novel taxon – ***Pocillopora bairdi* sp. nov.** (Schmidt-Roach, this study). Citation synonyms and type materials are presented.

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ADDITIONAL KEYWORDS: Australia – coral – cryptic species – evolution – fine-scale morphology – Great Barrier Reef – morphometric analysis – speciation – species boundaries – Unified Species Concept.

INTRODUCTION

In recent years, molecular systematics has frequently challenged the morphology-based taxonomy of scleractinian corals, and has significantly contributed to the understanding of coral phylogenetics and evolution (e.g. Chen *et al*., 1995; Fukami *et al*., 2004, 2008; Benzoni *et al*., 2010, 2012; Huang *et al*., 2011; Budd *et al*., 2012). In multiple cases, however, a combination of genetic evidence and skeleton morphology has resulted in a powerful approach for a comprehensive revision and delineation of coral species. For example, within the common scleractinian coral genus *Pocillopora*, phylogenetic inference and morphological data have revealed evidence of cryptic speciation (Flot *et al*., 2008; Schmidt-Roach *et al*., 2012a; Schmidt-Roach, Miller

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& Andreakis, 2013). However, some uncertainty remains in the link between morphological and molecular species boundaries in this genus (Pinzón & LaJeunesse, 2010; Pinzón *et al.*, 2013).

In *Pocillopora*, as in many other scleractinian genera, high levels of phenotypic plasticity encrypt species boundaries and complicate the definition of valid taxonomic units (see Todd, 2008). On the basis of skeletal variation, early taxonomists described more than 35 *Pocillopora* species (see Veron & Pichon, 1976), which is likely to be an overestimate. In recent revisions, however, several taxa were synonymized due to a lack of clear diagnostic morphological characters reflecting species boundaries, or due to the presence of obvious transitions among morphotypes within an acceptable morphological species range (e.g. Vaughan, 1907, 1918; Hoffmeister, 1925; Wells, 1954; Veron & Pichon, 1976; Veron, 2000). For example, Veron & Pichon (1976) suggested the extensively studied species *P. damicornis* (Linnaeus, 1758) comprised four intergrading ecomorphs, which were partly defined based on junior synonyms. These comprise: (1) the elongate ecomorph '*bulbosa*' (named after *P. bulbosa* Ehrenberg, 1834) found in very sheltered or turbid deep habitat; (2) an ecomorph from semi-disturbed habitats; (3) the stunted, compact ecomorph '*brevicornis*' (named after *P. brevicornis* Lamarck, 1816) found in exposed habitats; and (4) a long and thick branching ecomorph found in temperate regions (Veron & Pichon, 1976: 46). The feature that unifies the aforementioned ecological variants and ultimately defines *P. damicornis* is the absence of true verrucae, i.e. verrucae grade into fully developed sub-branches (Veron & Pichon, 1976).

Molecular studies have provided evidence for the separation of morphological variants within *Pocillopora*, with some confirming a link between morphology and phylogeny (Flot *et al.*, 2008; Schmidt-Roach *et al.*, 2012a, 2013), and others challenging it (Pinzón & LaJeunesse, 2010). From a phylogenetic perspective, Flot *et al.* (2008) confirmed five distinct genetic lineages in Hawaii that are linked to different morphologies. While most lineages were characterized by individual mitochondrial haplotypes, *P. eydouxi* Milne Edwards & Haime, 1860 and *P. meandrina* Dana, 1846 were resolved only by the nuclear ITS2 region (Flot *et al.*, 2008). This observation was mainly attributed to the nature of the mitochondrial coral genome, which evolves slowly compared with other metazoan mitochondria (Shearer *et al.*, 2002; Hellberg, 2006). Its limited inter-specific resolution has often challenged phylogenetic approaches in delineating taxonomic units in coral taxonomy (Shearer & Coffroth, 2008).

At the nuclear level, introgressive hybridization, incomplete lineage sorting or reticulate evolution further complicate phylogenetic interpretation in some corals (e.g. van Oppen *et al.*, 2001; Márquez *et al.*, 2002; Wolstenholme, 2004; Flot *et al.*, 2008; Schmidt-Roach *et al.*, 2012a). Additional lines of evidence are therefore often necessary to resolve taxonomic units. These may include: gross- and fine-scale morphology (e.g. Benzoni *et al.*, 2010, 2012; Budd & Stolarski, 2011; Gittenberger, Reijnen & Hoeksema, 2011; Stefani *et al.*, 2011), symbiont association (Pinzón & LaJeunesse, 2010; Schmidt-Roach *et al.*, 2012a) or reproductive traits (McFadden *et al.*, 2001; Schmidt-Roach *et al.*, 2012a, 2012b).

Using the aforementioned traits in combination, Schmidt-Roach *et al.* (2012a) showed that the previously reported ecomorphs *sensu lato* Veron & Pichon (1976) within *P. damicornis* actually represent distinct species rather than morphological variants attributed to local environmental conditions. Mitochondrial molecular phylogenies were found to be congruent with morphological groups within *P. damicornis*, indicating at least five genetically distinct lineages. Nuclear markers, by contrast, recovered only three lineages (Schmidt-Roach *et al.*, 2012a). However, additional information from gross morphology, associated *Symbiodinium* clades, reproductive mode, and timing indicated intra-specific diversification patterns that were not revealed by the nuclear DNA data, probably due to introgressive hybridization. Most importantly, much of the reproductive plasticity perceived within species could be attributed to cryptic species (Schmidt-Roach *et al.*, 2012b).

Corals often do not meet the criteria of conventional species concepts due to extreme phenotypic plasticity and/or instances of hybridization along the geneological history of the species (e.g. Veron, 1995; Willis *et al.*, 2006). In these cases, the 'unified species concept' (USC; De Queiroz, 2007) may represent an appropriate taxonomic approach in delineating valid taxonomic units (Schmidt-Roach *et al.*, 2012a). The USC assumes that species are represented by separately evolving metapopulations whereby criteria associated with previously accepted species concepts are used in synergy to assess metapopulation boundaries. Each criterion therefore represents an independent component in a global line of evidence to support species formation (De Queiroz, 2007).

In this study we formally revise species within the genus *Pocillopora* by means of morphological analyses and data on fine-scale skeletal structure from voucher colonies collected from different locations around Australia. In addition to morphological and molecular data collected here, we combine molecular, reproductive evidence, and symbiont associations inferred from previous studies (Flot *et al.*, 2008; Flot, Couloux & Tillier, 2010; Pinzón & LaJeunesse, 2010;

Schmidt-Roach *et al*., 2012a, b, 2013; Pinzón *et al*., 2013) to strengthen species delineation. Finally, the identified valid taxonomic units are compared with type material and specimens from taxonomic collections for *Pocillopora* species identification and nomenclature.

MATERIAL AND METHODS

Specimen collections

Seventy-eight *Pocillopora* colonies/fragments were collected from different habitats throughout its range in Australian waters (Table S1). A fragment of each colony was preserved in ethanol for DNA extraction. Colonies were bleached using 0.5% sodium hypochlorite solution and air-dried for examination of morphology. Type material of the newly described species as well as a selection of specimens was deposited at the Museum of Tropical Queensland (MTQ), Townsville, Australia.

Specimen identification and phylogenetic analysis

The mitochondrial open reading frame (ORF) region (Flot & Tillier, 2006) was sequenced from each colony to ascertain mitochondrial lineage (following protocols in Schmidt-Roach *et al*., 2012a). Individuals of a potentially new species identified at Lizard Island were further investigated using the nuclear HSP70B region (following protocols in Schmidt-Roach *et al*., 2012a). PCR products were purified and sequenced in both directions for the mitochondrial marker and in reverse direction for the HSP70B marker by Macrogen Inc., Korea. Electropherograms were edited using Sequencher 4.9 (Gene Codes) and aligned manually in BioEdit v7.0.5.3 (Hall, 1999). Sequences generated by Schmidt-Roach *et al*. (2012a) were used as reference for the sequence alignment (NCBI accession numbers: JX985584–JX985620). MEGA4 (Tamura *et al*., 2007) was used to generate phylogenetic hypotheses using the neighbour-joining algorithm under the JC correction and 1000 bootstrap pseudo-replications for nodal support (Felsenstein, 1985; Saitou & Nei, 1987) for the mitochondrial ORF region. Network v4.5.1.6 (http://www.fluxus-technology.com) was used to examine genealogical relationships in the HSP70B region among the newly identified morphotypes and those identified by Schmidt-Roach *et al*. (2012a) using the median-joining algorithm (Bandelt, Forster & Röhl, 1999) (NCBI accession numbers: JX624847–JX624903). The sequences generated from novel species can be accessed online (NCBI accession numbers: KF709239–KF709244). The same method was used to compare our data with described genetic lineages of previous studies (inclucing: Flot *et al*., 2008; Pinzón & LaJeunesse, 2010; Souter, 2010; Schmidt-Roach *et al*., 2012a, b; Pinzón *et al*., 2013).

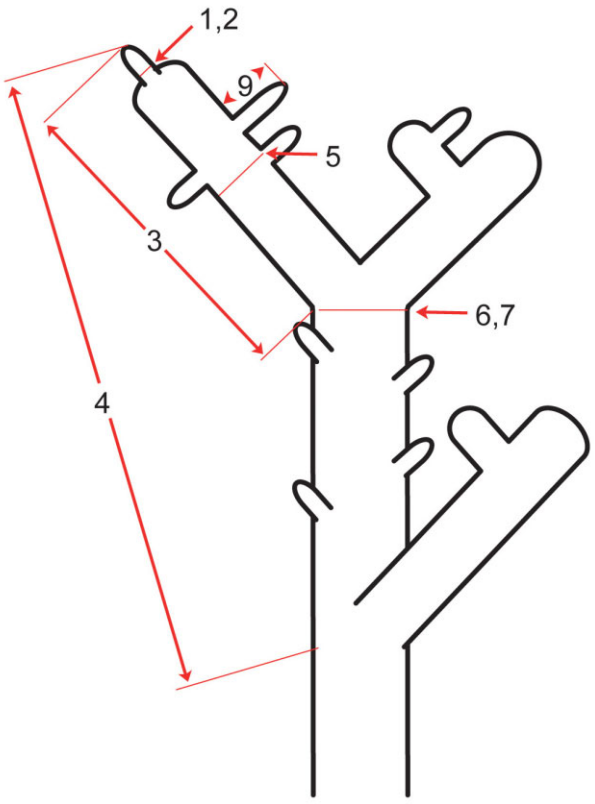

Figure 1. Schematic illustration of morphometric measurements taken of corallum (side view). Numbers refer to morphometric measurements taken from each colony (see Table 1).

Morphological analysis

For morphometric analysis of the identified genetic lineages, a subset of 68 colonies representing all candidate species was analysed, excluding *Pocillopora* Type ε due to a lack of skeletal material. Ten skeletal variables (Fig. 1, Table 1) were measured on each of two branches per colony using an electronic calliper. The dataset included the following numbers of branches examined per genetic lineage: $\alpha = 62$; $\beta = 24$; $\gamma = 22$; $\delta = 6$; $e = 4$; $m = 7$; $x = 8$. Branches were selected randomly from the top of the colony. For multivariate analysis a non-parametric permutational MANOVA (i.e. 'PERMANOVA') was performed using a two-factor nested model (with genetic lineage as a fixed variable, colony as a random variable, and branch as the lowest level of replication) in the PERMANOVA+ add-on package for PRIMER 6 (999 permutations, D1 Euclidean distance resemblance).

Table 1. Gross morphological measurements analysed in morphometrics of *Pocillopora* colonies

	Morphological measurements
1	The maximal diameter of most distal branchlet/verruca 1 mm under tip, at most distal branch
2	Minimal diameter of most distal branchlet/verruca 1 mm under tip, at most distal branch
3	Distance between most distal branch tip and the base of the most distal ramification of a main branch with secondary branching
4	Distance between most distal branch tip and the base of the second most distal ramification of a main branch with secondary branching (or base of colony)
5	Maximal diameter half way between most distal branch tip and the base of the most distal ramification of a main branch with secondary branching
6	Maximal diameter of branch at this most distal ramification of a main branch with secondary branching
7	Minimal diameter of branch at this most distal ramification of a main branch with secondary branching
8	Number of primary branches (branchlets/verrucae) between tip of most distal branch and most distal ramification of a main branch with secondary branching (with numbers exceeding 100 estimated to the closest decade)
9	Length of longest primary branch (branchlets/verrucae) between tip of most distal branch and most distal ramification of a main branch with secondary branching
10	Number of branches with secondary (or higher) branching originating from investigated branch between tip and 4 cm below tip (or base of colony)

Discriminant analysis of principal components (DAPC) using a priori defined groups based on the mitochondrial phylogeny was performed to describe clusters of morphologically similar individuals (using the adegenet-1.3-5 package (Jombart, 2008). Furthermore, a canonical discrimination analysis (CDA) was performed in StatistiXL v1.9, which produced an identical plot to that from DAPC, but enabled the creation of a bi-plot to examine the relative contribution of each of the morphological characters to the separation of species groups. Based on the discriminant functions, cluster-based reassignment probabilities were calculated to test for robustness of the identified clusters as well as to estimate levels of separation (Fig. 3). In the same manner, individual branch-based reassignment probabilities were calculated to identify intra- and inter-colony variation [whereby values can range between 1 (full assignment) and 0 (no assignment); see Figure 3B].

A subset of 26 colonies was analysed for fine scale morphological differences among genetic lineages using scanning electron microscopy (SEM; Jeol JSM5410LV). Skeleton samples were cleaned in 70% ethanol and air-dried before vacuum gold coating. The smallest and largest diameter of 6–10 fully developed calices of three colonies per candidate species was measured either by SEM or light microscopy to estimate the size range of calices. For this measurement, specimens were orientated horizontally.

Historical specimens and type material originating from the Ehrenberg collection in Berlin, Lamarck collection in Paris, the international coral collection at the Museum of Tropical Queensland (MTQ) and photos of additional historical samples were examined. Due to a lack of tissue availability for molecular comparisons we could only compare morphological characteristics between our present-day collections and the historical specimens examined. Furthermore, the sampling location of several holotypes examined here (e.g. Ehrenberg's samples) is not recorded, or only the broad geographical regions are reported from which they are collected. This prevented the collection of equivalent fresh samples at the original locations for molecular analysis.

Definition of species

Species are here defined according to the USC proposed by De Queiroz (2007), whereby criteria associated with previously accepted species concepts are used in synergy to assess species boundaries. All available information was considered to assess species integrity for each candidate species including molecular phylogenies, gross- and fine-scale morphology, and where obtainable or known, reproductive and symbiont differences.

RESULTS

Genetic identification of specimens and phylogenetic analysis

In a previous study, molecular phylogenies inferred from mitochondrial (ORF, COI) and nuclear (HSP70, ITS2) markers together with symbiont association and reproduction were used to identify six different

lineages of *Pocillopora*: Type ε, Type β, Type α, Type γ, and Type δ (Schmidt-Roach *et al*., 2012a). Four of these lineages (Types β, α, δ, ε) exhibited distinct morphologies previously attributed to *P. damicornis*, generally defined by the absence of true verrucae (Veron & Pichon, 1976); one lineage (*P. damicornis* Type γ) resembled *P. verrucosa* (Ellis & Solander, 1786) in terms of morphology and another lineage resembled *P. meandrina* morphology. The validity of the genetic lineages identified by Schmidt-Roach *et al*. (2012a) was recently further supported by Pinzón *et al*. (2013) sampling various locations throughout the global distribution of the genus *Pocillopora* (see Fig. 5). Unfortunately, this study was conducted without consideration of morphological characteristics, thus limiting comparisons to species identified here.

The colonies examined in our study encompassed the previously identified genetic lineages within *Pocillopora* in Australia with a final alignment of the mitochondrial ORF region consisting of 67 sequences, 708 bp in length (Table S1, Fig. 4), with the exception of one newly identified haplotype that corresponded to a distinct morphotype (*x*, Fig. 4). Lineages were grouped into four main clades (Clades 1–4, Fig. 4). Clade 1 consists of *P. damicornis* Type α, *P. damicornis* Type β and *P. damicornis* Type δ described by Schmidt-Roach *et al*. (2012a). Clade 2 comprises *P. damicornis* Type γ/*P. verrucosa* and a new morphotype (referred to as *x*). Although two individuals of this new morphotype were characterized by a unique mitochondrial haplotype, others exhibited shared haplotypes with *P. verrucosa*/*P. damicornis* Type γ (Fig. 4). However, further testing of the nuclear HSP70 region found a > 3 bp divergence for all sampled individuals of this morph compared with congenerics investigated by Schmidt-Roach *et al*. (2012a) (including *P. verrucosa*/*P. damicornis* Type γ; Fig. S1). Clade 3 comprises *P. meandrina*, a well-distinguished species used by Schmidt-Roach *et al*. (2012a) for outgroup comparisons against species within *P. damicornis*. Interestingly, the morphospecies *P. eydouxi* shared an identical ORF haplotype with *P. meandrina*, confirming previous findings from Hawaii, where only limited support for genetic differentiation in these species based on the nuclear ITS2 region was found (Flot *et al*., 2008). Clade 4 was previously described by Schmidt-Roach *et al*. (2012a) as *P. damicornis* Type ε.

The aforementioned clades (1–4) comprise most (excluding species of clade 5, *P. ligulata* and *P.* cf. *effusus*, and one unidentified species) of the known genetically distinct lineages within the genus *Pocillopora* as shown in Figure 5, integrating publicly available sequences from various geographical locations.

Morphometrics

The assessed morphological characters were largely overlapping among the genetic lineages, except for *P. eydouxi* (*e*) which is morphologically distinct from other taxa based on characters 3, 4, 5, 6, and 8 (Fig. 2). *Pocillopora eydouxi* has larger branch diameters (> 2 cm) and greater distances between tip and first ramification (> 5 cm) and between tip and second ramification (> 10 cm) than other species. *Pocillopora meandrina* is intermediate between *P. eydouxi* and other taxa for these characters (Fig. 2). Both *P. eydouxi* and *P. meandrina* have high numbers (> 38) of primary branches (branchlets/verrucae) between the tip of the first ramification with secondary branching compared with other taxa. There were some differences among the *P. damicornis* types; in particular, *P. damicornis* Type δ had larger distal branchlets/verrucae (2.9–8.3 mm) than other taxa. The opposite was true for the newly identified morphotype (*x*), which had generally smaller distal branchlets/verrucae (0.2–2.6 mm) than other taxa.

Non-parametric multivariate analysis identified significant morphological differences among the genetic lineages (PERMANOVA, d.f. = 6, *Pseudo*-F = 28.024, $P = 0.001$, unique permutations = 999), but there was also significant variation among colonies within a genetic lineage (PERMANOVA, d.f. = 61, *Pseudo*-F = 8.6146, $P = 0.001$, unique permutations = 999). For the discriminant analysis of the principal components (DAPC) *a*-score calculation suggested that all ten principal components of the principal component analysis should be considered to receive maximum resolution of differences among clades (see Fig. S2). Furthermore, eigenvalues suggested that the first four discriminant functions should be included. DAPC indicated morphological differences between *P. eydouxi* (*e*), and *P. meandrina* (*m*), *P. damicornis* Type δ and the new morphotype (*x*), while the remaining groups were overlapping (Fig. 3A). A similar outcome was found conducting pair-wise tests using the PERMANOVA approach (see Table S2).

Full reassignment of colonies to their genetic lineages was observed only for *P. eydouxi* (*e*), while the remaining clusters were moderately to weakly defined (9–82.25%) in the group-based reassignment test (Fig. 3B). Reassignment probabilities were lowest for the *P. damicornis* Type γ/*P. verrucosa* cluster (9%) due to the morphological similarity to *P. damicornis* Type α (Fig. 3B). The morphometric data indicate high levels of morphological plasticity for *P. damicornis* Type α, including several morphologies similar to other lineages. Thus, the species overlaps in its morphology with several other species and encrypts the clear definition of these groups based solely on gross morphology. Group-based reassignment probabilities of

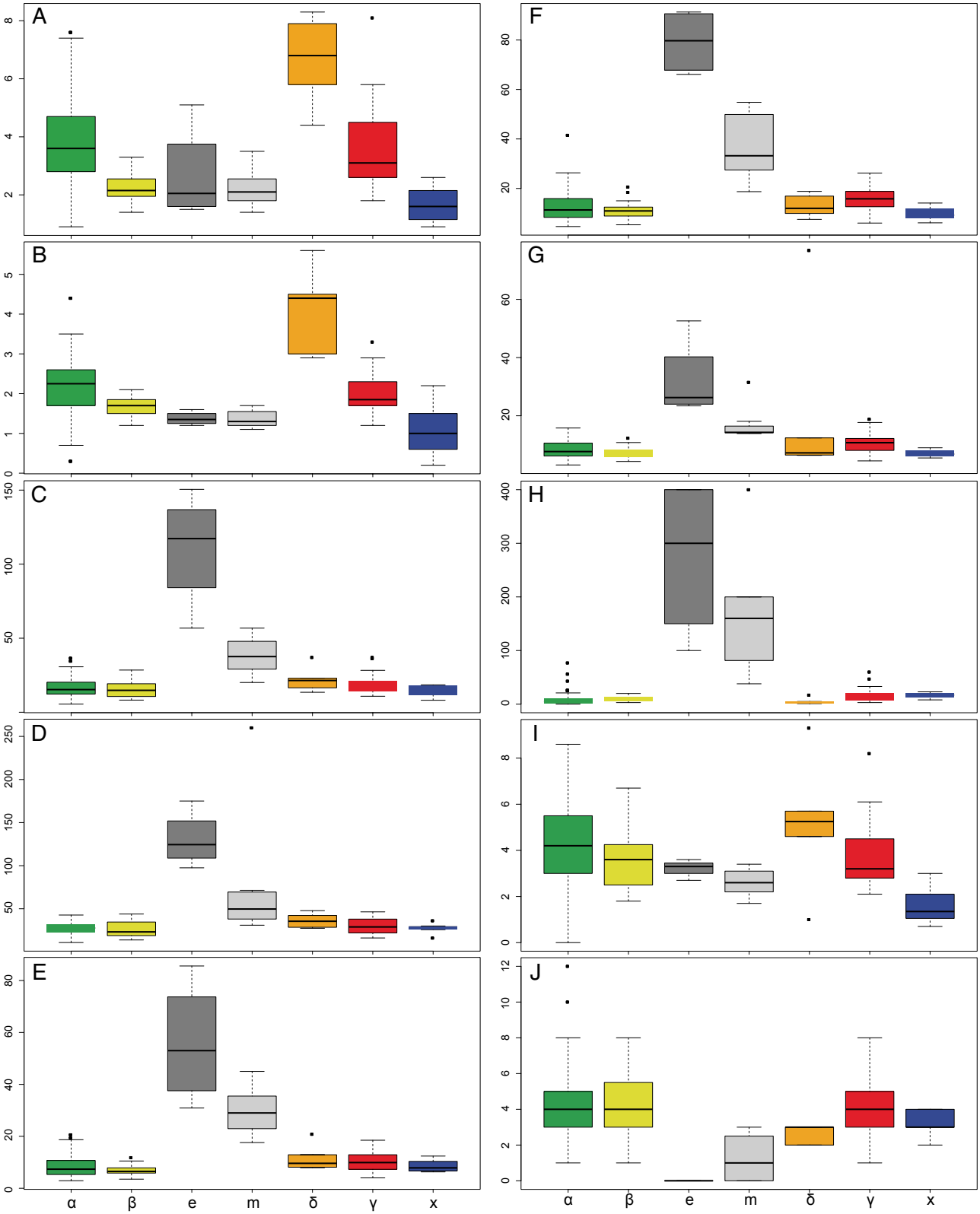

Figure 2. Box plots of morphological variables for each identified group; colours indicate genetic lineages labelled at the bottom. Plots A-J represent morphological variables 1-10 respectively as listed in Table 1.

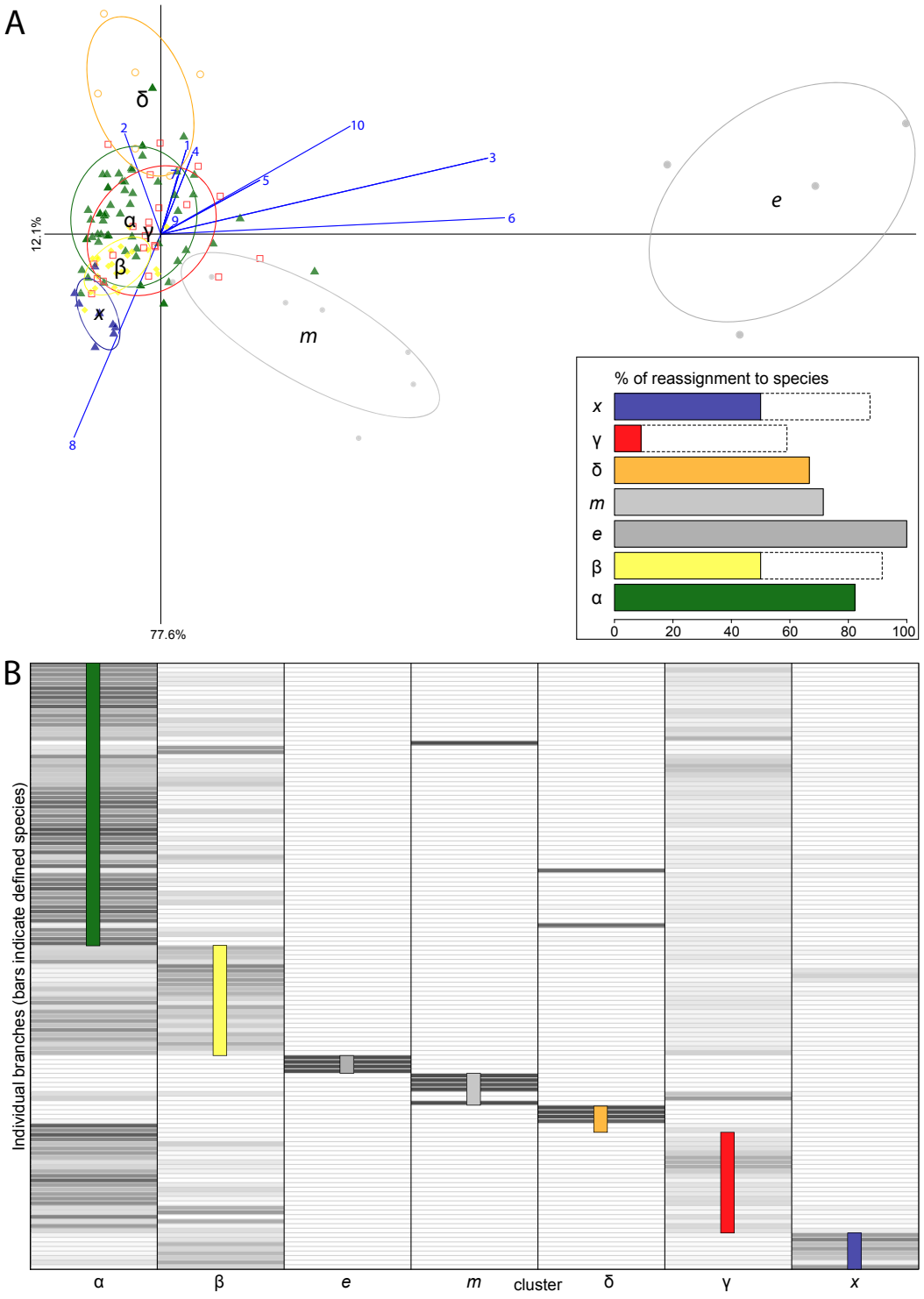

Figure 3. A, DAPC of gross morphological characters. Bi-plot indication of character (see Table 1 for explanation of characters) contribution is shown in blue. Individuals are represented by dots and groups by elipses. Box, cluster-based reassignment probabilities (dotted lines indicate probabilities if Type α is excluded from calculations). B, branch-based reassignment probabilities for each cluster; bars indicate genetic lineages [probability of reassignment of a branch (N = 133) (horizontal bars, y-axis) to a certain cluster (genetic lineage) (vertical bars, x-axis) is indicated by shades: white = 0, dark grey = 1]. Clusters: α, *Pocillopora damicornis*; β, *P. acuta*; *e*, *P. eydouxi*; *m*, *P. meandrina*; δ, *P. aliciae*; γ, *P. verrucosa*; *x*, ***P. bairdi sp. nov.***

genetic lineages were indeed much higher if *P. damicornis* Type α was excluded from the calculations of the DAPC (*P. damicornis* Type β: 87.5%, *P. damicornis* Type δ: 83.3%, *P. damicornis* Type γ/*P. verrucosa*: 72.7%, *P.* Type *x*: 62.5%, *P. meandrina*: 85.7%, *P. eydouxi*: 100%; Fig. 3B dotted lines). Furthermore, moderate reassignment was observed for *P. bairdi* sp. nov. (*x*) due to similarity to *P. damicornis* Type β (Fig. 3B). Character 8, the number of primary branches between the tip of the most distal branch and the most distal ramification with secondary branching, contributed most to the divergence of these lineages from the others (bi-plot, Fig. 3A). In general, reassignment of individual branches to the pre-defined morphological clusters produced similar results to that based on colonies, with the highest reassignment of individual branches to the species *P. eydouxi* (*e*), *P. meandrina* (*m*), and *P. damicornis* Type δ. However, reassignment probabilities did result in some individual branches recovering with higher probability within a different morpho species from that which it was originally assigned, stressing high levels of intra-colony variation and overlap in gross morphological characters among the genetic groups/lineages (Fig. 3B).

Fine-scale morphology

Clear fine-scale morphological differences were found among the four genetic clades, and there was little variation among the lineages within each of the clades. Colonies within Clade 1 are characterized by a flat columella ornamented with short spinulae (Figs 4, 6C, 8C, 9C). Calices are 0.8–1.4 mm in diameter and round to oval. Septa are rudimentary, often only indicated by spinulate septa teeth arranged hexamerally in two equally developed cycles. The coenosteum is ornamented sparsely to densely with short spinulae. Two lineages within Clade 1 (*P. damicornis* Type α and *P. damicornis* Type β; Figs 6C, 8C) have identical fine-scale morphological features, whereas *P. damicornis* Type δ has a reduced columella in comparison with the other two linages within the clade (Figs 4, 9C).

Clade 2, comprising *P. verrucosa*/*P. damicornis* Type γ and the new identified morphotype (*x*), was characterized by absent to styloid columellae, often only indicated by its ornamentation with long spinulae which may be arranged in a line (Figs 4, 10C, 10H, 11C, 13C). Calices are round and usually smaller (0.4–0.7 mm) than those of Clade 1. Septa are only indicated by irregular, but long (~100–150 μm) spinulate septa teeth and arranged hexamerally in two equally developed cycles. The coenosteum is ornamented sparsely to densely with spinluae. Although some variation regarding the development of spinulae covering the strongly reduced columellae as well as the coenosteum can be acknowledged within and between specimens, overall individuals within the clade are very similar in fine structure.

The highest level of intra-clade variation was observed for Clade 3 (Fig. 4), consisting of *P. eydouxi* and *P. meandrina*. The former has a styliform columella, with one to three distinct stylae originating from a diagonally arranged, bridge-like columella (Fig. 14C). The latter is more variable and characterized by oval-convex to styloid, rarely obsolete columellae (Fig. 15C, D), which is consistently more predominant than that of *P. eydouxi*. Both show septa that are hexamerally arranged in two cycles and vary in their development from almost reduced to well developed, indicated by long spinulae, and where the second septal cycle may be slightly less developed than the first. The coenosteum is ornamented with short spinulae. Calices are 0.5–1.6 mm in diameter for *P. meandrina*, and are usually > 1 mm in *P. eydouxi*.

Unfortunately, material of Clade 4 comprising *P. damicornis* Type ε was limited to DNA and a field photo, and thus no skeleton features could be assessed.

Links between genetic/morphological groups and described species

The morphological differences scored among the genetic lineages enabled us to link our taxonomic units to earlier descriptions of *Pocillopora* spp. and formally re-describe species. The observations gathered from previous taxonomic descriptions and the skeleton morphology of type material showed that the specimens investigated could be classified as belonging to (a) four existing species (*P. damicornis*, *P. verrucosa*, *P. eydouxi*, *P. meandrina*), (b) one recently described species (*P. aliciae*), (c) two species that had previously been synonomized with *P. damicornis* and that should be resurrected (*P. acuta* and *P.* cf. *brevicornis*), and (d) one new species that is here described as *P. bairdi* sp. nov.

Due to the lack of type material for *P. damicornis* (Linnaeus, 1758) (the holotype is temporally lost), corallite structures between our samples and the type specimen could not be compared. However, the original description of *P. damicornis* by Linnaeus (1758) and his illustrations correspond well with the morphology observed for subtropical *P. damicornis* Type α. The latter shows high levels of phenotypic plasticity (Fig. 3) and graduates in its branching from elongate in subtropical regions to robust and cespitose in tropical regions (Fig. 7). Indeed, the apparent differences between latitudinal morphs led Ehrenberg (1834) to describe the tropical form as a separate species,

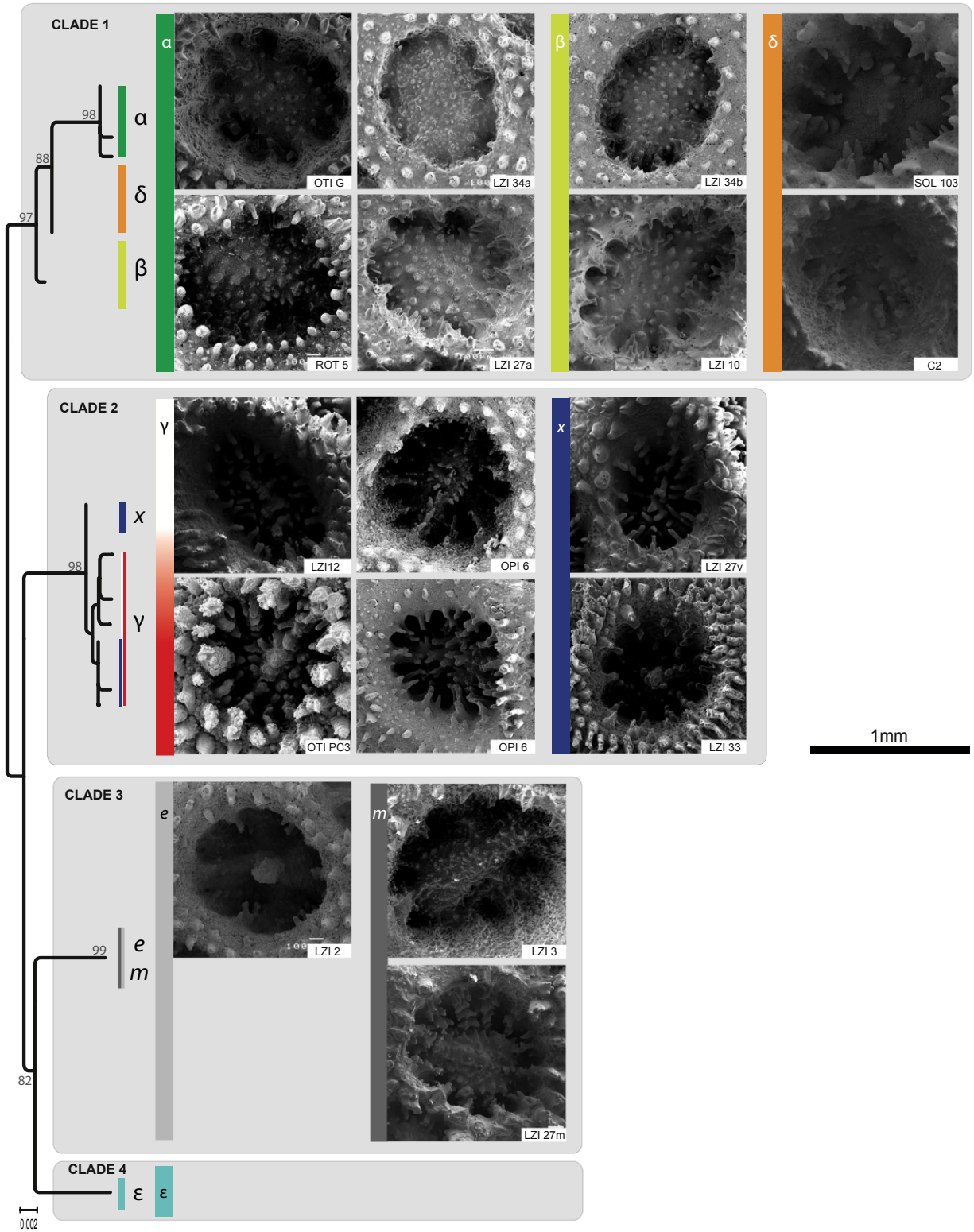

Figure 4. Fine-scale skeletal differences between genetic lineages. Left: phylogeny based on ORF region resolving in four main clades (bootstrap values over 70 are shown as grey numbers). Right: scanning electron micrographs of different species (bar on the left indicates scale). Clade 1: *Pocillopora damicornis* Type α (*P. damicornis*), *P. damicornis* Type β (*P. acuta*), *P. damicornis* Type δ (*P. aliciae*); Clade 2: *P. damicornis* Type γ (*P. verrucosa*), *Pocillopora* Type *x*, ***P. bairdi* sp. nov.**; Clade 3: *P. eydouxi e*, *P. meandrina m;* Clade 4: *P. damicornis* Type ε (*P.* cf. *brevicornis*) (no micrograph available).

P. favosa. *Pocillopora damicornis* Type β matched the holotype of *P. acuta* and agreed well with its columella structure (Fig. 8E). The name is derived from its characteristic pointy to sharp branch endings, which differentiate this species from morphs of *P. damicornis* (Table 2). The species varies from the elongate morphs found in sheltered environments to more compact morphs found in exposed environments. *Pocillopora damicornis* Type δ has already been described as *P. aliciae* (Schmidt-Roach *et al*., 2013).

Both *P. damicornis* Type γ and *P. verrucosa* (Ellis & Solander, 1786) share five mitochondrial haplotypes with minor divergence from one another and no clear morphological pattern. Furthermore, nuclear markers failed to recover genetic discontinuities between *P. damicornis* Type γ and *P. verrucosa* (Schmidt-Roach *et al*., 2012a). Thus, we conclude that Type γ and *P. verrucosa* are a single species, morphologically ranging from a typical *P. verrucosa* morphology (i.e. equally sized and distributed verrucae) to a *P. damicornis*-like morphology [i.e. a lack of true verrucae and unequally sized and distributed branchlets; which initially led Schmidt-Roach *et al*., (2012a) to differentiate between *P. verrucosa* and *P. damicornis* Type γ]. As the type material of *Pocillopora verrucosa* (Ellis & Solander, 1786) is also lost to science, a neotype was defined for this species (see systematic account).

Fine-scale skeleton structure suggested little differentiation between *P. verrucosa* and the new putative species (*x*) (Fig. 4). However, distinct gross morphology, partial mitochondrial and strict nuclear divergence (HSP70) supported the separation of the new morphotype from *P. verrucosa*. Due to its mismatch with existing *Pocillopora* descriptions, it is here described as a new species named *P. bairdi* sp. nov. (Schmidt-Roach, this study).

For clade 3, the original descriptions of *P. eydouxi* Edwards & Haime, 1860 and *P. meandrina* Dana, 1846 agree morphologically well with our samples and the fine-scale morphological characteristics. Edwards & Haime (1860) illustrated well the styloid columella development of *P. eydouxi*. Thus, the different columella development seems to be of value in differentiating these two species.

The sample of *P. damicornis* Type ε corresponded well with the description of *P. brevicornis* Lamarck, 1816. However, due to the lack of skeleton material and additional specimens a formal revival of this species is not possible at this time.

DISCUSSION

We provide clear lines of evidence for morphological differentiation of multiple genetically distinct lineages previously recovered within *Pocillopora damicornis* (Schmidt-Roach *et al*., 2012a). Mitochondrial molecular phylogenies were congruent with gross morphological groups at the species level. Fine-scale skeleton differences supported clade-level and even some species-level divergence, confirming the taxonomic utility of fine-scale skeleton structure reported for other coral taxa (Benzoni *et al*., 2010, 2012; Gittenberger *et al*., 2011; Stefani *et al*., 2011). Comparisons between the morphotypes recovered in this study and type specimens or original descriptions of *Pocillopora* spp. demonstrated that, with one exception (*P. bairdi* sp. nov.), each of these genetically distinct lineages corresponds to previously described species.

Nevertheless, classification of species solely on the basis of skeleton morphology remains unreliable due to high levels of gross morphological plasticity and partial cryptic morphologies (Fig. 3). Indeed, colonies or branches within colonies exhibiting an apparent gross morphological transition from one species to another can be found for almost all species within the genus, which has led to taxonomic confusion in the past. In addition, conventional species concepts (i.e. biological, phylogenetic) fail to fully resolve species boundaries if applied singularly. For instance, *P. damicornis* and *P. verrucosa* could not be assumed as two biologically or phylogenetically distinct taxa given the limited resolution power of the nuclear regions (ITS2, HSP70), due to apparent occasional introgressive hybridization (Schmidt-Roach *et al*., 2012a). Fine-scale morphological analyses, by contrast, could strictly resolve both species.

Here we reliably differentiate species within the genus based on a multi-level approach combining morphological and genetic data (including data of previous studies on molecular phylogenies; Flot *et al*., 2008; Schmidt-Roach *et al*., 2012a, 2012b), complemented by findings from previous studies on reproductive traits (Schmidt-Roach *et al*., 2012a, 2012b) and symbiont association (Pinzón & LaJeunesse, 2010; Schmidt-Roach *et al*., 2012a) (see below). Thus, applying species criteria in synergy as proposed by the USC (De Queiroz, 2007) we achieve reliable differentiation among these species and we assess speciation levels in *Pocillopora*.

Species evolution in *Pocillopora*

The degree of variation found in each of the criteria applied to delineate *Pocillopora* species depicts the genealogical history of the distinct taxa assigned by our approach as well as the mechanisms underlying speciation within the genus. Reproduction based on asexual brooding and sexual spawning constitutes a synapomorphic character for clade 1 (*P. damicornis*, α; *P. aliciae*, δ; *P. acuta*, β). It is therefore plausible

Table 2. Summary of morphological differences between the investigated *Pocillopora* species

Clade	Species	Initial designation	Code	Columella	Septa	Gross form	Branch tips	Colour and pigmentation of the live colony
1	*P. damicornis*	*P. damicornis* Type α	α	flat, ornamented with very short spinulae	rudimentary, often only indicated by spinulate septa teeth	cespitose, rather stout, with increased ramification towards the apex in the tropics – elongate, slender, partly flattened branching in the subtropics	round	evenly pigmented (often pink to brown, rarely green). Less pronounced darker pigmentation around oral opening than *P. acuta*.
	P. acuta	*P. damicornis* Type β	β	flat, ornamented with very short spinulae	rudimentary, often only indicated by spinulate septa teeth	compact in exposed environments to elongate, spaced in sheltered environments	pointy, sharp, acute	pale (sometimes greenish, pinkish) with characteristic darker pigmentation surrounding oral opening of polyps (giving appearance of brown rings outlining polyps)
	P. aliciae	*P. damicornis* Type δ	δ	weakly developed and flat	robust, almost horizontally branching, small short sub-branches arise vertically from the main branches	round	green	
2	*P. verrucosa*	*P. damicornis* Type γ	γ	absent to spinulate	septa indicated by irregular, long (~100–150 μm) spinulate septa teeth	branches almost cylindrical, robust, sometimes slightly flattened towards branch tips to swollen ends and commonly growing in high stalks (> 40 cm)	round	usually brownish to pale, rarely pink, with darker pigmentation around oral opening, similar to *P. acuta*
	***P. bairdi* sp. nov.**	*Pocillopora* sp. *x*	*x*	absent to spinulate		corallum is fragile, with evenly sized branches and evenly arranged small verrucae	round	mostly pale to light brown, rarely pink.
3	*P. eydouxi*	*P. eydouxi*	*e*	styliform columella, with one to three distinct stylae	septa often indicated only by short (~100 μm) septa teeth	corallum is ramose, verrucate, branching varies from meandering-lamellar, broad-ended to cylindrical	round, long verrucae	evenly pigmented brown to pink
	P. meandrina	*P. meandrina*	*m*	oval-convex to styloid, rarely obsolete	septa vary in their development from almost reduced to well indicated by long spinulae	corallum cespitose, very neatly verrucose, summits often naked, mostly lamellar and sinuous branches	round	evenly coloured, yellow, brown, pink, blue, or green.
4	*P.* cf. *brevicornis*	*P. damicornis* Type ε	ε	n/a	n/a	compact, even-topped, irregular but short subbranching	round, short	pale, brownish

that clade 1 originated from a shift in its reproductive strategy (i.e. ancestral spawning) to a mixed mode of asexual brooding and sexual spawning, leading to reproductive isolation from its congeneric lineages and divergence (Schmidt-Roach *et al*., 2012b). The same mechanism seems to have induced divergence between the brooding genus *Isopora* and the spawning *Acropora* (Wallace *et al*., 2007). Seemingly, divergence between *Pocillopora* and the sister genera *Stylophora* and *Seriatopora* is based on the evolution of a different reproductive mode (spawning versus brooding in *Stylophora* and *Seriatopora*; Shlesinger, Goulet & Loya, 1998). Furthermore, a mismatch in reproductive timing may have reinforced speciation of *P. acuta* and *P. damicornis* with both maintaining reproductive cycles at opposite lunar phases in the Great Barrier Reef and Hawaii (Richmond & Jokiel, 1984; Schmidt-Roach *et al*., 2012a). However, introgressive hybridization suggests that different reproductive traits do not necessarily lead to complete reproductive isolation (e.g. a putative hybrid between *Stylophora pistilata* and *Pocillopora damicornis* was identified at Lord Howe Island; Miller & Ayre, 2004).

In *Pocillopora*, symbiotic algae are transferred maternally and co-evolve with the host, leading to apparent consistent species-specific associations observed over variable geographical scales (Pinzón & LaJeunesse, 2010; Schmidt-Roach *et al*., 2012a). On the other hand, Bongaerts *et al*. (2010) identified habitat-specific symbiont associations characterizing genetically highly divergent *Seriatopora hystrix* Dana (1846) populations. Therefore, both host and symbiont play a role in influencing processes related to the coral's niche adaptation, a key process for reproductive isolation and genetic differentiation of a sub-group from the rest of the population. Selective pressure acting at the symbiont level may, in particular, increase isolation of populations in high latitudinal environments by limiting successful migration of less adapted individuals. Indeed, *P. aliciae* at the Solitary Islands and *P. damicornis* at Lord Howe Island are characterized by endemic symbiont associations (Wicks *et al*., 2010; Schmidt-Roach *et al*., 2012a). However, further research is necessary to understand the impact of the association between specific *Symbiodinium* types and host in the speciation process.

Clade 2 comprises *P. verrucosa* (γ) and *P. bairdi* sp. nov. (*x*), which is characterized by an absence of styloid columella, a character opposed to flat developed columella of species within clade 1. Interestingly, a distinct morphology was not recovered for several mitochondrial haplotypes found within the *P. verrucosa* cluster (Fig. 4, excluding the new species described), confirming that high plasticity and fluent phenotypic transitions characterize this species (Schmidt-Roach *et al*., 2012a). Indeed, microsatellite data show that *P. verrucosa* has a homogeneous population structure over several thousand kilometres (Pinzón *et al*., 2013). Reticulate evolution is probably responsible for the mitochondrial and nuclear sequence diversity in *P. verrucosa*, i.e. temporally isolated populations may have accumulated sequence divergences, before reticulating into their ancestral lineage by hybridization. Furthemore, reticulation may explain a distinct mitochondrial lineage described as Type 7 by Pinzón *et al*. (2013) for the Indian Ocean (Fig. 5), which shows no genetic divergence from *P. verrucosa* using microsatellites. The species' gross morphological variation has led to much confusion in the past; i.e. *P. damicornis* from the Tropical Eastern Pacific is most likely *P. verrucosa* based on molecular phylogenies (Schmidt-Roach *et al*., 2012a). On the other hand, incomplete lineage sorting or introgressive hybridization seems to support the limited mitochondrial divergence of *P. bairdi* sp. nov. from *P. verrucosa*, a common phenomenon in the genus (e.g. Combosch *et al*., 2008; Flot *et al*., 2008; Schmidt-Roach *et al*., 2012a).

Clade 3 comprises *P. eydouxi* (*e*) and *P. meandrina* (*m*). A clear difference in columella development has been recovered between these two species, confirming them both as valid taxonomic units (Fig. 4) despite the absence of mitochondrial divergence and the limited differentiation recovered by the nuclear regions (Flot *et al*., 2008). In addition, Pinzón *et al*. (2013) found two distinct population clusters within this lineage (Type 1 & 9). Given their fossil age (Pliocene < 2.6 Myr, Felix, 1913; Veron & Kelly, 1988; late Pleistocene < 0.0117 Myr, López-Pérez, 2012) and estimated cnidarian mitochondrial mutation rates (0.055% per Myr, Hellberg, 2006), we consider the time elapsed since differentiation insufficient for mitochondrial lineage sorting in these two species.

Finally, clade 4 comprises a genetically distinct species probably corresponding to *P. brevicornis*. However, as mentioned previously, additional samples are necessary to confirm the taxonomic validity of this species.

Species within the genus *Pocillopora* have independent evolutionary trajectories. This conclusion is supported by microsatellite data finding no indication for recent hybridization between different *Pocillopora* species (Types 1, 3, 5, and 9; Pinzón *et al*., 2013), a finding that further confirms that these species are stable over time, hence explaining the accumulation of morphological, molecular, and reproductive divergences. However, limited nuclear divergences indicate that rare introgressive hybridization is likely to occur even between more distant species such as *P. damicornis* and *P. verrucosa*. The exchange of genes responsible for gross morphology during these events

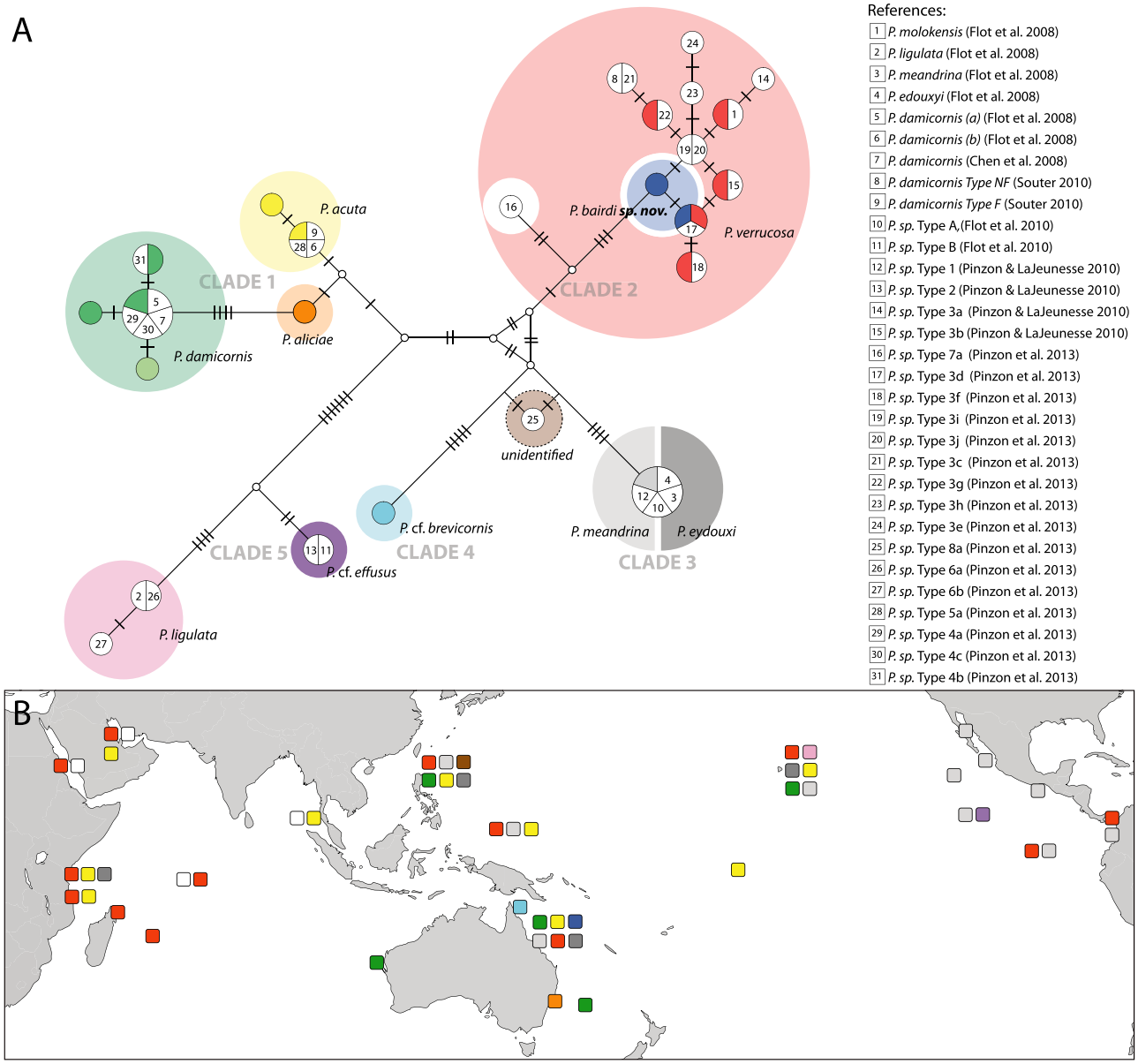

Figure 5. A, haplotype network based on ORF DNA sequence data and incorporating published *Pocillopora* sequence data from other locations across the Indian and Pacific Oceans (total alignment length 594 bp). B, geographical account of these lineages on a global scale based solely on genetic lineages.

may explain the apparent similarity between some of these species. Indeed, interspecific introgression is thought to increase the adaptive potential and reduce the risk of extinction. It may allow for the exchange of beneficial genetic variation among species (Seehausen, 2004), for example genes supporting adaptation to major environmental shifts. Thus, the apparent genetic transfer at evolutionary time scales between these species within *Pocillopora* may reduce the individual risk of extinction and accelerate evolutionary rates, leading to a high potential for adaptation.

In addition to the eight species described here, genetic data indicate that the well-defined morphospecies *P. ligulata* and *P.* cf. *effuses* also represent valid taxa (Flot *et al*., 2008; Pinzón *et al*., 2013). Furthermore, the genetically distinct lineage described as Type 8 by Pinzón *et al*. (2013) from Taiwan (Fig. 5) probably represents a valid species. Future research may identify or confirm additional rare species in the genus *Pocillopora*. However, the initially reported species diversity of 17 species (Veron, 2000) may have been overestimated. Further studies using the multidisciplinary approach applied here are needed to test for

the validity of such rare species that may have been missed in previous studies.

SYSTEMATIC ACCOUNT

ORDER SCLERACTINIA

FAMILY POCILLOPORIDAE GRAY, 1842

GENUS *POCILLOPORA* LAMARCK, 1816

Diagnosis

Hermatypic, plocoid, generally ramose, rarely massive or encrusting; septa are generally poorly developed and mostly arranged in two cycles; the columella is mostly poorly developed (Veron & Pichon, 1976), strong tabular endothecal dissepiments. Verrucae are common, although in some species reduced or absent.

SYNOPSIS OF SPECIES AND VARIETIES OF *POCILLOPORA* SPP. STUDIED*

**Footnote*: Due to the lack of fine-scale morphology data for *P.* cf. *brevicornis*, this species is not included in the key.

1. Columella weak to well developed, flat and irregular ornamented with short spinulae; brooding or spawning....2
- Columella obsolete, spinulate, oval-convex or styloid.....6

2. Corallum cespitose, bushy, irregular sized branchlets.....3
- Branches, ascending horizontal from the base, reticulate branching forming flat, plate-like appearance, verrucae are obsolete.....*Pocillopora aliciae*

3. Branches with increasing ramification towards the terminal branch end, branch endings blunt, rounded; living phenotype evenly pigmented, often brown or pink.....4
- Branches with elongate, pointy to sharp, thin branchlets of various length; living phenotype pale with characteristic darker pigmentation surrounding oral opening of polyp (brown rings).....5

4. Branches slender, round to flattened, deer-antler-like in subtropical locations to almost cylindrical, robust branches with swollen ends in tropical locations.....*Pocillopora damicornis*

5. Branches fine, elongate, slender to bushy branches (high sub-branching), crowded towards terminal end.....*Pocillopora acuta*

6. Reduced, irregularly developed verrucae, and cespitose sub-branching at branch endings, robust, often swollen ends and commonly growing in high stalks (> 40 cm). Verrucae reduced or absent on main stems.....*Pocillopora verrucosa*
- Verrucae well developed and equally distributed over corallum.....7

7. Branches compressed, mostly round and separate; phenotype pale, brown, rarely pink, darker around oral opening of polyp; columella obsolete or styloid.....8
- Branches compressed and meandering, robust with very equally sized verrucae; columella styloid or oval convex; often bright pink, blue or yellow, very evenly pigmented.....9

8. Branches spaced, robust (mostly > 1.2 cm), mostly cylindrical to terminal branch end. Summits verrucose.....*Pocillopora verrucosa*
- Branches thin (mostly < 1.2 cm), flattened towards branch end. Thickness relative equal from origin to terminal branch end. Verrucae equally distributed and short (~1 mm), mostly obsolete at summit.....***Pocillopora bairdi* sp. nov.**

9. Branches meandering, robust; equally sized, short verrucae covering branches; columella oval convex.....*Pocillopora meandrina*
- Branches spaced, meandering to cylindrical, larger then other species of the genus (mostly > 2 cm), very reduced sub-branching, large distances between ramifications; verrucae, evenly sized, and obsolete on summits; columella styloid.....*Pocillopora eydouxi*

POCILLOPORA DAMICORNIS (LINNAEUS, 1758) (FIGS 6, 7)

SYNONYMY

Millepora damicornis 1758 p. 791

Madrepora damicornis Pallas, 1766 p. 334, Esper (1791) pl. 46 & pl. 48

Pocillopora favosa Ehrenberg, 1834 p. 351

Taxonomic history

Linné (1758) based his description of *Pocillopora damicornis* on three references: Gualtieri (1742: pl. 31) (see Fig. 6H), Rumphius (1741: 243) (which shows a specimen of *Seriatopora hystrix*, later described by Dana, 1846), and Bauhin (1650: p. 846) (suggested to show *Millepora alcicornis* by Boschma, 1948). Initially described as *Millepora damicornis* by Linné (1758), the species was placed in the genus *Madrepora* by Pallas (1766), and subsequently into *Pocillopora* by Lamarck (1816). The genus *Pocillopora* was erected by Lamarck based on *Pocillopora acuta*, a taxon later synonymized under *P. damicornis* (Veron & Pichon, 1976). Three other species

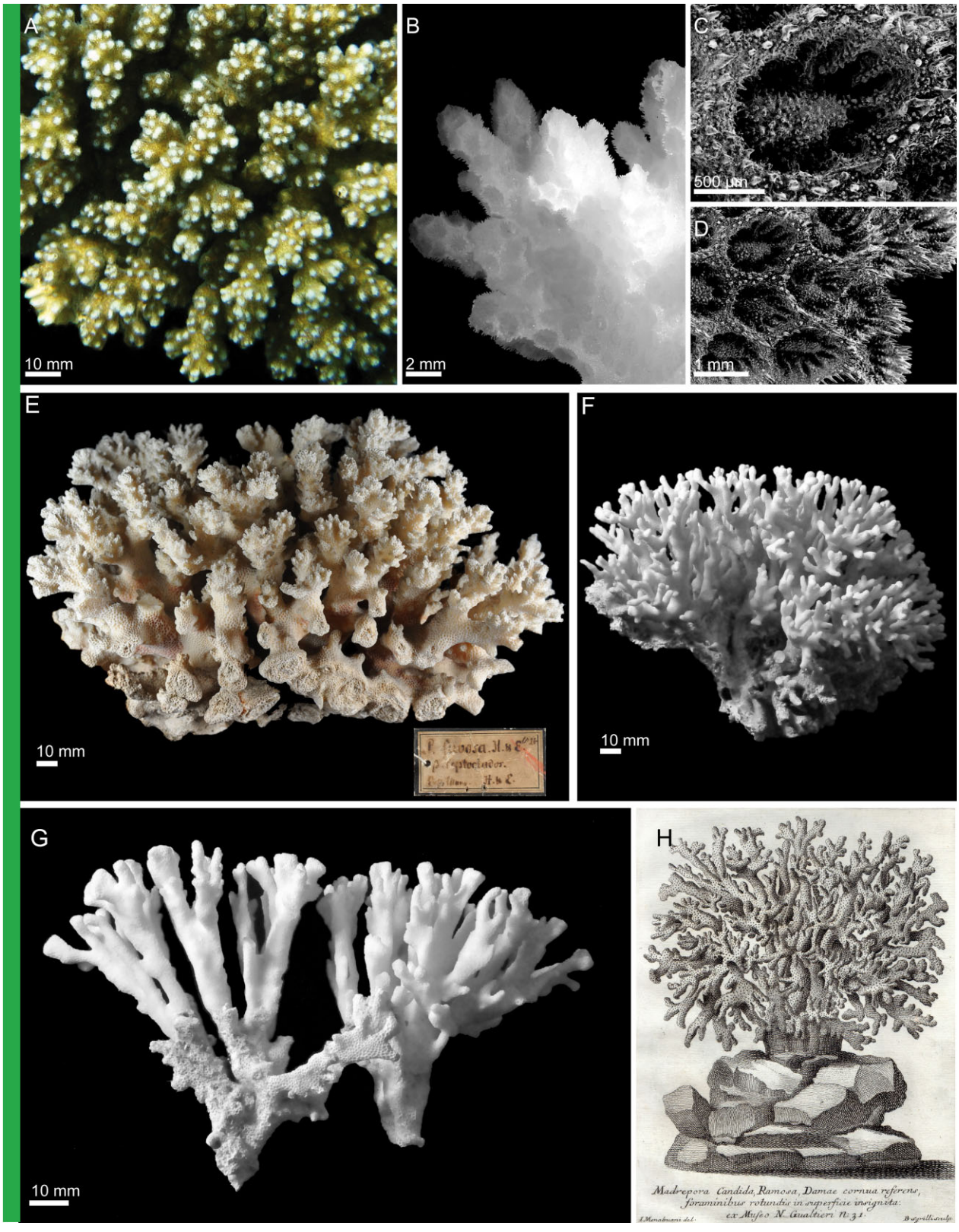

Figure 6. *Pocillopora damicornis*. A, *in situ*. B, skeleton of branch (side view). C and D, scanning electron micrographs (photos: Paul Muir). E, eorallum of type specimen of *P. favosa* Ehrenberg, 1834 (side view). F and G, elongate morphs of *P. damicornis* (side view; MTQ-G66090). H, first illustration of *P. damicornis* by Gualtieri (1742).

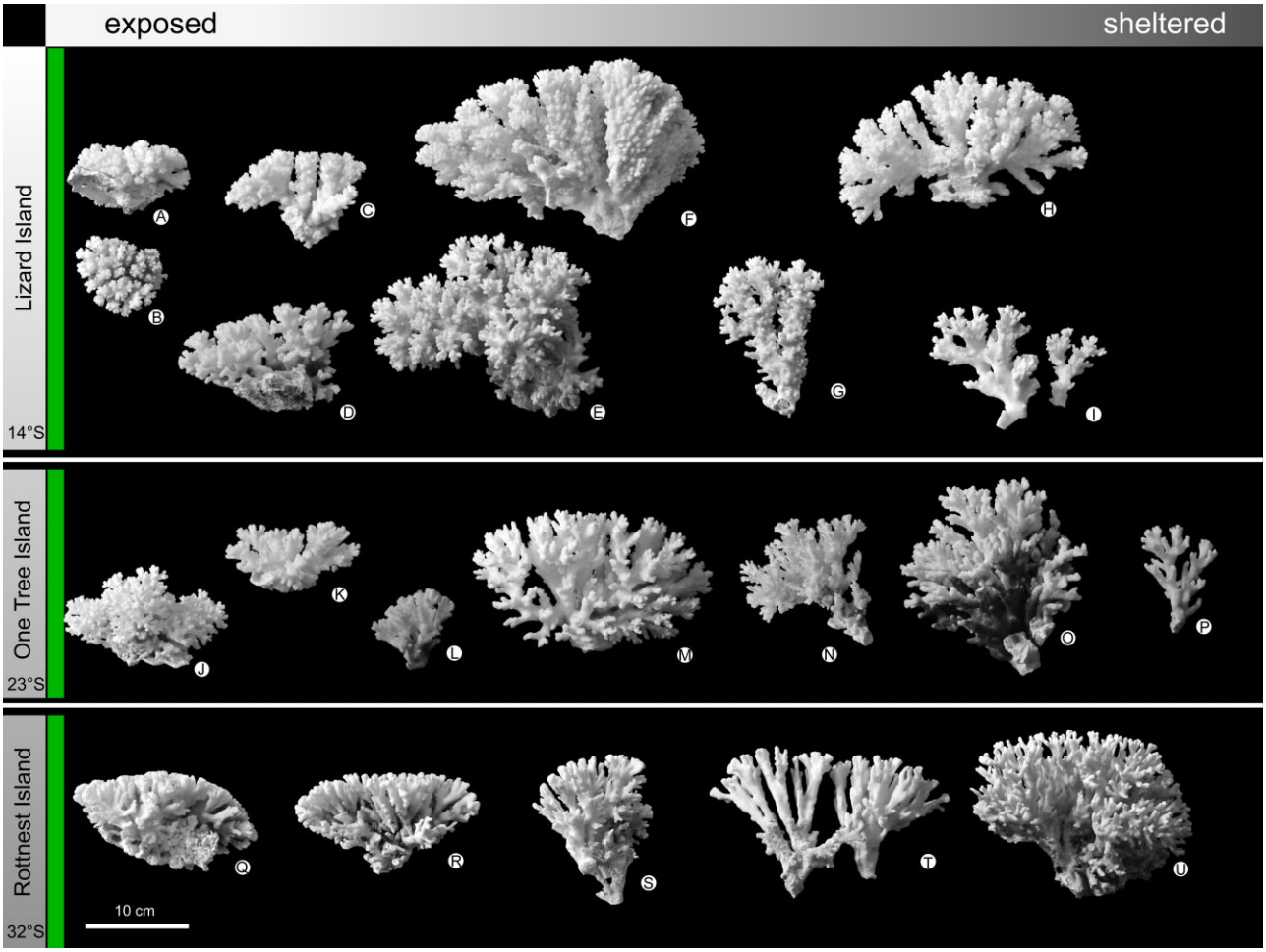

Figure 7. Illustration of morphological plasticity of the corallum of *Pocillopora damicornis* in different environments and at different latitudes (side views). MTQ-sample numbers: A, G66102; B, G66131; C, G66126; D, G66136; E, G66109; F, G66107; G, G66095; H, G66127; I, G66134; J, G66123; K, G66097; L, G66103; M, n/a; N, G66098; O, G66099; P, G66100; Q, G66093; R, G66094; S, G66121; T, G66091; U, G66090.

(*P. bulbosa*, *P. brevicornis*, *P. cespitosa*) were additionally synonymized under *P. damicornis* (Veron & Pichon, 1976), all considered to be morphological variants of a single taxon associated with different environments. Unfortunately the type specimen of *P. damicornis* is temporarily lost to science. The specimen is part of the royal invertebrate collection of Lovisa Ulrika of Prussia, Queen of Sweden, which is now curated by the Uppsala University Museum of Evolution, Uppsala. Linné examined her collection ('Museum Ludovicae Ulricae'), housed at the castle of Drottingholm near Stockholm, on several occasions to describe these specimens, later partly published in the 10th edition of Systema Naturae (Linné, 1758) (Wallin, 2001). However, Linné produced no labels or inscriptions for the specimens, making subsequent identification of the type specimens extremely difficult (Wallin, 2001). Linné adopted the name '*damicornis*' from Gualtieri (1742) who labelled his illustration: 'damae cornua'. Considering Linné's description of branches 'formed like Fallow Deer antlers' (a deer species he described himself; *Dama dama* Linneaus, 1758), it is likely that he examined a specimen of *P. damicornis* Type α, which has antler-shaped branching in some geographical locations (Fig. 7Q–U), including the Indo-Pacific where the type specimen was sampled. However, the species has been the subject of much confusion, particularly the differentiation between *P. bulbosa* and *P. damicornis*. Hoffmeister (1925) synonymized *P. bulbosa* Ehrenberg, 1834 and *P. ceaspitosa* Dana, 1846 as varieties of *P. damicornis*. The most recent revision of these taxa supported this idea but differentiated four ecomorphs, including *P. brevicornis* and *P. bulbosa* as varieties of *P. damicornis*, all considered habitat-specific morphological varieties of a single

phenotypically plastic species (Veron & Pichon, 1976).

Holotype
Temporarily lost to science. Last reported in the castle of Drottingholm near Stockholm (Wallin, 2001).

Material studied
MTQ samples: G33397 (AIMS MCC) Wheeler Reef, Australia (18°48′S, 147°32′E); G33366 Bowl Reef, Australia (18°31′S, 147°32′E); G33365 North-West Reef, N of Thursday Island, Australia (10°33′S, 142°15′E); G33622, G33628 Shrimp Reef, QLD, Australia (18°53′N, 145°05′E). G33618 Bewick Island, QLD 0–12 m (14°26′S, 144°49′E); G3397 Wheeler Reef, QLD (18°48′S, 147°32′E). Further material: Lizard Island (11 specimens), Rottnest Island (6 specimens), One Tree Island (10 specimens) (see Table S1).

Corallum
Compact to elongate, very plastic in its branching, and rounded branch endings. Two morphological variants can be differentiated, which are found at different latitudes. Subtropical *P. damicornis* is elongate, slender, partly flattened branching, verrucae obsolete (Fig. 7P–U). *Pocillopora damicornis* in lower latitudes in Australia (> 20°S) shows a cespitose corallum, is rather stout, with increased ramification towards the apex (Fig. 7A–I). Main stems are robust and range in height from short in exposed environments to a more cespitose, elongate growth with higher ramification of the main stems in sheltered environments. There is a gradual gradation between these morphological variants in Eastern Australia from the tropics to the subtropics (Fig. 7J–P).

Corallites and coenosteum
Calices are 0.8–1.4 mm in diameter and mostly round, but can be oval towards the branch ends. The columella is flat and ornamented with short spinulae, septa are rudimentary often only indicated by spinulate septa teeth. The coenosteum is ornamented sparsely to densely with short spinulae.

Colour and pigmentation of the live colony
Phenotype evenly pigmented (pink to brown, rarely green).

Habitat and biology
In the Central and Northern Great Barrier Reef this species is common on the exposed side of reefs in high-energy environments. It was observed from lagoons, back reef habitats, and the deeper habitats of the reef slope (> 8 m), but is most abundant at the reef crest where it occurs partly in sympatry with *P. acuta*. In the Southern Great Barrier Reef this species is very abundant and occurs in most habitats. *Pocillopora damicornis* has a mixed mode of reproduction. It reproduces asexually through the production of brooded larvae (Stoddart, 1983; Ayre & Miller, 2004; Sherman, Ayre & Miller, 2006) and reproduces sexually by broadcast spawning gametes (Schmidt-Roach *et al.*, 2012b). It releases brooded larvae around full moon on the Great Barrier Reef (Tanner, 1996; our pers. observ.), but releases brooded planulae close to new moon in Western Australia (Ward, 1992).

Remarks
A rapid genetic assay for the identification of this genetic lineage on the Great Barrier Reef has been recently developed and successfully employed in a population genetic study, further confirming reproductive isolation of this lineage from *P. acuta* (Torda *et al.*, 2013).

Distribution
Pacific Ocean, Indian Ocean. Specimens were identified from various locations along the Great Barrier Reef down to the subtropical reefs of Lord Howe Island, as well as at subtropical locations in Rottnest Island in Western Australia. Sequences from public databases indicate an Indo-Pacific distribution of this species from Taiwan and Hawaii to the Indian Ocean; it seems to be absent in the Tropical Eastern Pacific and possibly the Western Indian Ocean as the genetic lineage could not be identified in this region (see Flot *et al.*, 2010; Pinzón & LaJeunesse, 2010; Pinzón *et al.*, 2013) (Fig. 5).

POCILLOPORA ACUTA (LAMARCK, 1816) (FIGS 8, S2)

SYNONYMY

Pocillopora acuta Lamarck, 1816 p. 274
Pocillopora bulbosa Ehrenberg, 1834 p. 351 (p 127)
Madrepora damicornis 1766 p. 334, Esper (1791) pl. 46A
Pocillopora apiculata Ehrenberg, 1834 p. 351
Pocillopora cespitosa Dana, 1846 p. 525, pl. 49, fig. 5, 5a
Pocillopora subacuta Edwards & Haime, 1860 p. 303

Taxonomic history
Pocillopora acuta Lamarck (1816) defines the genus *Pocillopora* (type specimen Fig. 8E). Esper (1791) illustrated a colony of Pallas's (1766) *Madrepora damicornis* type 8F as an elongate, fine branching morph, later in literature commonly referred to as Ehrenberg's (1834) species *Pocillopora bulbosa*. Dana's (1846) interpretation of this elongate morphology as

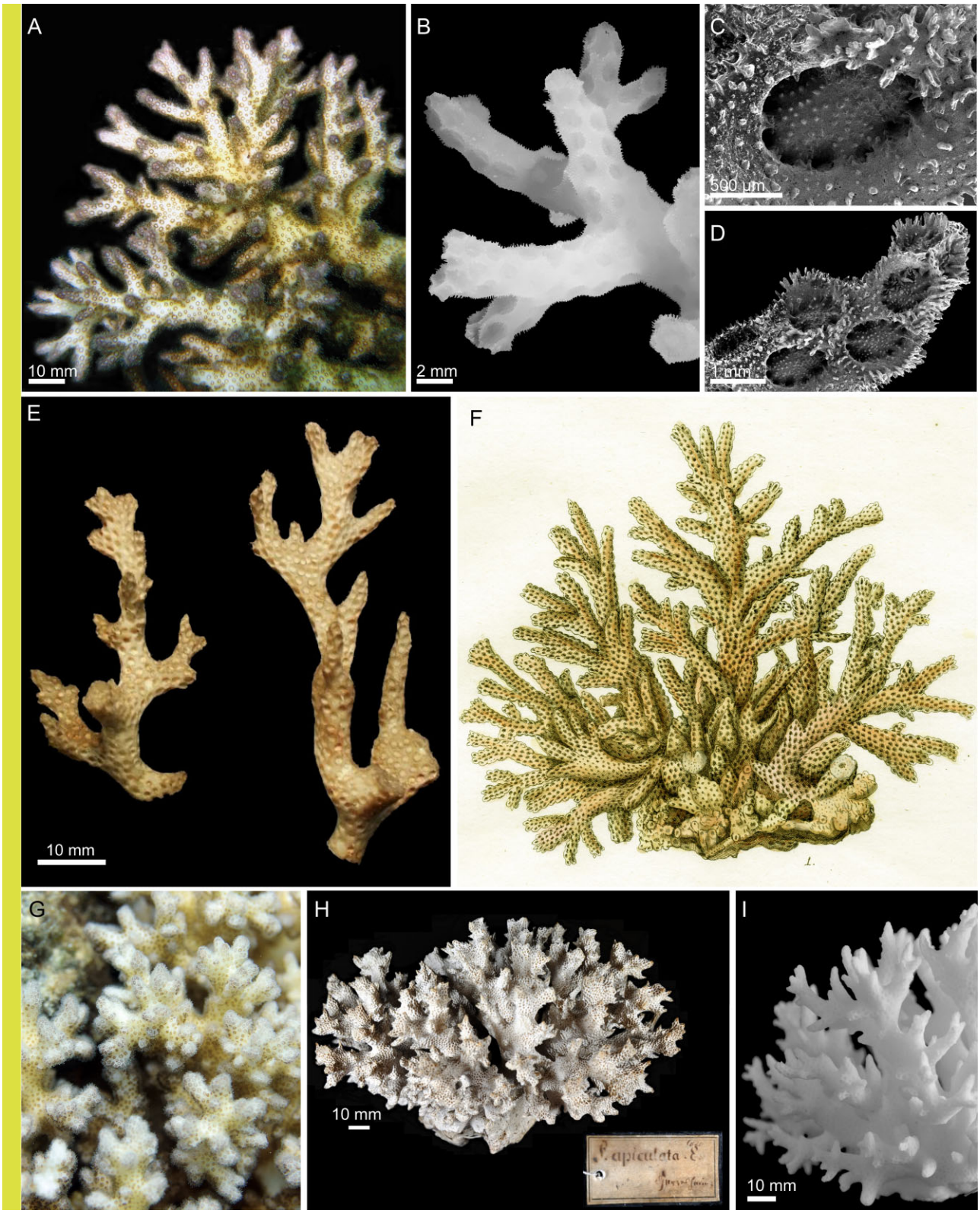

Figure 8. *Pocillopora acuta*. A, *in situ* appearance. B, skeleton of specimen. C and D, scanning electron micrographs of specimen (photos: Paul Muir). E, side view of corallum of holotype of *Pocillopora acuta* Lamarck, 1816 (photo: Michel Pichon). F, drawing by Esper (1791). G, *P. acuta* morph *in situ*. H, holotype of *Pocillopora apiculata* Ehrenberg, 1834. I, skeleton of compact morphology of *P. acuta* (MTQ-G66112).

P. bulbosa led to much confusion in consecutive descriptions. However, Lamarck (1816) referred to Esper's (1791) illustration as representing *P. acuta*. The type specimen of *P. bulbosa* (a relatively small fragment) shows a compact morphology and does not match what has been referred to as *P. bulbosa* in the literature. Furthermore, Ehrenberg's collection contains a specimen labelled *P. acuta*, which matches Lamarck's description. Thus, *P. bulbosa* represents a junior synonym of *P. acuta*. In addition, Ehrenberg (1834) described a moderately compact morph of this taxon as *Pocillopora apiculata* (Fig. 8H). Dana (1846) described and illustrated this species as *P. cespitosa* (plate 49, fig. 5).

Holotype
MNHN-IK-2010-792 (Fig. 8E). Origin: Indian Ocean.

Material studied
MTQ samples: G37619 China Sea, Pratas Reef (21°50′N, 117°00′E); G33370 Orpheus Island (18°36′S, 146°29′E); 51948 Gulf of Aden, Yemen (12°47′N, 045°03′E); G33627 Shrimp Reef, QLD, Australia (1853′S, 14805′E); G33376 Fantome Island (Palm Islands), QLD, Australia (15–20 m) (18°41′S, 146°31′E). G33375 Houghton Island, QLD, Australia (14°31′S, 144°58′E). G35114 Flinders Reef (Coral Sea), 5 m (17°40′S, 148°20′E). Further material: Orpheus Island (2 specimens), Lizard Island (12 specimens) (see Table S1).

Corallum
Compact in exposed environments to elongate in sheltered environments (Fig. S3). Cespitose, much branched, branches mostly round and rarely flattened. This species shows consistently pointy branches, with sharp tips, a feature that differentiates it from its sister taxon *P. damicornis*. Two morphological variants can be differentiated, which are found in exposed and sheltered environments, respectively. *Pocillopora acuta* in sheltered environments is characterized by elongate, fragile, slender branches almost approaching *Seriatopora hystrix* Dana, 1846 (Fig. S3E–J) but no seriate cells. *Pocillopora acuta* in exposed environments resembles *P. apiculata* Ehrenberg, 1834. The corallum is compact to compressed, but still cespitose with crowded branches (Fig. S3A–D).

Corallites and coenosteum
Calices are 0.7–1.3 mm in diameter, often oval due to the narrow, slender growth. The columella is flat and ornamented with short spinulae, septa are only rudimentarily developed, often only indicated by spinulate septa teeth and arranged hexamerally in two equally developed cycles. The coenosteum is ornamented sparsely to densely (mostly towards the branch endings) with short spinulae.

Colour and pigmentation of the live colony
Pale (sometimes greenish) with characteristic darker pigmentation surrounding oral opening of polyps (giving appearance of brown rings outlining polyps).

Habitat and biology
In the Central and Northern Great Barrier Reef this species is common on the leeward site of the reefs, but compact morphs can also be found in exposed environments. It occurs in lagoons, back reef habitats to the deeper (> 12 m) habitats of the reef slope. In sheltered habitats the fine morphology is exhibited. At One Tree Island in the southern Great Barrier Reef this species was not recorded. *Pocillopora acuta* releases brooded asexual larvae after new moon (Schmidt-Roach *et al*., 2012a), supporting earlier observations of brooding in this species (Marshall & Stephenson, 1933). Although it has not been observed to spawn, it is expected to have a mixed mode of reproduction as observed in its sister species *P. damicornis* (Schmidt-Roach *et al*., 2012b).

Remarks
A rapid genetic assay for the identification of this genetic lineage on the Great Barrier Reef has been recently developed and successfully employed in a population genetic study, further confirming reproductive isolation of this lineage from *P. damicornis* (Torda *et al*., 2013).

Distribution
Specimens were identified from various locations along the Great Barrier Reef, but no colonies were observed at One Tree Island in the Southern Great Barrier Reef. Sequences from public databases indicate a wide distribution of this species reaching from the central Pacific to the Indian Ocean; it seems to be absent in the Tropical Eastern Pacific as the genetic lineage was not identified in the region (see Flot *et al*., 2010; Pinzón & LaJeunesse, 2010; Pinzón *et al*., 2013) (Fig. 5).

POCILLOPORA ALICIAE SCHMIDT-ROACH *ET AL*., 2013 (FIGS 9, S4)

Taxonomic history
Pocillopora aliciae was previously considered a temperate ecomorph of *P. damicornis* (e.g. Veron &

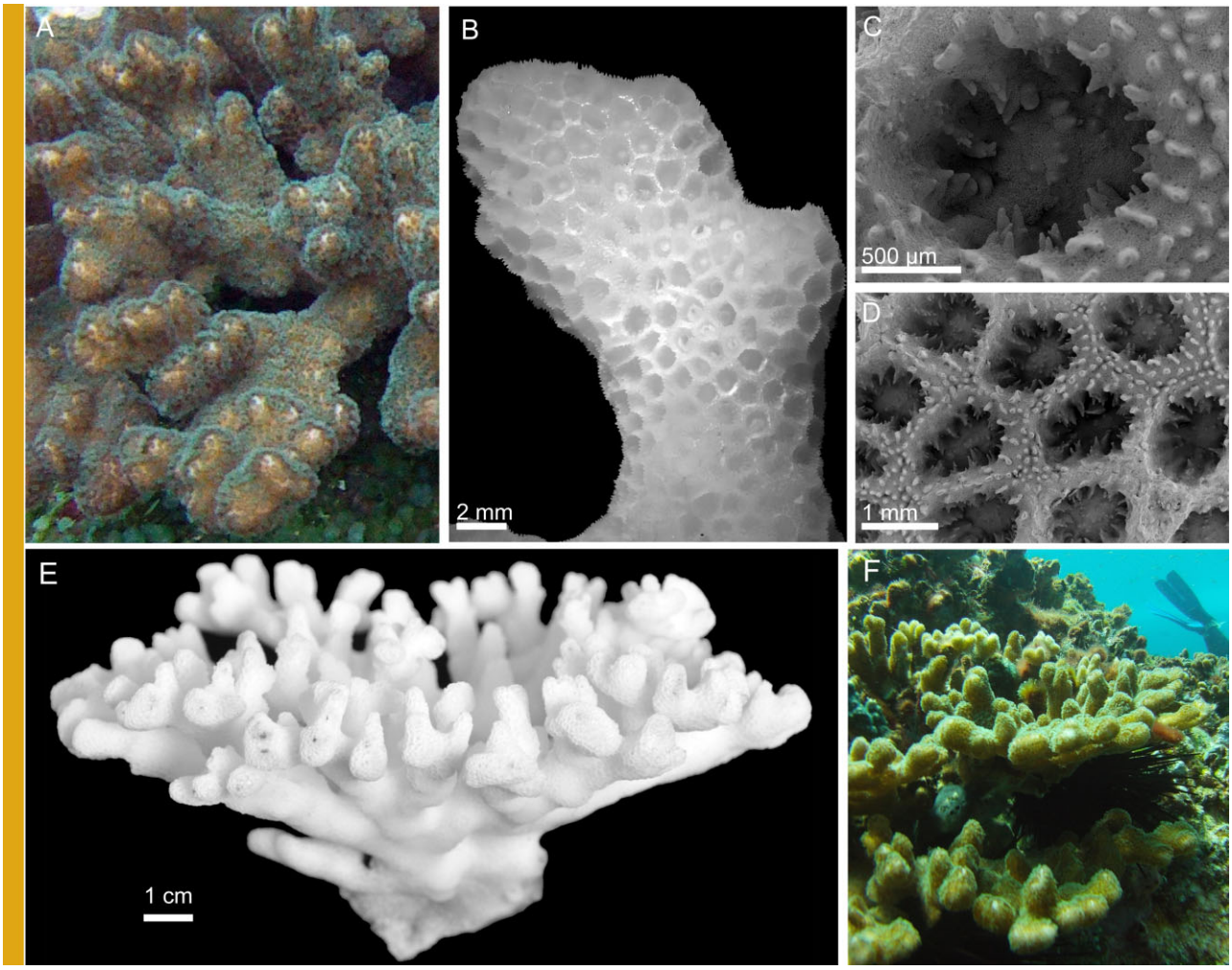

Figure 9. *Pocillopora aliciae*. A, field appearance. B, skeleton of branch. C and D, scanning electron micrographs of corallite structure. E, corallum of holotype (MTQ-G65423) (Schmidt-Roach *et al*., 2013). F, typical growth from on reef slope.

Pichon, 1976), but was recently described as a separate species (Schmidt-Roach *et al*., 2013).

Holotype
MTQ-G65423. Black Rock, off South Solitary Island, NSW, Australia (30°12′0.55″S, 153°15′27.05″E).

Other material studied
MTQ samples: G65424 (Paratype) same as holotype. G65425 Smoky Cape, NSW, Australia (30°54′22″S 15°35′9″E). G65900 Bryon Bay, NSW, Australia. G666153 Bryon Bay, NSW, Australia.

Corallum
Pocillopora aliciae is characterized by its robust, almost horizontal branching. Small sub-branches arise vertically from the main branches, but are generally short, giving the colony an overall flat appearance. Colonies seldom exceed 30 cm in diameter. Branch endings are rounded and verrucae reduced to entirely absent.

Corallites and coenosteum
Calices are 0.8–1.1 mm in diameter, the columella is weakly developed and flat, ornamented with short spinulae. The septa are hexamerally arranged in two cycles and weakly developed, often only indicated by spinulae. The coenosteum is ornamented with short spinulae.

Colour and pigmentation of the live colony
Green.

Habitat and biology
The species was observed on rocky habitats at depths of 2–32 m. *Pocillopora aliciae* releases brooded

larvae after full moon (Schmidt-Roach *et al*., 2012a). Although it has not been observed to spawn, it is expected to have a mixed mode of reproduction as observed in its sister taxon *P. damicornis* (Schmidt-Roach *et al*., 2012b).

Remarks
See Schmidt-Roach *et al*. (2013) for a more detailed description.

Distribution
The species has only been recorded on the east coast of New South Wales, Australia, from Byron Bay to Port Stephens. Genetic samples analysed originated from the Solitary Islands.

POCILLOPORA VERRUCOSA (ELLIS & SOLANDER, 1786) (FIGS 10, 11, S5)

SYNONYMY

Madrepora verrucosa Ellis & Solander, 1786 p. 172
Pocillopora hemprichii Ehrenberg, 1834 p. 352
Pocillopora danae Verrill, 1864 p. 59
?Pocillopora molokensis Vaughan, 1907 p. 91

Taxonomic history
Pocillopora verrucosa was described by Ellis & Solander (1786). Together with Joseph Banks, Solander joined the *Endeavour* voyage under Captain Cook. Returning from the Providential Channel in Northern Queensland, Australia, Banks notes in his journal the collection of 'many curious fish and mollusks besides corals of many species' (see Beaglehole & Banks, 1962). After returning to England, specimens collected at this and other locations visited by the HMS *Endeavour* were examined and described by Ellis & Solander (1786). Unfortunately, the type specimen could not be located in the Hunterian collection of the Museum of the University of Glasgow, which curates the corals described by Ellis and Solander. Eighteenth century specimens are largely unlabelled and confirmation of samples originating from Ellis and Solander is based on their illustrations, which are not known to exist for *P. verrucosa*. Due to this loss, a neotype is here defined from a geographical region likely to be the origin of the type specimen. The neotype was sampled at Lizard Island, which was visited by the *Endeavour* on the 12th of August 1770.

Holotype
Hunterian Museum in Glasgow was contacted, but a type could not be identified and is thus considered lost.

Neotype
MTQ-G65923 Lagoon, Lizard Island, QLD, Australia (14°41′14.94″S, 145°27′57.42″E). 2 m (19.11.2011) (Coll. S. Schmidt-Roach) (Fig. 10G–I).

Other material studied
Pocillopora verrucosa: MTQ-samples: G33427 Tijou Reef, QLD, Australia (13°10′S, 143°57′E) 0–10 m; G33405 same as before (1–2 m); G33424 Great Detached Reef, QLD, Australia, 0–15 m (11°42′S, 144°00′E); G33422 Bowl Reef QLD, Australia (0–10 m) (18°31′S, 147°32′E). G33417, G33619 Hope Island, QLD, Australia (0–3 m); G46830 South China Sea, Pratas Reef (20°35′N, 116°46′E); G43835 Philippines, Coron Island, Calis Point (11°34′N, 120°07′E), USNM no. 696 Type specimen of *Pocillopora danae* Verril, 1864 (based on photograph by Vaughan, 1918). MTQ samples: G66150 Galapagos, Ecuador; G66151 Gulto Dulce, 4–5 m, Costa Rica. G33384 Great Detached Reef, QLD, Australia 0–1 m (11°48′S, 144°03′E); G33383 AIMS site no. 33; G35117 Flinders Reef (Coral Sea), QLD, Australia (17°40′S, 148°20′E). G33392 AIMS site no. 33. G33393 QLD. Further material: Orpheus Island (4 specimens), Lizard Island (11 specimens), One Tree Island (1 specimen) (see Table S1).

Skeletal characteristics of the neotype
The corallum measures 188 mm in length, 161 mm in width, and 145 mm in height. The corallum is hemispherically cespitose, with spaced (approx. 8–10 mm between branches), robust and almost straight branching (diameter of main branches mostly > 12 mm). Two-dimensional ramification of two or more branches at branch tips may give some branches a flat appearance. Verrucae are equally distributed but irregular in size and shape, summits are verrucose. Calices are mostly round and usually smaller (approx. 0.4–0.7 mm) than those of *P. damicornis*, *P. acuta*, and *P. aliciae*. The columella is absent to styloid, mostly just indicated by its ornamentation with long spinulae, which may be arranged in a line; septa are only rudimentarily developed, often only indicated by irregular, but long (~100–150 μm) spinulate septa teeth and arranged hexamerally in two equally developed cycles. The coenosteum is ornamented sparsely to densely (mostly towards the branch endings) with spinluae, partly elongate in shape.

Corallum
Branches almost cylindrical, robust, sometimes slightly flattened towards branch tips to swollen ends and commonly growing in high stalks (> 40 cm). Verrucae evenly distributed over corallum, sometimes reduced or missing between branches; verrucae more irregular in height and width than those of

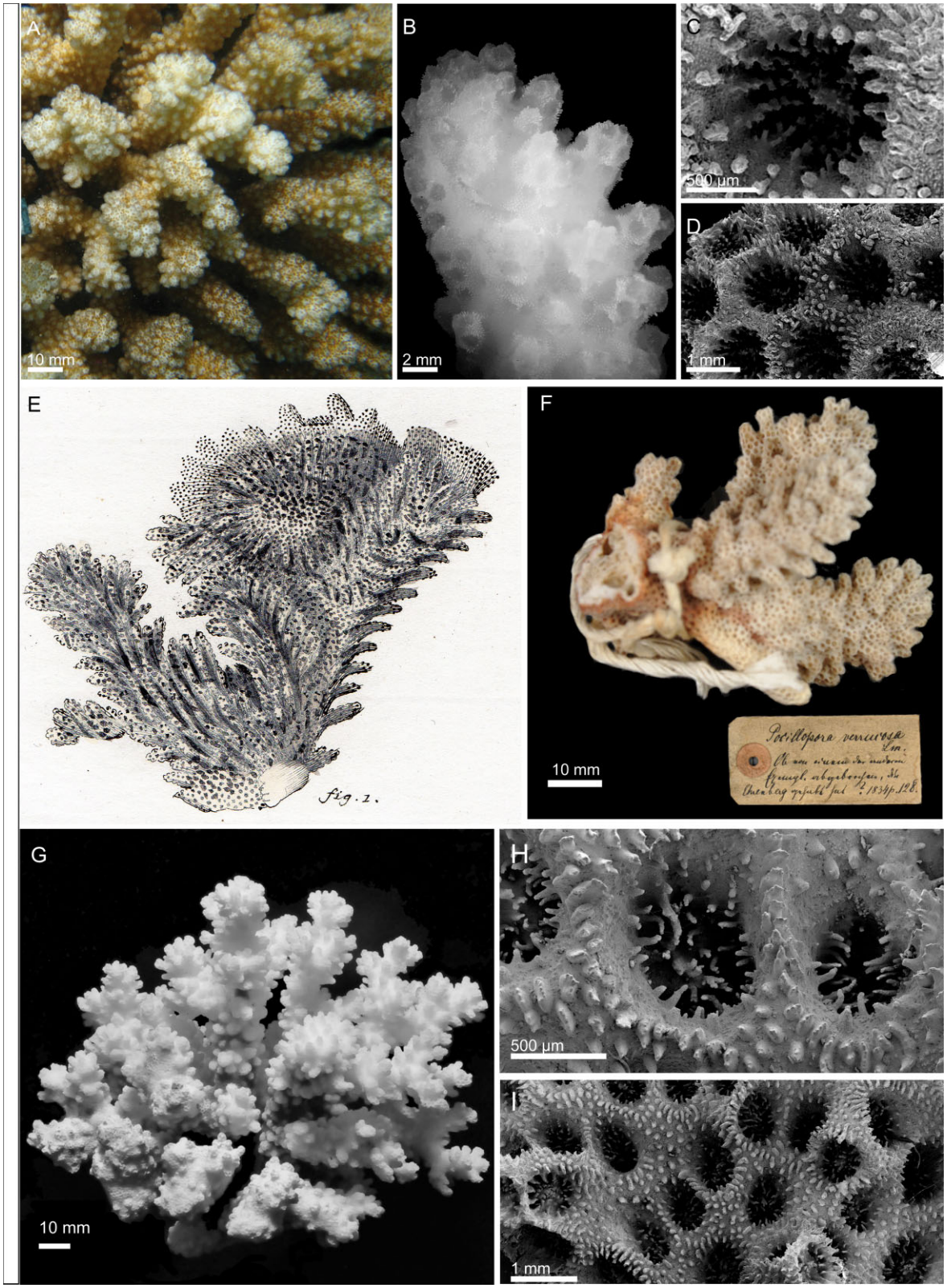

Figure 10. *Pocillopora verrucosa*. A, *in situ*. B, skeleton of branch. C and D, scanning electron micrographs (photos: Paul Muir). E, *Madrepora damicornis* Esper, 1791. F, specimen identified by Ehrenberg (1834) as *P. verrucosa*. G, sorallum of neotype (side view). H and I, scanning electron micrographs of neotype (MTQ-G65923).

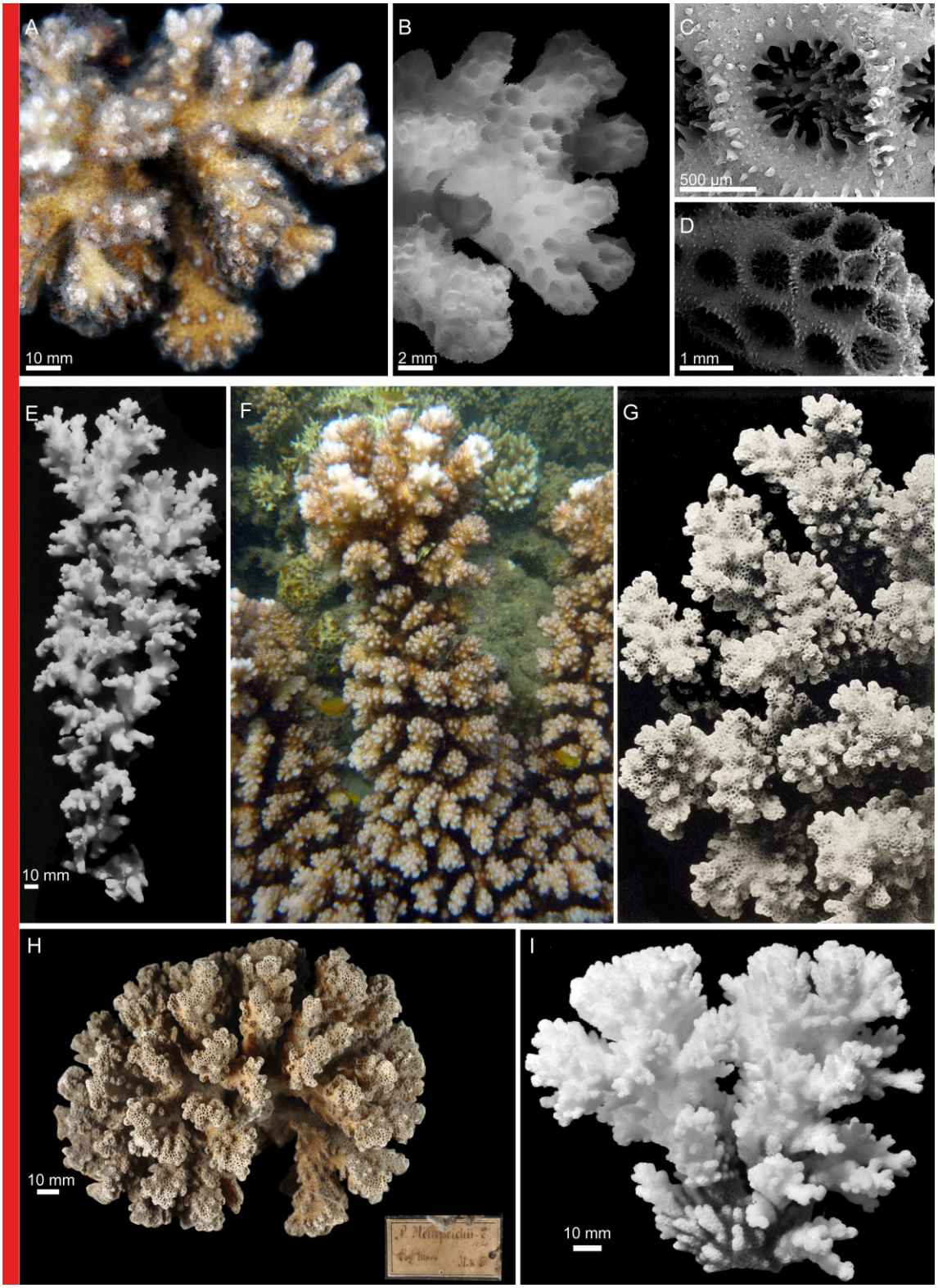

Figure 11. *Pocillopora verrucosa*. A, *in situ* appearance. B, skeleton of specimen. C and D, scanning electron micrographs of specimen (photos: Paul Muir). E, corallum of elongate 'damicornis-like' morph. F, colony at reef slope at Orpheus Island. G, corallum of holotype of *Pocillopora danae* (photo: Vaughan, 1918). H, corallum of holotype of *Pocillopora hemprichii* (side view). I, corallum collected at Lizard Island (side view) (MTQ-G66144).

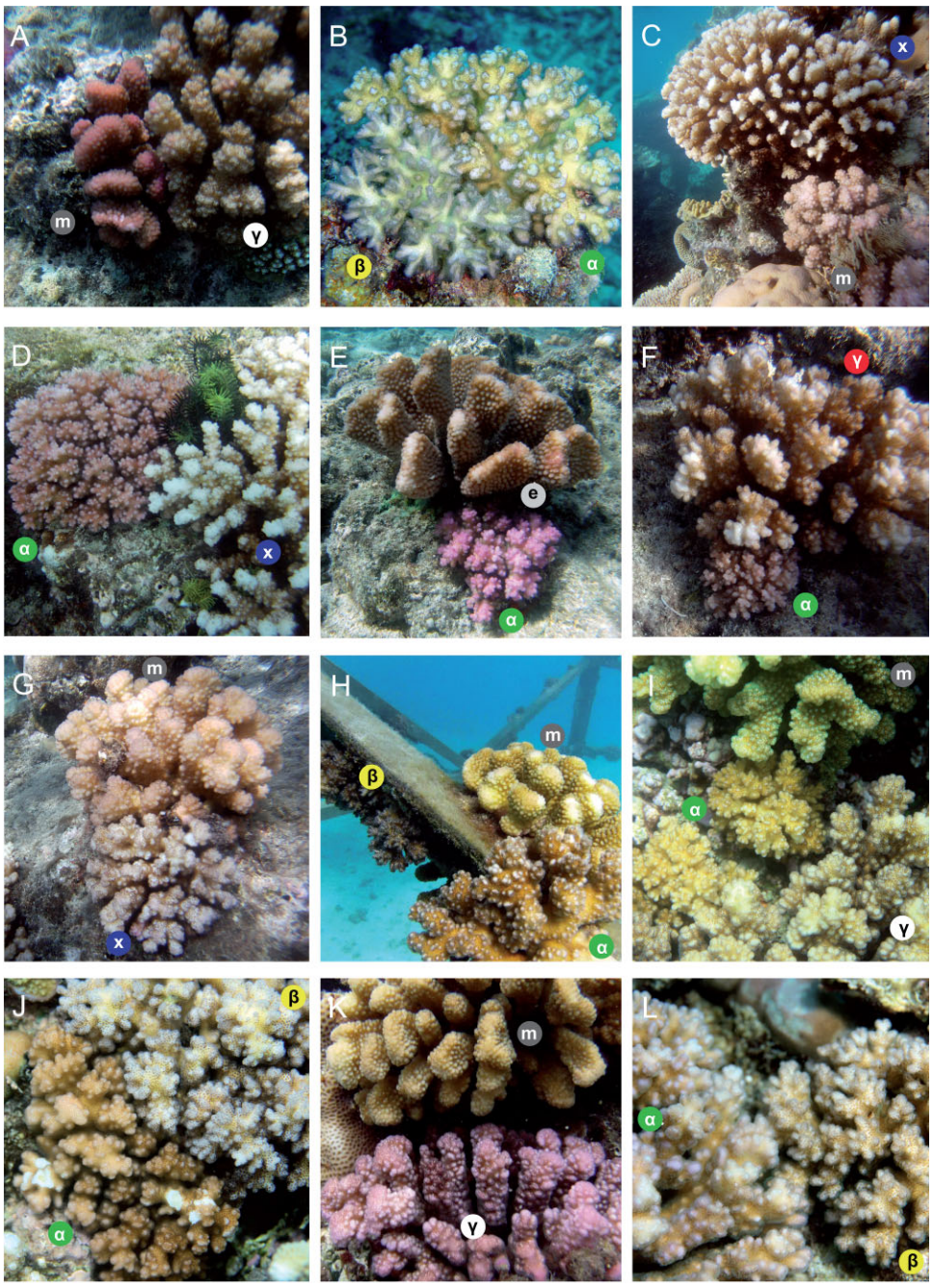

Figure 12. Field appearance of taxa in partial sympatry, when growing as mosaic colonies or in approximate distance to each other. α, *P. damicornis*; β, *P. acuta*; γ, *P. verrucosa*; *x*, ***P. bairdi* sp. nov.**; *e*, *P. eydouxi*; *m*, *P. meandrina*.

P. meandrina (see Fig. 12A, I, K) or verrucae reduced or absent on main stems, giving it a *P. damicornis*-like appearance. However, the branching is more spaced and less cespitose than in *P. damicornis*.

Corallites and coenosteum
As described for neotype.

Colour and pigmentation of the live colony
The colour of this species is usually brownish to pale, rarely pink, with darker pigmentation around oral opening, similar to *P. acuta*.

Remarks
As stressed by Schmidt-Roach *et al.* (2012a), specimens of *P. verrucosa*, *P. damicornis* Type γ and Tropi-

cal Eastern Pacific *P.* cf. *damicornis* are recovered within one mitochondrial clade and share identical haplotypes. Furthermore, the fluent morphological transition between *P. verrucosa* and *P. damicornis*-like morphs from the Tropical Eastern Pacific and of Type γ (reduced to absent verrucae) further strengthens that both present morphotypes of the same taxon. Thus, these lineages are here synonymized with *P. verrucosa*. We also agree with Sheppard (1987) that *P. danae* Verrill, 1864 presents a synonym of *P. verrucosa*. Genetically *P. molokensis* (Vaughan, 1907) seems to be recovered within *P. verrucosa* and may present a deep-water morph of this species (Schmidt-Roach *et al*., 2012a). Furthermore, the columella structure is similar to *P. verrucosa* (Vaughan, 1907: 91). However, the holotype morphology is quite distinct from *P. verrucosa* and further investigations including additional lines of evidence are needed to decide about the status of this taxon.

Habitat and biology
The species is often found to arise vertically with monopodial stems (see Fig. 11E, F) and commonly covers large areas of the reef slope of several square metres. Although the species has been reported to brood larvae, this probably relates to incorrect identification and the true *P. verrucosa* is a broadcast spawning species (see Schmidt-Roach *et al*., 2012b).

Distribution
Sequences from public databases indicate a cosmopolitan distribution from the Indian Ocean, Red Sea, and the Tropical Eastern Pacific (Fig. 5), which matches its distribution based on morphology (see Veron, 2000).

POCILLOPORA BAIRDI SP. NOV. SCHMIDT-ROACH, THIS STUDY (FIGS 13, S6)

Holotype
MTQ-G65918 Mermaids Cove, Lizard Island, QLD, Australia (14°38′46.4″S, 145°27′19.03″E). 3 m, (Nov 2011) (Coll. S. Schmidt-Roach) (Fig. 13B–E).

Paratypes
MTQ-G65921 same location as the holotype, 3 m (Nov. 2011) (coll.: S. Schmidt-Roach); MTQ-G65919 same as previous; MTQ-G65920 Trimodal Reef, Lizard Island, QLD, Australia (14°41′56–91″S, 145°26′52–54″E) (Fig. 13F). Other material studied: Lizard Island (1 specimen) (see Table S1).

Skeletal characteristics of the holotype
The corallum measures 197 mm in length, 147 mm in width, and 119 mm in height. Branches are thin (most < 1.2 cm in diameter), often flattened towards branch endings. Branch thickness is similar from origin to terminal branch end, which differentiates this species clearly from other *Pocillopora* species. Branch growth is directed upward, with sub-branches following this direction shortly after ramification, with spacing between branches of approximately 6 mm. Branches are of similar height and densely arranged, giving the corallum an overall round shape. Calices are 0.4–0.6 mm in diameter. Verrucae are equally distributed and short (~1 mm), strongly reduced to obsolete at summits.

Corallites and coenosteum of holotype
The columella is absent to styloid, often indicated just by its ornamentation with long spinulae, which may be arranged in a line (similar to *P. verrucosa*); septa are only indicated by irregular, but long (~100–150 μm) spinulate septa teeth and arranged hexamerally in two equally developed cycles. The coenosteum is ornamented sparsely to densely with spinulae. The specimen was pale to light brown when sampled and was found in a mosaic colony in sympatry with *P. damicornis* and *P. meandrina* (Fig. 13G, H).

Corallum
The species is very distinct in its growth from other taxa of the genus and easy to identify in the field. The corallum is fragile, with evenly sized branches and evenly arranged small verrucae. Overall, all specimens were very similar, but with one having branches that were slightly more elongate and thinner than the holotype (Fig. 13F).

Corallites and coenosteum
As described for the holotype.

Colour and pigmentation of the live colony
Mostly pale to light brown, rarely pink.

Etymology
This species is named after Dr Andrew H. Baird for his achievements in the field of coral biology and ecology and his support and great company during fieldwork activities.

Remarks
Some specimens were characterized by a unique mitochondrial haplotype in the ORF region; however, others were found to share a haplotype with *P. verrucosa*. All individuals had a single HSP70 haplotype which was distinct from the haplotypes found in all other species (Fig. S1). The lack of clear divergence from *P. verrucosa* in the ORF region may be explained by introgressive hybridization or incomplete lineage sorting, as observed in other taxa of the genus (see Schmidt-Roach *et al*., 2012a).

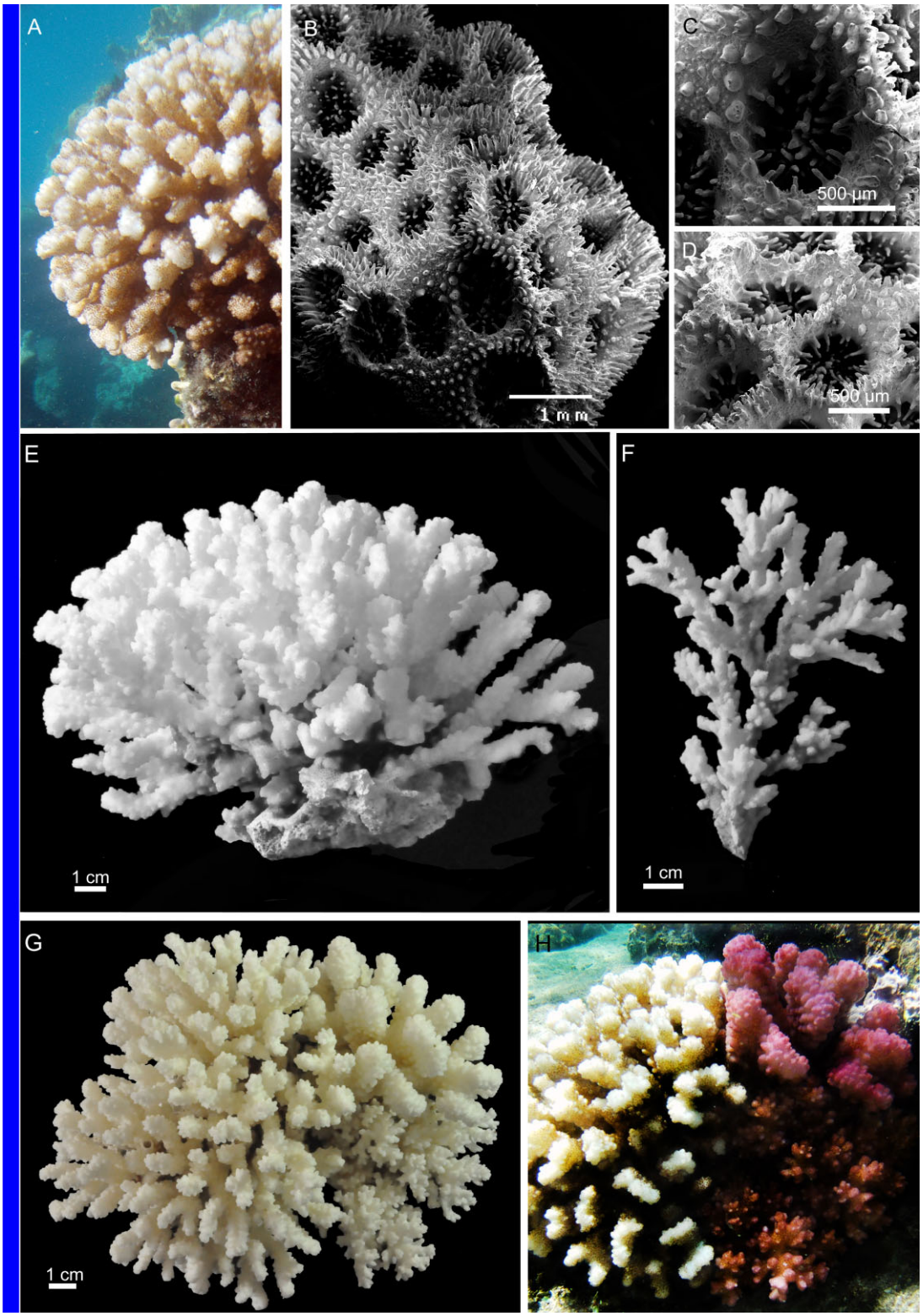

Figure 13. *P. bairdi* sp. nov. A, *in situ* appearance. B, skeleton of specimen. C and D, scanning electron micrographs of specimen. E, corallum of holotype (side view) (MTQ-G65918). F, corallum of paratype (side view) (MTQ-G65919). G, mosaic colony including holotype (left), *P. meandrina* (upper right), and *P. damicornis* (lower right). H, previous colony *in situ*.

Nevertheless, the strict divergence from *P. verrucosa* and *P. damicornis* in the nuclear region and its very distinct and consistent morphology strongly suggests it presents a separate species. Furthermore, it was found to grow close to typical *P. verrucosa* colonies (Fig. 12A, C, D, F, G; photographed at Mermaids Cove, Lizard Island).

Habitat and biology
Occurs predominantly in back reef habitats, but was also observed in less exposed habitats of the reef crest. Reproductive mode is unknown.

Distribution
Records are limited to the waters of Lizard Island.

POCILLOPORA EYDOUXI EDWARDS & HAIME, 1860 (FIGS 14, S7)

SYNONYMY

Pocillopora grandis Dana, 1846 p. 533
Pocillopora elongata Dana, 1846 1846 p. 531
Pocillopora eydouxi Edwards & Haime 1860
?*Pocillopora coronate* Gardiner, 1897 p. 949
Pocillopora rugosa Gardiner, 1897 p. 950

Taxonomic history
Pocillopora eydouxi was described by Edwards & Haime (1860). Although it presents a junior synonym of *P. grandis* Dana, 1846 and *P. elongata* Dana, 1846, these names are suppressed due to the common use of the name *P. eydouxi* for specimens of this taxon (Veron & Pichon, 1976).

Material studied
MTQ-samples: G33435, G33432, G33428 Tijou Reef, QLD, Australia (13°10′S, 143°57′E); G33430, G33434 Great Detached Reef, QLD (11°48′S, 144°03′E); 33429 Brisk Island, QLD, Australia (18°47′S, 146°42′E). G33433 Bowl Reef, QLD (18°31′S, 147°32′E); Great Detached Reef, QLD (11°42′S, 144°00′E); G52299 South China Sea, Scarborough Reef (15°07′N, 117°51′E); G50761 Seribu Islands, Indonesia (05°35′S, 106°32′E). Further material: Lizard Island (3 specimens) (see Table S1).

Corallum
The corallum is ramose, verrucate, branching varies from meandering-lamellar, broad-ended to cylindrical (Fig. S7). In adult specimens, branches are more robust then in other species (2–4 cm thick). Veron & Pichon (1976) observed colonies up to 95 cm high.

Corallites and coenosteum
The species is distinguished from *P. meandrina* by its styliform columella, with one to three distinct stylae (even within one colony, Fig. 14C) originating from a diagonally arranged, bridge-like columella. Calices are 0.6–1 mm in diameter. Septa are hexamerally arranged in two cycles and weakly developed, often only indicated by short (~100 μm) septa teeth. The second cycle may be weakly developed. The 1st and 4th septa of the first cycle eventually merge into the bridge-like columella connecting both sides of the calice. The coenosteum is ornamented with short spinulae.

Colour and pigmentation of the live colony
Evenly pigmented brown to pink.

Remarks
Although this species shares identical mitochondrial lineages with *P. meandrina*, Flot *et al*. (2008) found some indication of divergence in the nuclear DNA regions. The most striking difference between this species and *P. meandrina* is the columella development. All *P. eydouxi* colonies where characterized by a styloid columella development, a feature Edwards & Haime (1860) stressed in the illustration of the type specimen (Fig. 14F). In contrast, columellae of *P. meandrina* were mostly oval convex, rarely reduced, and if styloid with a significantly thicker stylus (Fig. 4) than *P. eydouxi* (Fig. 14B, C).

Habitat and biology
This species was found to occur predominantly in exposed to moderately exposed environments.

Distribution
This species is described to have a cosmopolitan distribution from the Tropical Eastern Pacific to the Indian Ocean and the Red Sea (see Veron, 2000). However, further research is needed to identify its actual range (Fig. 5).

POCILLOPORA MEANDRINA DANA, 1846 (FIGS 15, S8)

SYNONYMY

Pocillopora meandrina Dana, 1846 p. 533
Pocillopora nobilis Verill, 1864 p. 59

Taxonomic history
The species was described by Dana (1846). Vaughan (1918) notes that *P. meandrina* is closely related to *P. elegans* and *P. verrucosa*, and that it is probable that they are all variants of one species. Veron & Pichon (1976) first synonymized the species under *P. verrucosa*, before describing it as a separate species.

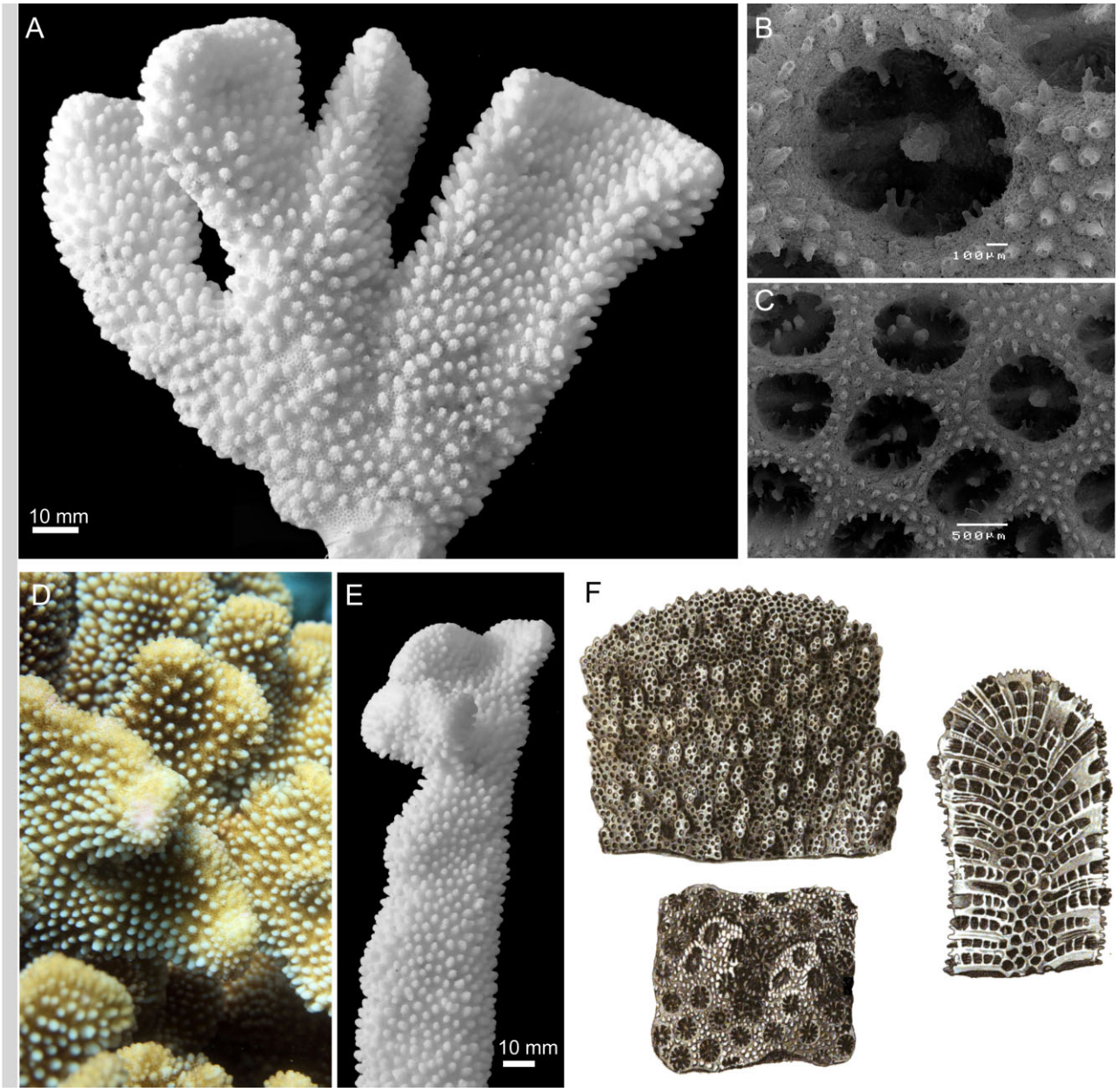

Figure 14. *Pocillopora eydouxi*. A, skeleton of specimen (side view) (MTQ-G66118). B and C, scanning electron micrographs of specimen. D, *in situ* appearance. E, corallum of cylindrical morph (side view) (MTQ-G66119). F, illustration of holotype by Edwards & Haime (1860).

Material studied

MTQ samples: G33035 Mellish Reef Lagoon, QLD, Australia (0–4 m) (19°09′S, 150°9′E); G33036 same as before (5–15 m); G33037 same as before (0–4 m); G52311 South China Sea, Pratas Reef (20°35′N, 116°46′E). Further material: Orpheus Island (4 specimens), Lizard Island (3 specimens), Davies Reef (2 specimen) (see Table S1).

Corallum

Cespitose, very neatly verrucose, summits often naked. Vaughan (1907) differentiated between two variants within the same species. Typical *P. meandrina* has mostly lamellar and sinuous branches, is evenly verrucate, summits mostly naked (Fig. 15A, B). However, it can also be very similar to *P. verrucosa* in gross morphology, but verrucae are more neatly and

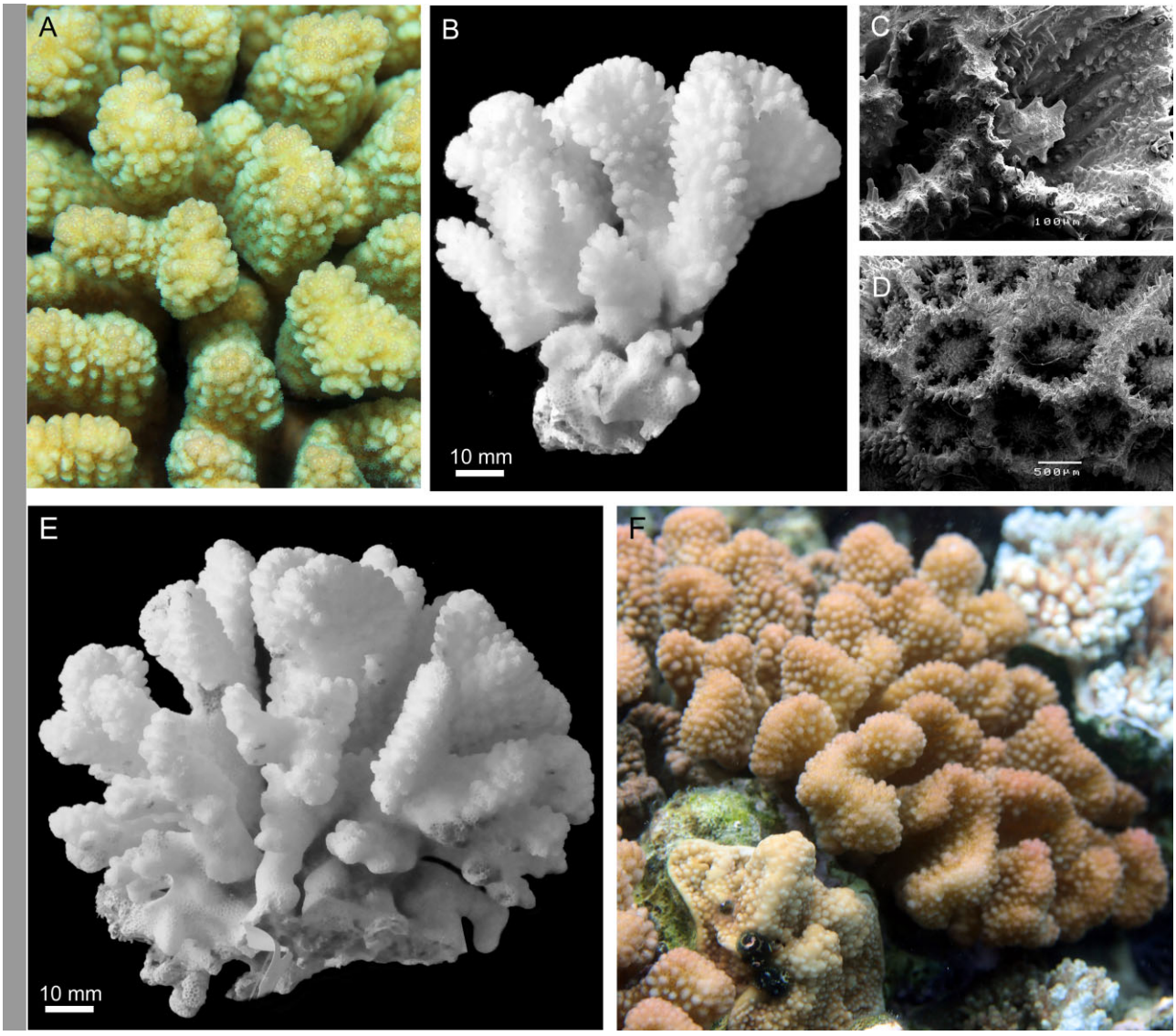

Figure 15. *Pocillopora meandrina*. A, field appearance of *P. meandrina* (side view). B, skeleton of previous variation (MTQ-G65917). C and D, scanning electron micrographs of previous specimen. E, corallum of *P. meandrina* (side view) (MTQ-G66117). D, *in situ* appearance.

equally arranged and branches are more flattened, forming meanders towards the tips (Fig. 15E, F).

Corallites and coenosteum

The columella and septa development of this species is very variable (Fig. 4 γ, Fig. 15C, D). The columella is oval-convex to styloid, rarely obsolete; similar to *P. eydouxi* the columella is diagonal in the calice, but consistently more predominant than that of *P. eydouxi*. Calices are 0.5–1.6 mm in diameter. Intracolony variation in the columellae is high, ranging from oval-convex to thick (> 200 µm) styloid, but characterized by a fine, short spinulate ornamentation. Septa are hexamerally arranged in two cycles and vary in their development from almost reduced to well indicated by long spinulae. Similar to *P. eydouxi* the second septal cycle may be slightly less developed than the first. The coenosteum is ornamented with short spinulae.

Colour and pigmentation of the live colony

Evenly coloured (yellow, brown, pink, blue, or green).

Remarks

Separation between *P. meandrina* and *P. verrucosa* has challenged previous studies (e.g. Vaughan, 1918;

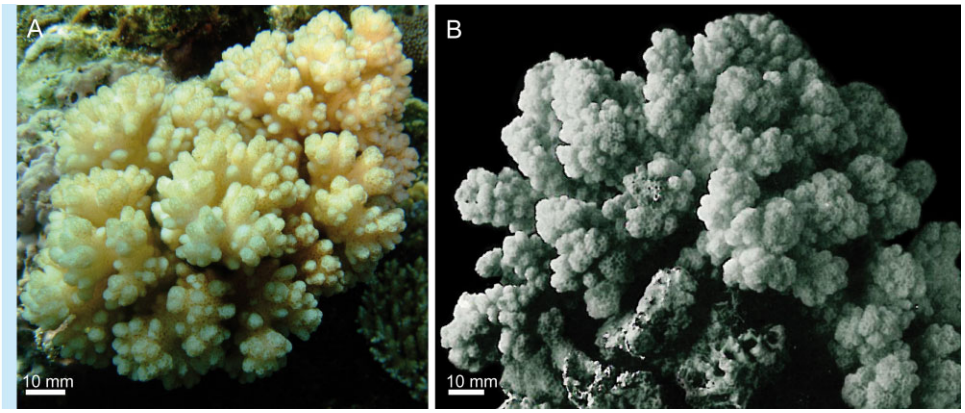

Figure 16. *Pocillopora* cf. *brevicornis*. A, field appearance. B, specimen collected and photographed by Hoffmeister (1925).

Veron & Pichon, 1976) due to the gross morphological similarity of some colonies. In contrast to the gross morphology, *P. verrucosa* and *P. meandrina* are very distinct genetically and *P. meandrina* is genetically much more closely related to *P. eydouxi* than to *P. verrucosa*.

Habitat and biology
Reef crest, back reef, and reef slope habitats, predominantly in exposed habitats.

Distribution
This species has a cosmopolitan distribution from the Tropical Eastern Pacific to the Indian Ocean (see Veron, 2000). However, further research is needed to identify its actual range (Fig. 5).

POCILLOPORA CF. *BREVICORNIS* LAMARCK, 1816 (FIG. 16)

SYNONYMY

Pocillopora brevicornis Lamarck, 1816 p. 275

Taxonomic history
Lamarck (1816) described *Pocillopora brevicornis*. Hoffmeister (1925) later added the subspecies *Pocillopora brevicornis setchelli*. The taxon was later synonymized under *P. damicornis* (Veron & Pichon, 1976).

Material and locations studied
Great Detached Reef (1 specimen) (11°45′0″S, 144°1′1″E).

Corallum
Branches short, compressed, thick, even-topped, and crowded with irregular but short subbranching/verrucae.

Corallites and coenosteum
Not recorded.

Colour and pigmentation of the live colony
Evenly pale to yellow.

Remarks
Unfortunately access was limited to a small fragment of one specimen, thus limiting a formal resurrection of this taxon. However, photographs of the specimen sampled correlate well with the description for *P. brevicornis*. Furthermore, its genetic divergence indicates strongly that it is a distinct species. Future investigations are needed to confirm the validity of this taxon.

Distribution
At this point its only confirmed location is the Northern Great Barrier (Fig. 5), although it may have been missed in other locations due to its rarity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Haploweb of HSP70B region. Red box indicates the newly identified species.
Figure S2. Background information for DAPC analysis (Fig. 3). A, variance explained by PCA. B, discriminant analysis eigenvalues.
Figure S3. Illustration of gross morphology plasticity of the corallum of *Pocillopora acuta* in different environments (side views). MTQ-sample numbers: a, G66130; b, G66106; c, G66105; d, G66133; e, G66129; f, G66132; g, G66127; h, G66112; i, G66089; j, G66111.
Figure S4. Illustration of morphological plasticity of the corallum of *Pocillopora aliciae* (side views) (skeleton photos: Schmidt-Roach *et al*., 2013). MTQ-samples numbers: a, G65423; b, G65424.
Figure S5. Illustration of morphological plasticity of the corallum of *Pocillopora verrucosa* in different environments. MTQ-sample numbers: a, G66146; b, G66114; c, G65923; d, G66142; e, G66144; f, G66139; g, G66140; h, G66143; i, G66145; j, G66147.
Figure S6. Illustration of gross morphology plasticity of the corallum of ***P. bairdi* sp. nov.** in different environments (side views). MTQ-sample numbers: a, G66104; b, G65918; c, G65919.
Figure S7. Illustration of gross morphology plasticity of the corallum of *Pocillopora eydouxi* in different environments (side views). MTQ-sample numbers: a, G66119; b, G66118; c, G66120.
Figure S8. Illustration of gross morphology plasticity of the corallum of *Pocillopora meandrina* in different environments (side views). MTQ-sample numbers: a, G66115; b, G65917; c, G66117; d, G66116; e, G66113.
Table S1. List of samples collected in this study and details of analysis applied.
Table S2. Average distance between/within groups (D1 Euclidean distance), *significant differences ($P_{perm} < 0.05$).