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Review

Review of Coral Taxonomy, Evolution and Diversity

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Abstract

To recast Theodosius Dobzhansky's famous 1973 quote: 'nothing in coral taxonomy makes sense except in light of reticulate evolution'. Coral species evolve through the continual intermixing of ancestral lineages forming a network of changing genetic interconnections rather than stable hierarchical trees. Most species are not discrete units but rather are components of continua with variable genetic, morphological, and geographic boundaries. Hybridisation and introgression are key processes maintaining reticulated networks, making polyphyletic species (those with mixed evolutionary origins) potentially the norm. This creates grey zones of speciation where taxonomic divisions are uncertain and gene flow is ongoing. With this understanding, we critically review: (1) Sources of information for taxonomic decisions, including biology, population dynamics and the need for comprehensive field and foundational molecular studies capturing environment-correlated and geographic variations; (2) Nomenclature (a human construct) and taxonomy (which endeavours to reflect nature's organisation): (3) Synonymy, including serial errors stemming from historical publications; (4) Type specimens, their use and misuse as a basis for taxonomic decisions; (5) Genus and species level agreements and disagreements between morphological and molecular taxonomies; (6) Use of the terms 'cryptic species', 'cryptic variant' and 'cryptic lineage'; (7) Taxonomic decisions based on inferences beyond the scope of individual studies, creating nomenclatural instability and concern, not least among those working to address the impacts of climate change. This review also provides context for an extensive array of Factsheets and linked documentation about each of the species included in CoralsOfTheWorld.org (2026 in prep.).

Keywords: coral taxonomy; molecular taxonomy; reticulate evolution; coral diversity

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Academic Editor: Juan Armando Sanchez

Received: 28 August 2025
Revised: 20 October 2025
Accepted: 21 October 2025
Published: 27 November 2025

Citation: Veron, J.E.N.; Stafford-Smith, M.G.; DeVantier, L.M.; Turak, E. Review of Coral Taxonomy, Evolution and Diversity. *Diversity* **2025**, *17*, 823. https://doi.org/10.3390/d17120823

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1. Introduction

Over the past decade or so, there has been a major shift in most taxonomy away from reliance on morphology to partial or total reliance on molecular technology as foreshadowed by Veron (1995) [1]. The molecular studies have provided much greater insight into the phylogeny of species, resulting in name changes at all levels. Corals are at the forefront of marine invertebrate taxonomy, with molecular studies providing insights into the relationships within and between species. As a result, there have been many changes to phylogenetic positions and a greater understanding of species relationships using population genomics. So far, however, there have been few fundamental challenges to the overarching biological units designated as species, a testament to the relative robustness of fieldwork and the morphology-based taxonomic foundation. Nevertheless, molecular studies are finding cryptic lineages—populations which have similar morphological characters but are genetically distinct. With

some exceptions the habitat and spatial scope of such studies is currently limited but some of these lineages may turn out to warrant species status.

This review on the taxonomy, evolution and diversity of reef-building corals assesses the morphological and molecular work to date and integrates new information with the existing taxonomic framework. In this endeavour, we have sought to develop a coherent and consistent strategy for assessing the synergies and conflicts between different approaches to 'the species problem'. Decisions are not always straightforward, so a basic purpose of this article is to provide a background to each influence on taxonomy, highlight the issues, offer examples of specific problems, and present our solutions to them (see Box 1).

Our approach is underpinned by the importance of maintaining taxonomic and nomenclatural stability unless evidence for change is clear and without contradictions, be they molecular, morphological, ecological or life history-related. This is consistent with the Code of the International Commission on Zoological Nomenclature (ICZN) [2] which repeatedly emphasises the need for stability.

Box 1. The purposes of coral taxonomy.

Whether morphological or molecular, modern coral taxonomy serves two purposes. The first is taxonomy isolated from all other endeavour (as is all pre-scuba taxonomy); the second is taxonomy that incorporates input from other disciplines in support of practical applications. Here, we delve into technicalities as befits any taxonomy, but our purpose is to provide accurate, reliable and stable taxonomic accounts integrated with other biological fields, identification and biogeography.

The 'species problem', of course, is not restricted to corals. It continues to challenge taxonomists across all major taxa. In our case, a key process, reticulate evolution, is central to understanding the question of 'what are species?'.

2. Overview of Reticulate Evolution

Reticulate evolution describes a mechanism for the origination of polyphyletic 'species' (see Glossary) through a mixing of ancestral lineages leading to a *network* of genetic change through time (Figure 1), rather than the growth of traditional hierarchical trees as classical phylogenetic perspectives implicitly assume. In so doing, it explains the origination of 'species' as well as their higher-level phylogenetic relationships. Herein, we use 'polyphyletic' in the general sense of a species that includes genes from different ancestral lineages.

The existence of reticulate evolution, a concept central to this article, was initially described as a peripheral issue in many groups of organisms, mostly plants (Refs. [3,4]; and see below). It was not considered a central explanation for species origination and phylogeny in the marine realm until proposed for corals by Veron (1995) [1], with genetic support from Hatta et al., 1999 [5].

With corals, along with a host of other marine taxa, larvae are subject to the vagaries of ocean surface currents for dispersal and population connectivity, and other types of physical, chemical, ecological and biological barriers which act as isolating mechanisms. These barriers vary across space and time giving rise to changing degrees of genetic mixing and isolation among gene pools. Most will die out, some may develop complete reproductive isolation leading to new lineages, whilst others may reconnect as physical or biological barriers are removed allowing genetic re-mixing (Figure 1). At any one point in time there may be some species that remain clearly definable across their entire distribution range, but most will be in different phases of speciation where processes of hybridisation and introgression (widely defined as the transfer of genetic material from one species into the gene pool of another by the repeated backcrossing of an interspecific hybrid with one of its parent species). These processes produce genetic continua where sister species are distinct in some regions and less distinct in others and where molecular

distinctions within a single morphology can occur in some regions but not in others as a result of geographic reticulation (see below and Figure 20). These patterns can be revealed with detailed molecular studies, but not morphologically except in studies which are both detailed and wide-ranging [1]. Indeed, some two-thirds (23 records from 39 cases) of nominal species represented in population genomic studies show evidence of gene flow linking partially reproductively isolated groups [7].

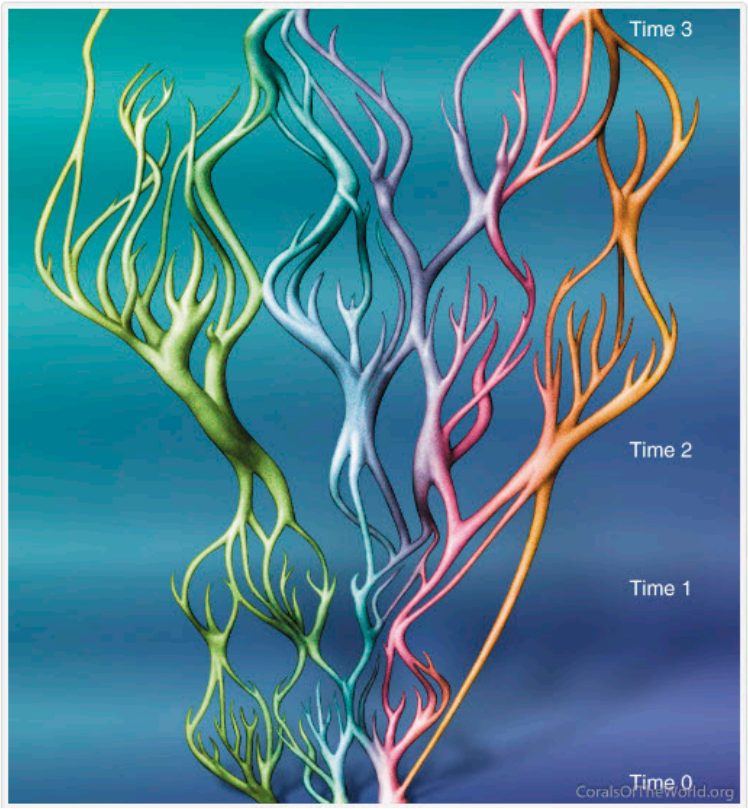


Figure 1. From Veron (2000) [6]. A hypothetical view of reticulate evolutionary change within a group of genetically linked taxa through time. At the bottom (Time 0), the group forms three distinct species each of which is widely dispersed by strong currents. At Time 1 the group forms many indistinct small species units that are geographically isolated because currents are weak. At Time 2, the group forms four species that are again widely dispersed by strong currents. Over the long geological interval to Time 3, the group has been repackaged several times. This repackaging is the source of polyphyletic species, those that include genes from different parent lineages, derived from more than one ancestor. Sometimes repackaging may result in a new lineage which remains isolated—this may be the ultimate fate of the left-hand lineage at Time 3. Colours represent hypothetical differences and similarities between lineages.

Reticulate evolution sees the 'species' that we name and describe, not as units—which are artificial constructs taxonomists impose on nature—but as components of *continua* that include components of other continua (other 'species'). We are commonly left with the complexity of defining species which have variable genetic boundaries, variable morphological boundaries, and consequently variable distribution ranges. The fact that a hypothetically detailed synonymy of these species may change geographically means that they may be clearly distinct in one area but become increasingly questionable in increasingly distant areas. It also follows that, with rare exceptions, boundaries between such 'species' are porous in both space and time. This has profound consequences for the age-old debate 'what are species?' Significantly, the concept is fundamental to taxonomy, biogeography and evolutionary theory alike, and therefore has the potential to increase confusion in an already complicated array of

discipline-related terminologies where the same word can have several different meanings. Although seldom explicitly stated, the morphology-based taxonomy of the pre-scuba era assumed that species are units whereas our understanding does not.

As a potential result of reticulation, different taxonomists working in different geographic regions may have good yet conflicting criteria for delineating related 'species'. Hence, detailed descriptions of them may be conflicting because they are likely to be based on different information. The more detailed the taxonomy, the more apparent the conflict. In cases where reticulation has clear taxonomic consequences, we identify and address apparent conflicts to maintain relevance to differing geographic regions and minimise information loss through synonymies.

A word of caution is needed here. Studies based on acceptance of 'neo-Darwinian evolution' and later the 'biological species concept' (reviewed for corals by Veron, 1995 [1]) and those accepting reticulate evolution use the same terminology including 'species', 'daughter species', 'sister species', 'cryptic species', 'species complex', 'taxon', 'hybrid', 'hybrid speciation', 'introgression', 'synonym', 'extinction', 'cross-fertilisation' and 'gene flow', because there are no alternatives. But the meaning of these terms is not always the same. For example, a neo-Darwinian synonym usually means 'the same as' whereas in a reticulate system it may simply mean 'a variation that is less than a species difference'. In the former case, the synonym is usually of interest only to establish nomenclatorial priority whereas in the latter it commonly retains information value especially as the difference between a 'species' and a synonym is usually a matter of opinion, not fact. For another example, the descriptor 'variable', which is applicable to most taxonomic and biogeographic species boundaries in a reticulate system, usually has little relevance in any neo-Darwinian taxonomic context (Box 2).

Reticulate evolution is not just relevant to corals. In one guise or another, it has surfaced in the taxonomy of many animal and plant taxa that have now been studied using molecular technology.

Box 2. Consequences of reticulate evolution.

Consequences of reticulate evolution for coral taxonomic units recognised as 'species':

- There is no easy definition of a 'species';
- There are no clear morphological or genetic boundaries between 'species', 'sibling species', 'hybrids', clades and 'subspecies';
- Many if not most recognised 'species' have variable distribution boundaries and as a result, 'sibling species' are likely to be common;
- A 'grey zone' commonly occurs between sibling species and subspecies where taxonomic divisions are uncertain and gene flow is ongoing;
- Taxonomic complexity exists for any 'species' both across its geographic range and among habitats in one place;
- Despite impressive dispersal capabilities via larvae and rafting, populations of very widespread species, at the edges of their ranges or those which have disjunctions, may be partly reproductively isolated on ecological and biogeographic timescales but not necessarily on evolutionary (or phylogenetic) scales;
- Polyphyletic species may be the norm, not the exception.

As a result:

- There are significant historical confusions;
- There is clarity of taxonomic units in some regions and confusion in others;
- There are significant conflicts between taxonomists working in different regions or with different molecular, museum and/or field experience;
- Molecular taxonomy can resolve some confusions as can reproductive studies, but others cannot be readily resolved by any methods;
- Broad field experience and significant sampling across ranges is essential to avoid misinterpretation of morphological and/or molecular results;
- There are no easy resolutions of these conflicts and grey zones.

3. Species Delineation in a Reticulate System

To set the stage, we first need to take a glimpse at the spectrum of issues that coral taxonomy confronts and to do this we turn to one of the most studied of all corals, the genus *Pocillopora*. The nomenclature of *Pocillopora*, summarised in Figure 2, illustrates the chaos that existed in pre-scuba taxonomy.

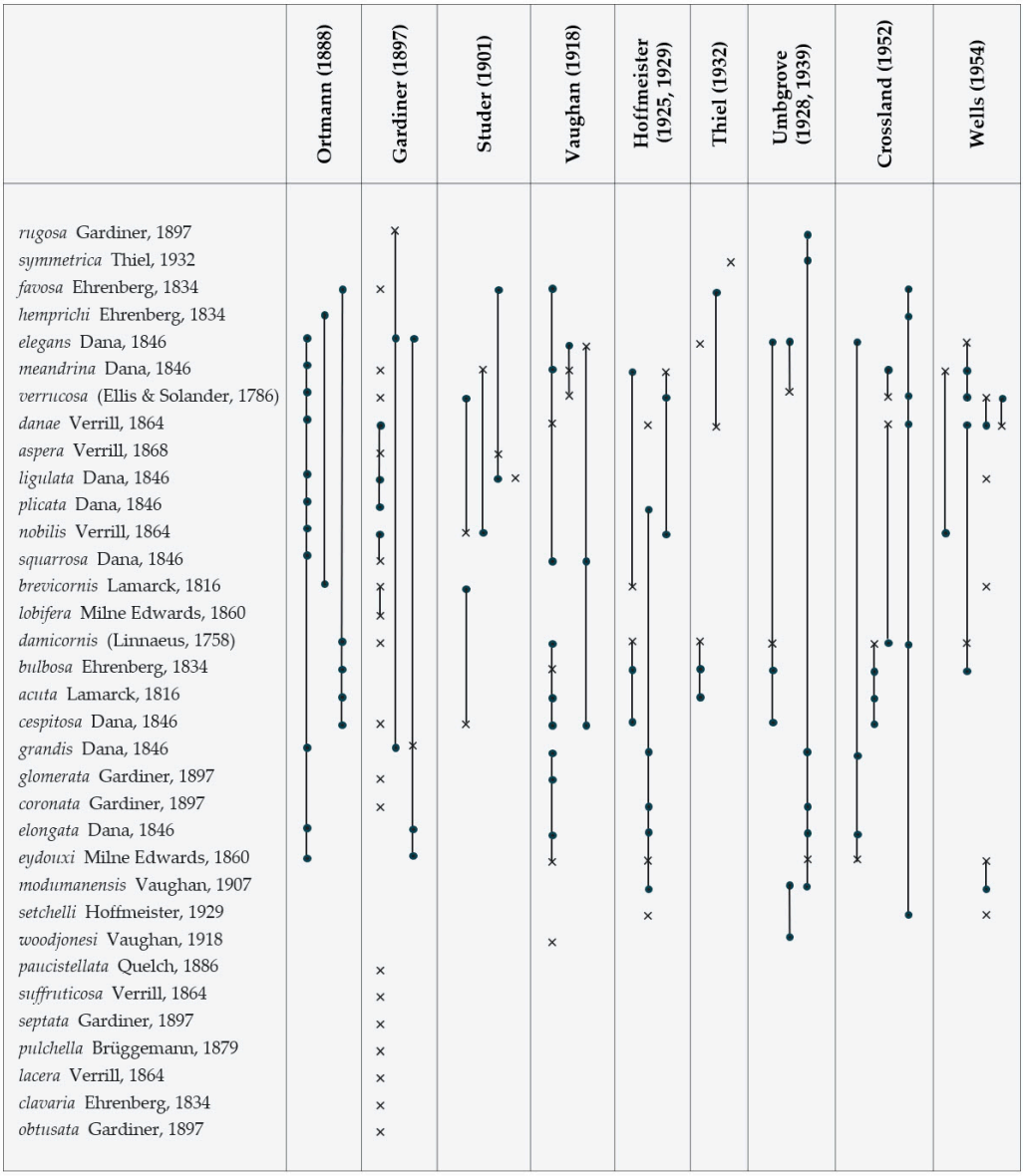


Figure 2. Species names of *Pocillopora* and the authors that used them. x = a supposedly valid name; • = supposed synonym. Lines linking species names indicate species included as synonyms by each author. Modified from Veron and Pichon (1976) [8] which includes source references.

Furthermore, it does not help that even widely accepted names are based on flimsy evidence and are open to challenge (Figure 3).

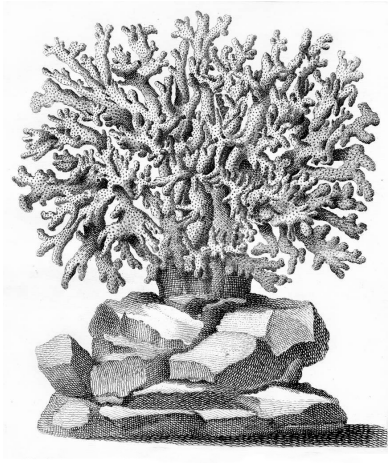


Figure 3. The name *damicornis* Linnaeus, 1758 is entirely based on this barely recognisable artist's engraving, captioned ambiguously "*Madrepora* Candida, Ramosa, Damae cornua referens foraminibus rotundis in superficie insignita: ex Museo N. Gualtieri n: 31". This loosely translates as 'White *Madrepora*, resembling the horns of a stag, marked on the surface with round pores: from the Museum of N Gualtieri, no. 31'. In the present taxonomic framework, this illustration could be interpreted as any of four other species.

The advent of scuba added a wealth of complexity to these names and did so against the background of synonyms figured above. At species level, the most studied *Pocillopora*, *P. damicornis* was seen to involve a previously unimagined range of environment-correlated variation (Figure 4).

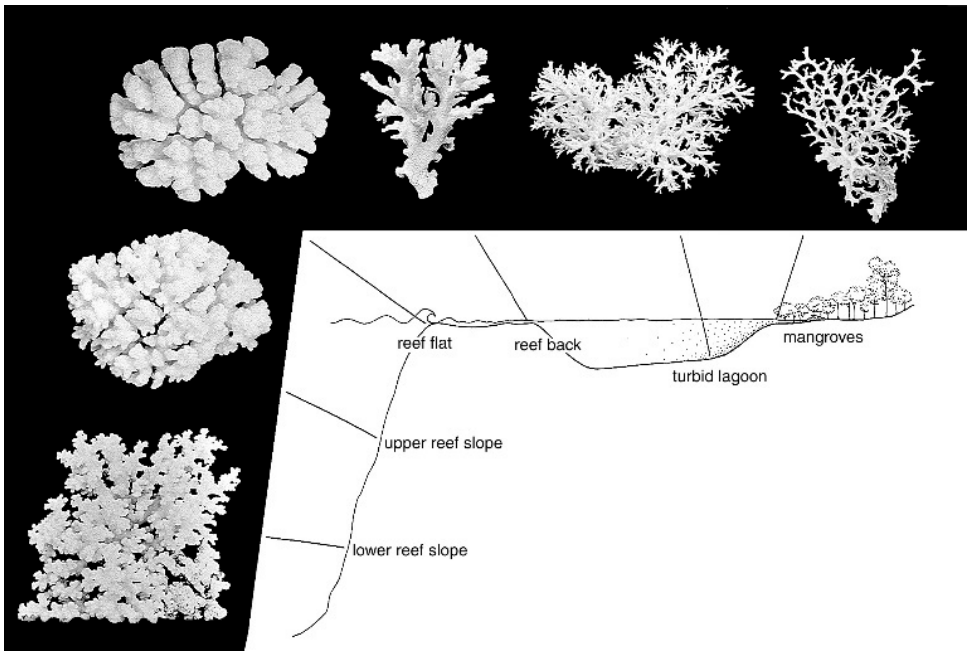


Figure 4. The morphological variation in a *Pocillopora damicornis* complex at a single location on the Great Barrier Reef. Modified from Veron and Pichon (1976) [8] and Veron (1995) [1].

Thirty-seven years on, with the advent of molecular taxonomy, Figure 4 (above) was modified by Schmidt-Roach et al. (2013) [9] (Figure 5). This compilation was again modified in CoralsOfTheWorld.org (2016) [10], changes based on further field observations.

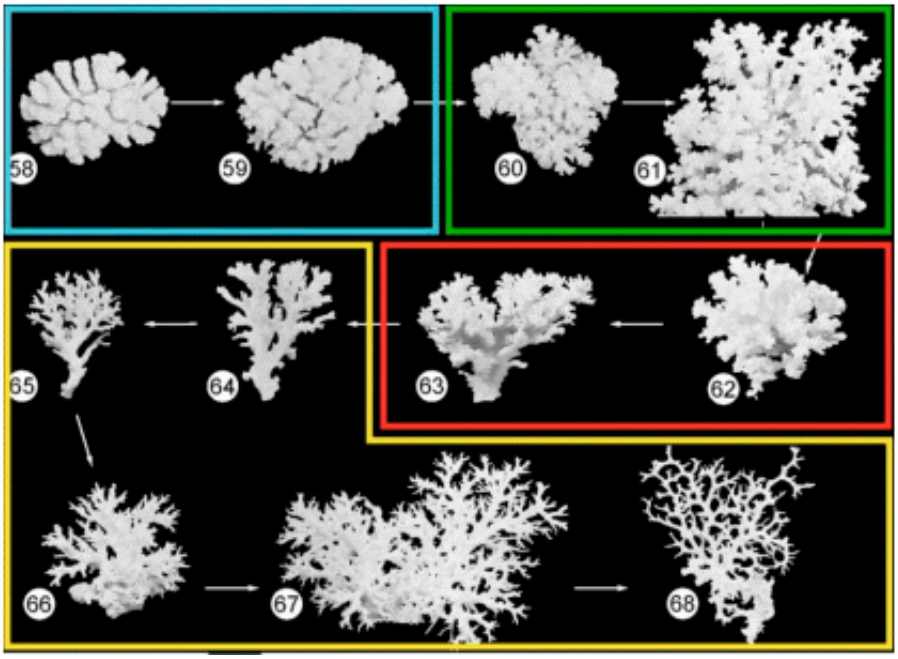


Figure 5. Modifications to the diagrammatic presentation of environment-correlated variation in *Pocillopora damicornis* from Veron (1995) [1] (represented in Figure 4 above) according to Schmidt-Roach et al. (2013) [9]. Coloured boxes represent different morphological groupings with some molecular differences. Diagram: Schmidt-Roach et al. (2013, their Figure 1) [9] (Courtesy: S. Schmidt-Roach).

Scuba-based studies also showed that colonies from similar environments, but widely separate geographic locations, are often very similar (Figure 6), but from other locations may be almost unrecognisably different.



Figure 6. *Pocillopora damicornis* from similar environments in different countries may be similar (from left to right: the South China Sea, the Great Barrier Reef and Fiji). Photographs: (from left to right) Lei Jiang and Hui Huang, Justin Marshall, and Russell Kelley.

Molecular taxonomy combined with studies of reproduction and population genetics ushered in another layer of complexity. Is there gene flow amongst all *Pocillopora damicornis* colonies? Do they have the same phylogeny? Are they reproductively isolated? The answers to these questions are highly relevant to deciding what the biological entity called *P. damicornis* is. Is it a species, a species complex or an incompletely defined part of a syngameon (see also Section 4.1)? And if so, what should we call it? These are questions we must ask and try to answer if coral taxonomy is to meet its obligations as the signpost to all biological information about *P. damicornis*.

This continues for all corals, albeit with most information missing for most of them.

To give further context: At least 2320 zooxanthellate species had been described before scuba studies took over in the 1970s. These have been reduced, mostly through synonymy,

into 546 of the species we accept today. In the fifty or so years since then, and with the above complexities and uncertainties notwithstanding, more than 328 new species have been added.

As we will see throughout this review, many molecular studies are distinguishing genetic lineages within coral species as currently delineated, which are more-or-less distinct. The presence of identifiable lineages within coral species is, of course, predicted by reticulation as well as by the selection constraints of different habitats and environmental conditions. A key question for the taxonomist is: Where should the species boundary lie?

Setting aside for the moment any technical differences in molecular methodologies, there are the following elements to consider: (a) the degree to which sampling has been undertaken across the morphological variability of the species (within and between habitats and across the known distribution range) to provide estimates of the natural genetic variance; (b) the degree of difference in genetic signatures; (c) the spatial distribution of the populations with different levels of genetic divergence/distinctiveness; (d) the temporal persistence of the different variation; (e) co-occurrence of different signatures (specifically existing in the same vicinity—including habitat and environmental gradations, not just in the same geographic region, see later).

In order to examine the delineation boundaries, we must first review some of the mechanisms leading to divergent genetic lineages.

3.1. Reproduction and Population Dynamics

Modes of reproduction are central to population dynamics in the short term and to biogeographic-scale dispersion and genetic divergence in the long term. Corals can reproduce sexually and asexually through a wide range of different mechanisms.

3.1.1. Reproductive Mode and Dispersion

Asexual Reproduction

Corals, along with other clonal invertebrates, show many asexual mechanisms of reproduction [11]. Some corals, including *Pocillopora damicornis*, can produce most of their larvae through parthenogenesis (where the egg develops without being fertilised). In some cases, the proportion of parthenogenetic larvae is as high as 94% [12] which could result in monoclonal populations with low local genetic variation.

Budding is an asexual process where new polyps develop from the parent and contribute to growth, producing genetically identical, modular colonies. Portions of colonies (ramets) can break off, particularly during storms, and subsequently form new colonies through fragmentation [13,14]. Colony fragmentation is a major form of local reproduction in some species, across a broad range of growth-forms, and including major reef-builders [13–16]. Again, this can result in monoclonal populations with low local genetic variation.

Under environmental stress of many kinds (temperature, salinity, or other chemical imbalance), individual polyps can become detached from the parent colony in a process known as polyp 'bail-out' [17–21]. In some cases, hundreds of genetically identical polyps may become detached and potentially disperse to more favourable conditions [22]. Bailed-out polyps (e.g., *Pocillopora acuta*) that survive can reattach and form new colonies under laboratory conditions [23,24]. This suggests that if large numbers of polyps settle en masse in a new location they may appear to be a well-defined distinct genetic lineage.

Sexual Reproduction

Corals reproduce sexually either by brooding larvae within the body of parent polyps (known in 74 species) or by 'broadcasting' gametes (known in 367 species) [25]. In the latter case, this is done by the release of bundles of combined egg and sperm in hermaphrodite corals or, in gonochoric species, separate bundles of eggs and sperm from female or male colonies, albeit with some fascinating exceptions (e.g., refs. [26,27]).

These bundles break apart on the ocean surface (Figure 7) where they may be widely dispersed. Contrastingly, brooding provides a relatively high level of larval survival but little opportunity for long-distance dispersal other than via rafting [28,29] (reviewed [30]). Broadcasting provides an opportunity for cross fertilisation among colonies of the same or different species when gametes are released synchronously. Synchronous mass spawning and release of brooded larvae have been observed at different times of the year in many countries and underpin the formation of patterns of distribution, genetic connectivity and divergence. For example, Rosser et al. (2020) [31] found that geography and spawning season drive genetic divergence among populations of *Acropora tenuis* from Indonesia and Western Australia. Duvane et al. (2025) [32] report that genetic divergence also occurs in *Acropora austera* populations between northern and southern Madagascar. These latter authors proposed that the apparent restricted connectivity is caused by short pelagic larval duration and/or oceanographic factors, notably eddies in the Mozambique Channel. In the western Pacific, Denis et al. (2025 preprint) [33] recently described four genetically distinct populations of *Acropora spathulata* from the central-northern and southern Great Barrier Reef, Coral Sea and New Caledonia. These authors found that larval dispersal estimated at 100 km per generation in major ocean currents promoted "asymmetrical gene flow" among geographically distant populations. The genetic structure of these populations resulted from the "opposing forces" of isolation and connectivity [33]. This is a good example of a reticulate evolutionary pattern for a broadcast spawning coral.



Figure 7. Egg and sperm bundles on the ocean surface of the Great Barrier Reef. The majority of species on these reefs will have contributed to these slicks and some may successfully cross-fertilise. Most of the resulting larvae will not survive but a tiny fraction will settle locally or be dispersed to nearby reefs or, extremely rarely, continue on to settle in more remote geographic regions. Photographs: Bette Willis (**left**) and Valerie Taylor (**right**).

Further, population genomic structure has been related to sexual reproductive mode for the brooding *Pocillopora acuta* and the broadcasting *Porites* sp., where the former had populations divided by the Malay Peninsula and the latter was panmictic [34]. On a much more local scale, Duijser et al. (2025) [35] reported two genetic clusters of *P. acuta* occurring on adjacent reef and mangrove sites in the northern Great Barrier Reef. Limited admixture suggested low levels of gene flow between the two lineages, with distinct dominant symbionts (*Cladocopium* in the reef population and *Durusdinium* in the mangrove population). 'Hybrid' corals exhibited greatest molecular heterogeneity.

In the Seychelles region of the Western Indian Ocean, a population genomic study of *Porites lutea* found connectivity greater than predicted from oceanographic model simulations despite a dispersal barrier between the Inner and Outer Islands [36]. A complementary broader-scale modelling study across the tropical southwestern Indian Ocean [37] found that remote reefs are connected by larval dispersal through eddies and a complex set of equatorial and boundary

currents. The oceanographic setting promotes bidirectional larval flow between reefs of the Chagos Archipelago, Seychelles (Inner Islands) and Mozambique Channel region, with most coral populations genetically connected within a few hundred generations of dispersal [37]. In the case of *Seriatopora hystrix*, a brooding species which has a short pelagic larval duration, eddies in the Mozambique Channel cause larval retention in northern Madagascar but facilitate dispersal from northern Mozambique towards southwest Madagascar [38].

Although the larvae of brooding species normally settle within a couple of hours after fertilisation [39] forming local populations in specific biotopes [40], they can survive and settle after as long as 100 days in experimental conditions [41]. They may also settle on floating objects and develop into juvenile corals which can be rafted for thousands of kilometres [28]. This has enabled, over evolutionary time scales, dispersal over ocean-wide distances (including to the far eastern Pacific), the long-term success of which is evident in the broad distribution ranges and taxonomic complexities (see below) of brooding pocilloporids and isoporids across large areas of the Indo-Pacific.

For some spawning species, settlement of larvae can occur as soon as two days after fertilisation, but some larvae can survive for more than 70 days before settling [30], creating complex genetic patterns among populations over wide geographic distances. Importantly, although there is some complementary evidence among brooding species, mass spawning—where large numbers of species release gametes simultaneously—is the principal mechanism facilitating hybridisation, albeit with some apparent anomalies (e.g., ref. [42]).

3.1.2. Hybridisation

It has long been clear that genetic isolation of related terrestrial plants and animals is maintained in the natural state by the many consequences of, most commonly, geographic separation [43–47]. Artificial removal of that separation, as has occurred with most domesticated plants and animals, may allow extensive hybridisation to result (e.g., Adavoudi and Pilot, 2021 [48] who review this for mammals). This process often occurs in the natural state, especially where related species' ranges overlap (e.g., refs. [49–51]) and particularly where both species are in low local abundance, or one species is common and the other rare (e.g., ref. [52]). Many publications discuss invasive species (e.g., refs. [53–55]).

The extent to which this applies to the marine realm of corals is not yet well understood, but it can be assumed that there is continual interaction between dispersal via surface circulation, which enhances genetic intermixing, and various physical and biological reproductive barriers which suppress it. These barriers can be investigated by artificially removing them either before the point of fertilisation (by combining eggs and sperm from different parent species), or after fertilisation (by tracking larval and post-larval survival). The result of either process can be revealed through molecular studies. It is important to note, however, that the results of both inter-species reproductive and genetic studies in one location may differ from those in another, adding yet more complexity to unravelling the reticulate evolutionary process. For example, two species of *Porites*, *P. lobata* and *P. evermanni*, were found to be fully isolated in Hawaii and American Samoa populations. In the eastern Pacific, introgression occurred from *P. evermanni* into *P. lobata* [56]. Divergence times between Hawaiian and eastern Pacific populations were consistent with an early Pleistocene recolonisation of the eastern Pacific by *P. evermanni* with a more recent arrival of *P. lobata*. Consequently, an absence of evidence of interbreeding in one location should not be assumed to be evidence of absence of this occurring elsewhere across species' ranges. Additional examples are provided below.

In their review, Hobbs et al. (2022) [57] found that 81 scleractinian species are reported to hybridise and that there has been a surge in reports of hybridisation among other coral reef organisms. This number, and its evolutionary consequences, seems certain to be greatly increased with future studies [58].

Returning briefly to *Pocillopora*: findings from two broadscale studies, one across the Pacific Ocean [59] and a second that included samples from the western Indian Ocean, tropical southwestern Pacific and south-east Polynesia [60] are relevant. Both reported complex phylogenetic patterns, with introgression events. The Pacific study confirmed three introgressions and identified potential for admixtures between each of the five species identified. Oury et al. (2023)'s [60] inter-ocean study also reported multiple introgression events among their 21 'genomic species hypotheses'. Although four main clades comprising the 21 species were proposed, species relationships were not fully resolved leading to multiple inferred species tree topologies. Thirteen species were, nonetheless, strongly supported by genetics, morphology, biogeography and symbiont associations. A further six species were considered to represent either undescribed species or incorrectly synonymised nominal species. Oury et al. [60] concluded that some recently diverged sister species might be actively speciating (in the grey zone, sensu De Queiroz, 1998 [61], see below), while some in allopatry may still be able to hybridise, forming species complexes. These included *P. damicornis* with two genomic species hypotheses and *P. acuta* with six.

We now turn from *Pocillopora*, with some 21 species in our current taxonomy, to *Acropora*, with 173 species, and make the point that most *Acropora* have some or most of the variations described above for *P. damicornis*. As with all major genera, extensive experience is therefore required to reliably identify *Acropora* species in the field and to separate them from similar species.

Caribbean *Acropora* species, of which there are only three, make a welcome exception to these identification difficulties, making studies of them all the more pertinent. In the Caribbean, *Acropora prolifera* is a hybrid between the other two species, *A. cervicornis* and *A. palmata*, and can be successfully backcrossed with both in the field and laboratory [62–64] (Figure 8). The timescale involved is interesting: Precht et al. (2019) [65] found *A. prolifera* has a Pleistocene fossil record indicating that it has an existence on a geological timescale. Yet populations can become genetically isolated in only a few years depending on surface circulation patterns [66,67] forming novel haplotypes [68]. These are unexpected findings for a species that shows little or no morphological geographic variability.



Figure 8. *Acropora prolifera* (**left**) is a hybrid between *A. cervicornis* (**centre**) and *A. palmata* (**right**), all in the Caribbean. Photographs: E. Weil (**left** and **centre**), N. Coleman (**right**).

Unlike the Caribbean, all Indo-Pacific *Acropora* show substantial geographic and habitat-related morphological variations (e.g., see Supplementary Figure S1), so it is unsurprising that these may form lineages or populations which are distinct, especially where they are semi-isolated in distant geographic regions. However, it is now clear that hybridisation can occur between species that are very different morphologically.

Acropora florida and *A. intermedia* (Figure 9) have been artificially hybridised in Japan [69–72] their gametes showing high rates of intercrossing. The last authors (Kitanobo et al., 2022 [72]) proposed that natural hybridisation may arise when sympatric colony numbers of parental species are low and spawning is synchronous or nearly so, and similarly for backcrossing of hybrids with each parent. In the latter case, competencies of

hybrid sperm outcompeted parental sperm even when the numbers of hybrid sperm were far lower than those of the parental species. They concluded that an occasional admixture event between *A. florida* and *A. intermedia* may be ongoing, although slight differences in spawning times place them, tentatively, at lower risk of hybridisation than other mass-spawning corals [72]. Nonetheless, *A. intermedia* has been reported as having high rates of crossing with other sympatric and synchronous spawning species [5].

It is also important to note that self-fertilisation in hybrids may decrease survival of offspring, a mechanism that might maintain separation of these species in the wild [70,73].



Figure 9. *Acropora florida* (**left**) can hybridise with *A. intermedia* (**right**). The centre image shows a putative hybrid of the former two widespread species. Photographs: (**left**) Palau, (**centre** and **right**) Coral Sea and Micronesia, E. Turak.

Acropora millepora can be artificially hybridised with *A. pulchra* (Figure 10) [74,75] and *A. hyacinthus* with *A. cytherea* (Figure 11) [76,77] on the Great Barrier Reef, but not in Japan [78].



Figure 10. *Acropora millepora* (**left**) can hybridise with *A. pulchra* (**right**) and likely also shares genes with *Acropora hyacinthus* (Figure 11) [79]. The centre image shows a putative hybrid of the former two widespread species. Photographs: (**left**) on the Great Barrier Reef, E. Turak; (**centre**) in Fiji, E. Turak; (**right**) in the Houtman Abrolhos Islands, J. Veron.

However, Márquez et al. (2002) [76,77] report that despite the potential for hybridisation and gene transfer, *Acropora hyacinthus* and *A. cytherea* remain genetically distinct.

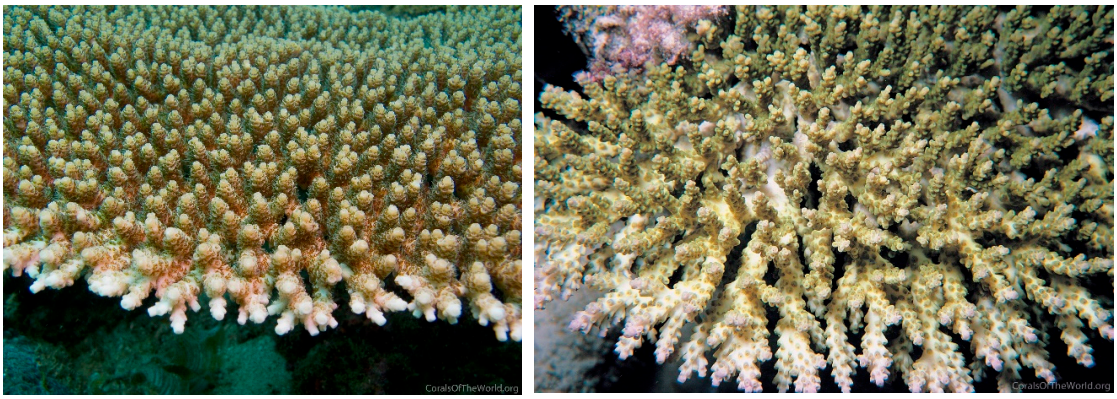


Figure 11. *Acropora hyacinthus* (**left**) can hybridise with *A. cytherea* (**right**). Photographs: (**left**) in Brunei, E. Turak; (**right**) in Ashmore Reef, NW Australia, J. Veron.

Ramírez-Portilla et al. (2022) [42] also found, from breeding trials in Japan, that *Acropora cytherea*, *A. bifurcata* and *A. hyacinthus* are all reproductively isolated, a finding supported by a broad spectrum of data also in Japan. Conversely, Ladner and Palumbi (2012) [80] found that *Acropora cytherea* and *A. hyacinthus* "form a global complex with consistent patterns of introgression over large distances", while also noting that *A. hyacinthus* is a species complex. Most recently, Rassmussen et al. (2025) [81], identified 16 lineages within this complex. These authors considered the lineages to represent distinct species, resurrecting nine nominal species names and designating five new species (see Section 7.3 Issues with species below).

In general, diversification of *Acropora* since the Miocene has been marked by both major introgression events and recurrent gene flow within networks of species [82]. Of contemporary consequence, hybridisation of *Acropora hyacinthus* with *A. millepora* was identified in a specific genomic region associated with increased bleaching tolerance in one *Acropora hyacinthus* clade relative to others [79].

In a molecular study of several rare *Acropora* species, polyphyletic patterns also provided evidence for introgressive hybridisation with allele sharing between species, either reflecting hybrid origins or secondary hybridisation following speciation [83]. Three of the species studied, *A. pichoni*, *A. kimbeensis* and *A. papillare*, were found to be monophyletic for mitochondrial DNA but polyphyletic with highly divergent alleles for nuclear DNA, even within individual colonies.

Lamb et al. (2024) [58] compared the fertility of aquarium-reared first-generation hybrid and purebred corals of two *Acropora* species, *A. loripes* and *Acropora kenti* (a likely geographic variant of *Acropora tenuis*, see below), on the Great Barrier Reef (Figure 12). Based on the probability of spawning and fertilisation success in crosses using gametes, these authors reported that F1 hybrids had greater reproductive fitness than the F1 *A. loripes* purebred stock. This clearly demonstrated the high fertility of interspecific hybrids, thus high reproductive fitness.



Figure 12. *Acropora loripes* (**left**) and *A. tenuis* (**right**) both on the Great Barrier Reef, see text. Photographs: J. Veron.

Molecular studies (as opposed to breeding trials) suggest that extensive hybridisation occurs between *Acropora millepora*, *A. papillare*, *A. pulchra* and *A. spathulata* in the Great Barrier Reef with occasional gene leakage to and from *A. aspera* [84].

Moving on to other genera, Forsman et al. (2017) [85] used several approaches to resolve the phylogeny of two very distinct species of *Porites* in Hawaii: the branching *P. compressa* and the massive Indo-Pacific-wide *P. lobata* (Figure 13). Failure to separate these phylogenies led the authors to the conclusion that they frequently hybridise. Intermediate morphotypes indicative of such crosses have never been reported in the wild, perhaps

because, in this case and likely others, there are fixed genotypic pathways which dictate specific phenotypic expression, irrespective of parentage, at least within this species pair.



Figure 13. *Porites compressa* (**left**) can hybridise with *P. lobata* (**right**). Photographs: both in Hawaii, J. Maragos.

Hybridisation occurs between *Porites lobata* and *P. evermanni* in the far eastern Pacific [56] and between *Montipora digitata* and *M. spumosa* (Figure 14) on the Great Barrier Reef [74].



Figure 14. *Montipora digitata* (**left**) can hybridise with *M. spumosa* (**right**). Photographs: (**left**) Philippines, J. Veron; (**right**) in Indonesia, R. Steene.

In another prophetic study on the Great Barrier Reef, Miller and Babcock (1997) [86] and Miller and Benzie (1997) [87] showed that seven *Platygyra* species (*P. daedalea*, *P. lamellina*, *P. pini*, *P. ryukyuensis*, *P. sinensis* and two unidentified *Platygyra* taxa) could cross-fertilise and successfully grow. Hybrids were later shown to have no or only slightly reduced fecundity. This should, if common and widespread in nature, coalesce into one species, but they remain distinct, again possibly relating to fixed genotypic pathways dictating phenotypes. Additionally, Miller (1994) [88] found that some *Platygyra* species hybridise with *Leptoria phrygia* on the Great Barrier Reef, the first record of cross-genus hybridisation in corals.

Clear field evidence of hybridisation can be well masked by identification uncertainties, genetically recent divergence, and complex patterns within syngameons (see also Section 4.1), so it is unsurprising that if present, or even common, it may go unobserved, particularly in the more morphologically plastic genera like *Acropora* and *Pocillopora*. In the latter, a second apparent case of generic-level hybridisation has been observed between *Pocillopora damicornis* and *Stylophora pistillata* at Lord Howe Island [89] (Figure 15) where adjacent colonies exhibit a full range of intermediate morphologies (Figure 69, below).



Figure 15. A putative hybrid colony combining the characters of *Pocillopora damicornis* and *Stylophora pistillata* at Lord Howe Island. Photograph: N. Coleman (**left**) and same colony enlarged (**right**).

Interestingly, similar hybrid colonies also occur at Norfolk Island 890 km away (Figure 16) the taxonomic status of which has yet to be investigated.



Figure 16. Putative hybrid colonies similar to those of Lord Howe Island (Figure 15) also occur at Norfolk Island, see text. Photographs: S. Prior.

We have also recorded putative hybrids in places which are not isolated and where species diversity is high. One such example is at southwest Wajh Bank, North Saudi Arabia, where a small number of colonies of an unrecognised *Seriatopora* occur alongside *S. hystrix* (Figure 17). Potentially, such occurrences are common but go unrecorded unless they have distinctive characters.

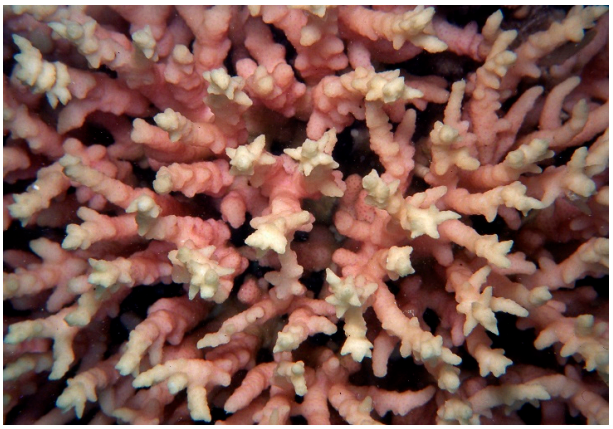


Figure 17. A possible hybrid between *Seriatopora hystrix* and an unknown species at North Red Sea, Saudi Arabia. *Seriatopora hystrix*, with much finer branches, occurs at the same locality. Photograph: E. Turak.

Reports of hybridisation and genetic divergence coming from many sources strongly indicate the presence of widespread reticulation in corals at species or molecular lineage level (Box 3). In the case of *Pocillopora damicornis*, it seems likely that this entity is part of a syngameon containing components of other pocilloporid species [90]. Almost routinely, studies indicate the presence of cryptic molecular variants (e.g., in *Pocillopora:* [60,91–94]; in *Acropora:* [80,81,95,96])

Cryptic molecular divergence also occurs within *Stylophora pistillata* in the Red Sea and many locations in the western Pacific [97–99]. These divergencies may not be morphologically recognisable (Figure 18) especially as this species is genetically diverse, see 'case study' below of *Stylophora.* On the Great Barrier Reef, Meziere et al. (2024) [100] found limited evidence of recent hybridisation among five *S. pistillata* variants, while concluding that assortative mating and the accumulation of genetic differences between locally adapted clades was consistent with niche differentiation. These authors concluded, as have others, that this can lead to speciation within dispersal ranges, but continuing gene flow during transition from within populations to isolation can blur species boundaries (see also Roux et al., 2016 [101]). Hence, as with *Pocillopora* [60], the different molecular variants of *Stylophora* were placed in the 'grey zone' of speciation, as defined (without specific reference to corals) by gene flow analyses in 60 taxa, as being between 0.5 and 2% of net synonymous divergence [101]. Most GBR *Stylophora* taxa were towards the species end of this speciation continuum, partly in agreement with our morphological species delineations and partly not (the latter in the case of *Stylophora mordax*, see Figure 24, bottom row). We provide further detail in the case study of the *Stylophora* syngameon below. The recent detailed study of *Acropora spathulata* in the western Pacific (whole-genome data from 1088 colonies from 29 reefs) [33] reported four lineages with absolute divergence of around 1% but included evidence of connectivity and mixing via gene flow.

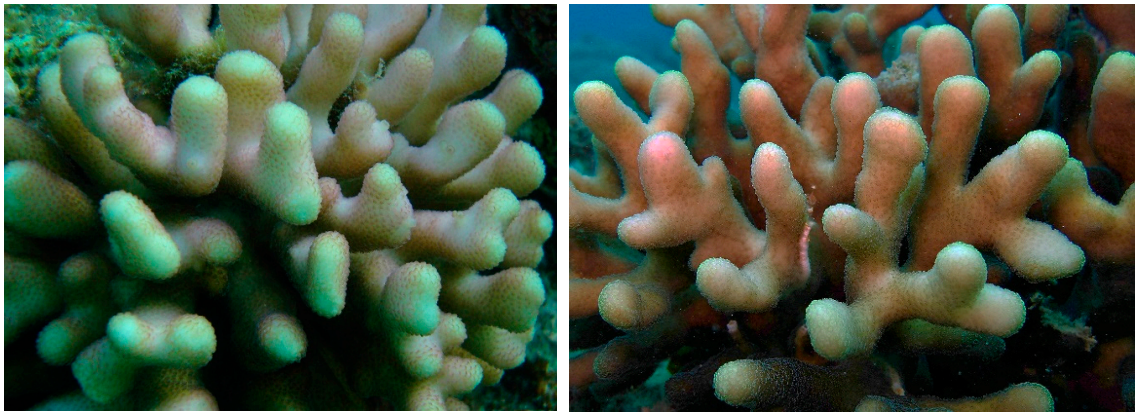


Figure 18. *Stylophora pistillata* in the Red Sea (**left**) and the Great Barrier Reef (**right**) are morphologically indistinguishable yet have different molecular signatures as predicted by reticulate evolution, see text. Photographs: E. Banguera (**left**) and R. Kelley (**right**).

Hybridisation in most other Indo-Pacific species is less studied. Nakajima et al. (2016) [102] found that *Galaxea fascicularis* has two sympatric variants in Japan. This was followed by Wepfer et al. (2020) [103] who found that this species has three well-differentiated lineages over large ranges and, more to the point, that *G. horrescens* is the only monophyletic *Galaxea*.

Of particular interest given longstanding debate on species boundaries in the Atlantic genus *Orbicella*, the three species presently recognised—*O. faveolata*, *O. franksi* and *O. annularis* (once considered a single polymorphic species [104])—all hybridise in the Florida Keys [105–107]. Similarly, Prata et al. (2022) [108] found that *Agaricia grahamae* and *A. lamarcki* are not genetically isolated and neither are *Madracis decactis*, *M. formosa* and *M. pharensis* [109],

all in the Caribbean region. These findings in Caribbean species are particularly pertinent on two points. Firstly, if intra-species divergence and porous species boundaries are common in the Caribbean, these are likely to be overwhelmingly common throughout the entire Indo-Pacific. Secondly, if Caribbean species are morphologically well defined (and most if not all are) yet many are polyphyletic, many if not most Indo-Pacific species are also likely to be polyphyletic.

Box 3. The consequences of hybridisation in corals.

Hybridisation in corals

- Is centre stage for any concept of reticulate evolution;
- Leaves no clear distinction between species (however defined), subspecies and hybrids;
- Occurs to an unknown extent but could be widespread across most major scleractinian taxa;
- Creates uncertainty in both morphological and molecular taxonomy;
- Is not readily accommodated by binomial nomenclature;
- Creates uncertainty and unpredictability in geographic boundaries;
- Reinforces a widespread view that conservation needs to be on finer spatial scales than distribution boundaries suggest.

While hybridisation and introgression may be the most important processes involved in maintaining the reticulated networks in corals, there are many other mechanisms which have significant importance to the development of divergent genetic signatures and thus relevance to contemporary taxonomy.

3.1.3. Reproductive Mechanisms and Taxonomy

Different reproductive strategies have significant consequences for population genetics. Alvarado-Cerón et al. (2023) [110] and Pinsky et al. (2023) [111] examine some of the ways in which reproduction, including fragmentation, contribute to genetic diversity and structure within populations. The latter authors emphasise the roles of gene flow, selection and hybridisation in adaptation to environmental changes.

Nevertheless, as far as taxonomy is concerned, there are few clear links between taxa and mode of reproduction. Many species within the Pocilloporidae brood their larvae, although others are principally broadcasters (*Pocillopora grandis* and *P. elegans*). Most Acroporidae with the exception of *Isopora* are broadcast spawners. Some corals are known to have both modes of reproduction. These include *Acropora digitifera*, *A. humilis*, *A. palmata*, *Cyphastrea serailia*, *Fungia fungites*, *Goniastrea aspera*, *Heliofungia actiniformis*, *Leptastrea purpurea*, *Oulastrea crispata*, *Pocillopora damicornis*, *P. elegans* and *Porites cylindrica*, a list that may be greatly extended by future studies. For further details, see the review by Baird et al. (2009) [112] and the updated information in the Coral Traits Database (www.coraltraits.org) [113].

Brooding and many broadcast spawning corals are hermaphroditic and thus have the potential to self-fertilise. This has been shown or postulated in a few species: in *Favia fragum* and *Porites astreoides* [114], in *Isopora brueggemanni* [115] and in *Seriatopora hystrix* [116,117]. In broadcast spawning corals, cross-colony fertilisation is dominant, but self-fertilisation has been observed at low levels under laboratory conditions (e.g., refs. [74,118]). This has potentially positive and negative effects in different situations. For example, it may be of importance where population numbers are low or colonies are isolated, but can result in reduced larval output or suppression of thermal tolerance in embryos: in *Goniastrea favulus* and *G. aspera* [119,120], in *Orbicella faveolata* [105], in *Diploria strigosa* [121] and in *Acropora palmata* [118]. In the case of *Acropora palmata*, self-fertilisation occurred in 7 out of 12 colonies isolated under laboratory conditions [118]. If similar levels of self-fertilisation occur under natural conditions in low-density or isolated populations, this could contribute to

the formation of localised, genetically homogeneous (monoclonal) communities with distinct genetic signatures.

The fact that so many corals participate in mass spawning events has many consequences for both contemporary and evolutionary processes. There is huge potential for gene mixing both within and between species. When a coral spawns, its eggs may be fertilised by sperm from a wide range of individuals, providing a mixed gene pool for settlement. If particular gene combinations are more suited to certain light levels, depths or turbulence levels, they will be favoured in those environments and may result in selective gene signatures in different habitats. Provided there are no reproductive barriers (such as timing of spawning), the next time a spawning event takes place, re-mixing may occur and, if conditions have changed, a new gene signature may be favoured in the modified environment. As we shall see below, different genetic lineages are being distinguished in certain habitats but, as yet, it is not clear whether this is a result of past genetic divergence or of local selection. Where there are developing mechanisms of partial reproductive isolation such as via asynchronous spawning, these may represent and support ongoing genetic divergence. However, these may turn out to be detrimental to the survival of the genetic lineage in the face of present environmental stresses unless they are reversed. Henley et al. (2022) [122] suggest that *Montipora flabellata*'s aperiodic spawning may be detrimental under changing climate conditions for this reason.

There are only a few studies linking reproductive mode, time of spawning and/or aspects of larval dispersal to a taxonomic position. According to Yasuda et al. (2021) [123], the genetic variation in *Goniopora lobata* and *Goniopora djiboutiensis* is better explained by surface circulation patterns than by differences in morphology. Rosser et al. (2020) [31] found that differences in spawning times are likely to be the principal cause of genetic divergence between populations of *Acropora tenuis* in Indonesia and Western Australia. van Oppen et al. (2002) [84] found that differences between *Acropora aspera* and four sister species could be explained by asynchrony in the time of release of gametes on the Great Barrier Reef. Furukawa et al. (2020) [124] found that differences in spawning time supports cryptic speciation within *Acropora divaricata* in Japan. Miller and Ayre (2004) [89] found that the genetic structure of *Pocillopora damicornis* populations of Lord Howe Island (Figure 15, above and Figure 69 below) appears to be maintained by localised recruitment of sexually produced larvae rather than asexual recruitment. Thomas et al. (2020) [40] found that there is wide variation in metapopulation connectivity in the brooding species *Isopora brueggemanni* and the spawning—brooding species *Acropora digitifera* on Rowley Shoals, an isolated offshore reef of Western Australia. Note that in most cases where differences in genetic signatures have been detected, there is still no clear evidence that these differences are stable over time or space—both important criteria for supporting taxonomic changes.

Among explanations for the presence of local genetic lineages, ongoing habitat selection for specific genotypes along with asexual propagation, as introduced above, are notable. Furthermore, factors such as genotype remixing during synchronous spawning, the unknown stability of minor spawning asynchronies, and the prevalence of hybridisation may all contribute to the temporal transience of lineages.

We conclude from these studies that reproductive biology, distribution and physical environment are inextricably inter-linked and that these subjects are essential contributors to our understanding of coral species however defined, a far cry from the museum-based taxonomy of yesteryear. We also conclude that coral reproductive mode, notably but not exclusively mass spawning in conjunction with hybridisation, combine to drive reticulation [1,5,75,125].

3.2. Other Mechanisms Causing Genetic Mixing and Divergence

Species hybridisation and genetic divergence are opposite sides of the same coin, both processes creating taxonomic complexity. Another is the relationship of corals with

their microbiome, termed 'the holobiont', once considered a simple one-on-one symbiosis between corals and a single species of dinoflagellate Symbiodinaceae (collectively termed 'zooxanthellae'), now understood to be highly complex [126].

3.2.1. The Holobiont

Climate change projections and the bleak outlook for corals have seen an explosion of studies focused on the responses of corals to associated temperature and chemical stresses (e.g., refs. [127,128]). These increasingly important selective forces, driving both acclimation and adaptation, are expected to exert significant evolutionary pressure on coral populations over the coming millennium with, as yet, unknown taxonomic implications. As a result, there have been significant advances in our understanding of the holobiont, particularly their photosynthetic dinoflagellates and bacterial communities.

Recent studies of the coral endo-symbiont and commensal community have revealed far more complexity than originally recognised [126,129–132], enabling corals to thrive in nutrient-poor waters ('Darwin's paradox' [133]; and subsequently [134,135]). Corals also occur in nutrient enriched waters where they appear to both 'farm' and feed on some components of their microbiome [136,137]. In the eastern Pacific, the depth-linked zonation of two dominant corals is explained by their association with different algal symbionts adapted to different light regimes [138].

Increasing numbers of coral species are being reported to host several species of Symbiodinaceae, along with a diverse array of other microbiota. These include bacteria, viruses, and other micro-eukaryotes. Specific composition of microbiomes varies in response to local environmental changes and cophylogenetics [139–144]. This remains an area of vigorous research, with both physiological and taxonomic relevance [145–152]. The work was initiated three decades ago by a provocative paper by Buddemeier and Fautin (1993) [153] proposing the 'adaptive bleaching hypothesis' (see also [154]).

Certain species of Symbiodiniaceae are more heat-tolerant than others and in adverse conditions some corals are able to benefit either by 'shuffling' the proportions of endosymbiont species or by 'switching' to a more heat tolerant species [155–161]. Bacterial populations also show significant changes in response to different environmental conditions and perturbations [162,163] and may be actively modulated by the coral through mechanisms such as quorum quenching, offering potential defence against microbial threats [164]. In some species of coral, vertical transmission of symbionts (both dinoflagellates and bacteria) can occur via the planula larvae in brooding species [39,165–168], via the oocytes in some spawning species [169–172], and potentially via mucus deposited around gamete bundles [173].

In other cases, corals can acclimatise to temperature stress [174–176], ocean acidification [176] and low-quality estuarine environments [177], often through epigenetic mechanisms [178,179]. Certain epigenetic stress modifications can be inheritable [180,181].

Not all studies suggest positive outcomes. Some coral species may not modify their dinoflagellate associations even under stress conditions either because more tolerant variants are not readily available or because they are not accepted by the coral host [182,183]. Not all coral species are able to pass their symbionts on directly to their progeny [184]. Furthermore, increased fungal diversity and pathogen abundance in the holobiont can increase thermal susceptibility [185] and the presence of other environmental stressors can limit tolerance even where heat tolerant symbionts are dominant [158].

Some differences in response to temperature can be attributed to specific genetic lineages [79,107,186–188]. Along with the scope for inheritable variation (e.g., refs. [106,189]) and reproductive consequences [190], these are obvious drivers of divergence and potential speciation which can lead to taxonomic uncertainties, particularly where lineages are not morphologically distinct.

The close relationship between host species and their microbiome led to the suggestion (based on coral bleaching studies of *Oculina patagonica*) that the holobiont may evolve as a single unit [191,192]. This has sparked considerable debate [193–196]. There are studies supporting vertical transmission of symbionts to offspring (in references above) and at least some evidence for horizontal gene transfer between symbiont and host [197–199]. Hence, there are good reasons to believe that environmental conditions will have effects on the resulting coral-symbiont association and potential selection influences on the coral genome. This assertion is supported by studies of genomic signatures in the coral holobiont through Holocene climate changes [200].

3.2.2. Chimaerism, Mosaicism and Somatic Mutations

Adding to this biological complexity, we do not yet know the full extent to which coral molecular signatures may be affected by chimaerism and mosaicism [201,202]. These authors noted that multi-genotype corals—mosaics—can arise from somatic mutations producing a neoplasm (Figure 19, right) [203], mitotic recombination, mitotic gene conversion or duplications, or exchange of genetically distinct components from different organisms, usually in early development stages, producing a chimaera (Figure 19, left) [204–206].

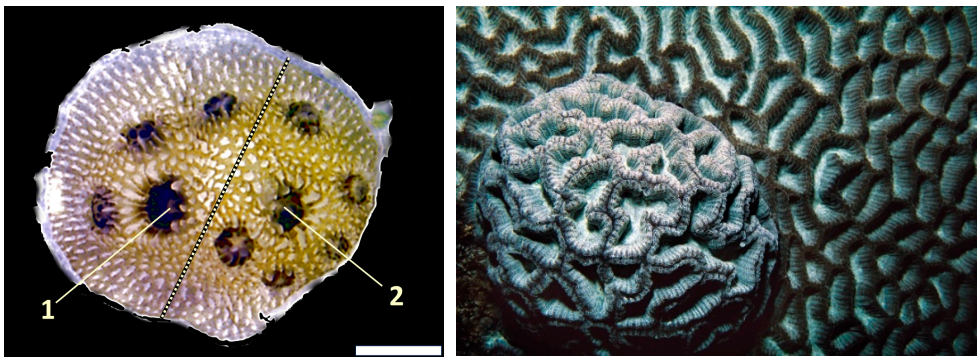


Figure 19. (**Left**) A single colony growing from fusion of spat from two parents (1 and 2). The broken line shows where fusion has occurred. (**Right**) Neoplasm on a *Platygyra daedalea* colony. *Photographs*: B. Rinkevich (**left**) and J. Veron (**right**).

Although field workers recognise somatic mutations in a wide range of coral taxa, including *Acropora*, *Platygyra* (Figure 19, right), *Hydnophora* and *Symphyllia*, other forms of intra-colonial genetic variability are much less obvious. As yet, there is little understanding of the effects of these processes on morphological variation, or their ecological [207] or taxonomic consequences despite studies dating back to the 1970s [201]. These studies evaluated interspecies [208] and allogeneic interactions, notably tissue fusions in spat, and natural chimaerism in *Pocillopora damicornis* [209], *Pocillopora acuta* [202], *Stylophora pistillata* [210], and *Pavona cactus* [211].

Chimaeric colonies have been experimentally cultivated in both the lab and field, typically developing in the 'chimaeric window' of ontogeny, between partners less than three months old, prior to the maturation of the allorecognition system [201,205]. It can, however, be delayed up to one to two years post-settlement [212]. In their molecular study of *Pocillopora acuta* at Reunion Island, Oury and Magalon (2024) [202] detected chimaerism and mosaicism in 12 and 7 percent of colonies, respectively. Both chimaerism and mosaicism led to intra-colonial allelic differences, some of which occurred in genes involved in a variety of biological processes. Recently, Rinkevich (2019) [201] noted that multi-chimaeras made of several genotypes may facilitate adaptive mutational opportunities to develop and become fixed in coral populations, increasing genetic variation. Oury and Magalon (2024) [202] similarly concluded that intra-colonial genetic variability is a source of genetic diversity and genetic plasticity, increasing

adaptive potential and aiding maintenance of populations and evolution. Also, of particular relevance to taxonomy, we note the apparent risks such intra-colonial genetic variability may pose for molecular analyses, particularly where sample sizes are minimal.

3.2.3. Contemporary Stressors

Environmental Impacts

Human-induced environmental impacts on corals, and particularly those resulting from climate change (increased temperature including prolonged heat waves, super storms, acidification, deoxygenation and sea level rise) seem certain to greatly accelerate natural selection. Mass bleaching is already decimating those individuals/lineages not well adapted to higher temperatures and although, as we have seen above, some species and genotypes have mechanisms to increase their tolerance, others may not [107]. It is not yet clear what effects such intense pressures on subpopulations of species will have on total genetic or morphological variability of taxa, or indeed whether there will be significant extinctions. It is clear, however, that reef-building corals are increasingly threatened [213,214]. Some species are now critically endangered (IUCN Red List, 2025 [215]), including two species of Atlantic *Acropora* (*A. cervicornis* and *A. palmata*) and the monotypic *Dendrogyra cylindrus* [216]. In the central Indian Ocean, the endemic *Ctenella chagius* has suffered major population decline, and is now considered ecologically and functionally extinct on Chagos [217]. Causes of these declines, and of those of many other species, include synergisms among increasingly severe heat waves and diseases and more localised impacts.

The overarching questions are multifarious and include

- Rates of evolution [218];
- Thermal tolerance;
- Acclimation;
- Adaptation to rapidly changing physico-chemical conditions [219–221];
- The value of thermal refugia [222,223];
- Their potential as a genetic resource for denuded reefs [224];
- Human intervention through selective breeding of heat- or other stress-tolerant cultivars [225];
- And other mechanisms of 'assisted evolution' [226].

The last involves the creation of cultivars via experimental manipulation of both corals and their symbionts, followed by mass cultivation of successful products and mass release of larvae [227]. Branching *Acropora* are usually assumed the best candidates for this work because of their rapid growth rates, their diversity in the Indo-Pacific, and their ability to form three-dimensional colonies to maintain essential ecological function.

Disease

According to the massive literature compilations of Montilla et al. (2019) [228] and Burke et al. (2022) [229] there are approximately 40 known diseases that affect more than 200 species of corals. In most cases these are linked to mass bleaching and other environmental stressors including acidification and pollution. Diseases have been most heavily studied in the Caribbean where disease has caused extinctions in regional areas. There is considerable variability in disease resistance among species [230–232]. As with temperature, different genotypes of corals show significantly different rates of disease susceptibility [232,233] and gene expression is also an important criterion [232]. Many aspects of disease resistance are heritable and thus may be detectable in lineage studies and may lead to divergence over time.

3.3. Observing Reality

Having briefly reviewed some of the many intricacies and complexities currently affecting genetic diversity and speciation of corals, we now turn to assessments of coral variation in the field and the taxonomic and nomenclatural consequences that follow. But before doing so, a brief diversion is warranted.

3.3.1. Blame It on Taxonomy?

We have seen that the advent of scuba-based fieldwork revolutionised the study of corals, including their taxonomy. Now, field studies are giving way to molecular studies, and it is not difficult to see why: it takes decades to acquire the expertise to make the sorts of observations described in the introduction to geographic reticulation below, time which few young people can afford if they are to follow a career path. At the same time, experienced field taxonomists are becoming ageing rarities. We are not reflecting here on the value of field versus molecular studies (discussed below), but rather on the extent of present-day field studies themselves. To take one example among hundreds, the differences between *Isopora palifera* and *I. cuneata* colonies illustrated in Figures 21 and 22 (below) is not now an issue for an experienced field taxonomist for they will have seen these sorts of intra-specific variations in many species, but it would certainly be an issue for an inexperienced observer (just as it once was for the present authors). Without further study, newer observers will have little confidence separating these species and deciding what their names should be.

The point at issue is that many hundreds of publications about topics addressed throughout this review find some 'fault' with the taxonomy of the species they treat. We pause here to distinguish genuine taxonomic problems (of which there are clearly many as this article reveals) from observer error—misidentification, as may arise from limited knowledge or field experience. Both may be flagged as 'cf' or 'aff' (abbreviations from Latin) to signify uncertainty. In some recent cases, such use appears to pay homage to 'the mantra' (below) where all morphological nomenclature is dismissed (but used anyway).

3.3.2. The Biological Entity

At species level, however defined, coral taxonomy is seldom simple. This is primarily because most corals, as we have seen, exhibit wide environment-correlated morphological variation in any particular place or country as well as extensive geographic variation, both morphological and molecular, over their full distribution range. Over great geographic distances, a 'species' may remain clear but more often it becomes uncertain because of reticulate pattern formation, as described above. In many if not most cases, the 'species' may cease to be a clearly defined unit, creating a level of uncertainty over space and time that has yet to be widely recognised, let alone accommodated.

We use the term 'biological entity' to denote a discrete 'species-level' taxonomic unit (whether named or unnamed, formally described or not) which has an identifiable suite of morphological variability in the field and is recognised across different environmental and spatial scales. Depending on the degree of confidence, a biological entity may be considered a 'valid entity', a 'probably valid entity' or 'possibly valid entity'.

The term 'species' is used here in the same somewhat vague and variable way it is used in other publications, but we distinguish 'valid species', which are entities that have been formally described and have a name, from 'valid entities' which may be undescribed. It follows that all valid species are valid entities, but the reverse is often not the case.

3.3.3. Biological Entities and Names

It is fundamentally important to understand the difference between a biological entity and a name. A biological entity is a group of organisms to which a name has or may

be given and which has certain characteristics in common. The biological entity can be described and linked to morphological, molecular, environmental, geographic, ecological, physiological or other information. A name, in contrast, is simply a label to denote a biological entity or group of biological entities.

The distinction between a biological entity and the name applied to it will become important when we examine the criteria for essential versus destabilising taxonomic changes. Fortunately, most biological entities have remained stable over two decades at least, generic name changes for some notwithstanding. Such changes are sometimes warranted but we do not undertake or accept them without good reason, for every time the name of a biological entity is altered, or it is divided or combined with another, there is potential for information loss and increased uncertainty.

3.3.4. Morphospecies

For those readers who are not specialist field biologists, it may be helpful to clarify the difference between the term 'morphospecies' as used in most molecular papers and 'biological entities', the focus of field taxonomists.

The term 'morphospecies' conjures the image of a species which is defined by its morphology, whether macro- or micro-, and suggests that it could be described from one or more skeletons of the species. This is how most early species descriptions were undertaken. But morphology is only one component of a wide range of criteria including soft tissues, behaviour, habitat types and associated community structure, that are absorbed, almost subliminally by the experienced field biologist to determine whether a suite of field variability is sufficiently different to be considered a potentially different species. Thus, a specialist's field identification of corals includes all aspects of environment-correlated variation and is usually based on extensive replication across multiple habitats, localities and geographic regions with all the variability that entails (e.g., Supplementary Figure S1). When an expert field taxonomist with broad geographic experience believes that a suite of observed colonies may be new, the chances are high that it is because the decision is based on an internal assessment of thousands of encounters of similar colonies and on a wide range of associated information.

3.3.5. Field and Museum Studies

Collectively, we have spent >20,000 h studying corals in situ in 91 of 150 ecoregions [234] wherever they occur across most of the world's reef provinces since the 1970s and we have collected approximately 30,000 specimens for studies of skeletal detail. These specimens are lodged in museums or similar curational institutes, in Australia, France, Germany, Brunei, Indonesia, Philippines, Papua New Guinea, Timor Leste, Pohnpei (Micronesia), Palau, Japan, Vietnam, Madagascar, Hong Kong, Yemen, Eritrea, Egypt, Saudi Arabia the UK and the USA. Throughout this time, we have also undertaken extensive photography of living corals augmented by a host of photos donated by collaborators. This work also included extensive studies of species descriptions, in situ images and collections from 52 of the remaining 59 ecoregions, providing an overall coverage of all but 7 (very isolated) of the 150 ecoregions.

For a previously unstudied ecoregion, our work initially involves broad-scale familiarisation. It then focuses on unfamiliar field occurrences to separate unfamiliar geographic variants from unrecognised species. The unfamiliar occurrences are reviewed against a background of thousands of similar occurrences we have encountered in the past.

This work is concurrently integrated with examination of previous taxonomic studies and collections relevant to that ecoregion or country. For example, Veron's many field studies of Philippine corals were intermixed with studies of the collections of Nemenzo and his colleagues and Veron's multiple studies of Japanese corals involved similar studies of the collections of Yabe and his co-authors. In most other geographic regions, earlier

taxonomic studies are less demarcated. Thus, previous studies of Red Sea corals involve a complex mixture of historic and recent taxonomies and previous studies of Caribbean corals involve the world's oldest taxonomic publications and collections, most in European and American museums. Need it be said that this work has endless shades of grey, stemming from both fieldwork and the taxonomic issues described below.

In our collation of this large body of work, it became clear that some species were endemic to a particular region or, in a few cases, a single ecoregion, but most had much wider distributions of multiple ecoregions and many had ocean-wide distributions [234,235] see CoralsOfTheWorld.org (2016, 2026 in prep.) [10,236] maps for details.

The various patterns resulting from this geographic variability are summarised and discussed in more detail by Veron (1995) [1] (Figure 20). The additional fieldwork that has taken place since 1995 has not materially changed our understanding, although it has greatly added to our knowledge of all individual species.

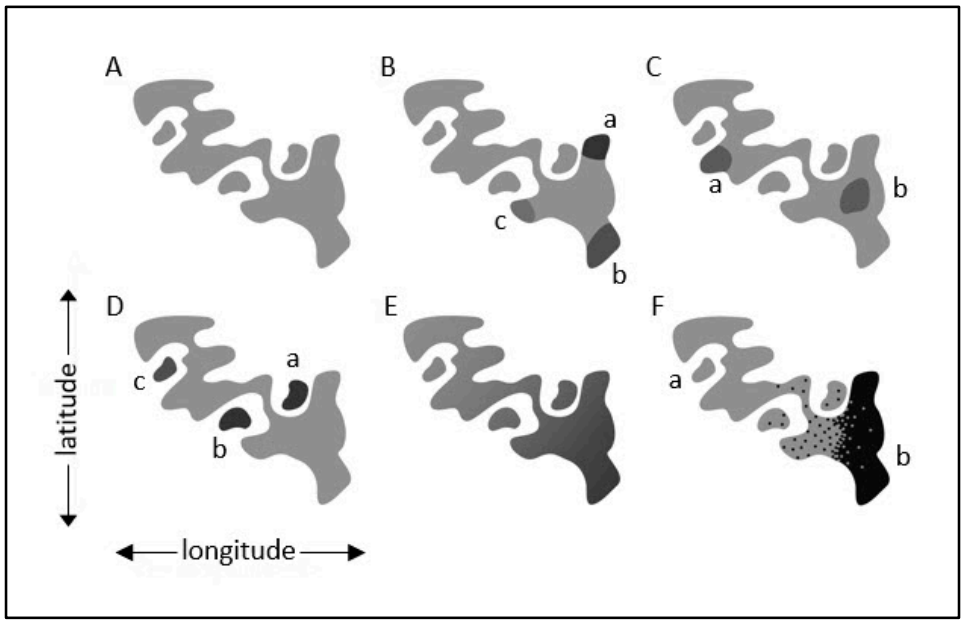


Figure 20. Concept diagram of common types of geographic variation with widespread Indo-Pacific species and species complexes: (**A**) no taxonomically significant morphological variation occurs throughout the range; (**B**) morphologically distinct disjunct—geographic variants (a, b, c) occur in high latitudes; (**C**) morphologically distinct variants occur in geographically marginal (a) or central (b) regions; (**D**) morphologically distinct disjunct variants or geographic variants occur in isolated regions. These groups may be similar (a and b) or individually distinctive (c). (**E**) Continuous variation with a species becomes increasingly marked over distance so that coralla from opposite ends of the longitudinal range are very distinct, but at no point are there two overlapping or distinctive groups. (**F**) As with E, except that there is a region of overlap, or hybridisation, between geographic variants a and b (modified from Veron, 1995 [1], p. 204).

A second component of these studies is environmental, with some corals restricted to particular habitats. Not unexpectedly, habitat details are usually strong indicators of species likely to be present.

Within these various ranges, both geographic and habitat, some corals show little variation while others show more-or-less consistent gradations from one habitat and/or region to the next. These fall into several overlapping categories. The most common is where the biological entity is morphologically variable and where part of that variability is more common in specific habitats or geographic areas than others. To an observer who is not familiar with the full range of variability in a region, or who has a search image which focuses on only part of that variability, the same species in another habitat or region may

appear to be different. To an observer who is familiar with the full variability of the taxon, the same taxon in a different habitat or region will initially be less familiar until it is clear that the difference is merely a difference in the frequency of a particular variant (see below).

Another form of variability is where the biological entity is gradually changing across its full distribution range such that its full variability can only be characterised with reference to its full spatial extent. In this case, even an observer who is aware of the full variability in one region but has not sampled intervening regions, may mistakenly consider a species in a geographically distant region to be a different species.

3.3.6. Habitat and Environment-Correlated Variation

By now the complications that molecular and morphological variability impose on coral species delineation will be obvious. There are, however, some implications for taxonomy that are less obvious and less appreciated, but which persist today.

3.4. Habitats

Reefs are exceptionally heterogeneous environments in respect of their geomorphology, habitats and environmental regimes all of which are compressed into small amounts of three-dimensional space. These collectively interact to determine the composition and morphology of all corals present.

3.4.1. Back Reef, Lagoonal and Wave Hammered Reef Crests

Wave energy, current flow and illumination are all powerful forcings on coral morphology. These are at their most divergent in sheltered, often turbid, lagoons (Figure 63, below) compared with open ocean-facing, wave-hammered reef crests (Figure 64, below), each habitat type being characterised by corals with distinctive growth forms (as depicted for *Pocillopora damicornis* in Figures 4 and 5). Different habitats may well have morphological and genetic divergence linked in tandem (illustrated, for example, in the case study of *Stylophora pistillata* below).

We need not revive images of reef flats nor re-describe the corals found on them, but differences between these corals and those on lower reef slopes are often debated. One example predates molecular taxonomy by decades. Veron and Wallace (1984) [237] separated the sister species *Isopora palifera* and *I. cuneata* (then called *Acropora*) (Figure 21) and provided extensive morphological details and skeletal photographs of both species. Subsequently, Veron (1986 pp. 132–133) [238] illustrated the range of variation in *I. palifera* from a protected reef slope to a very exposed reef front where colonies of these species may be problematic to distinguish (Figure 22).

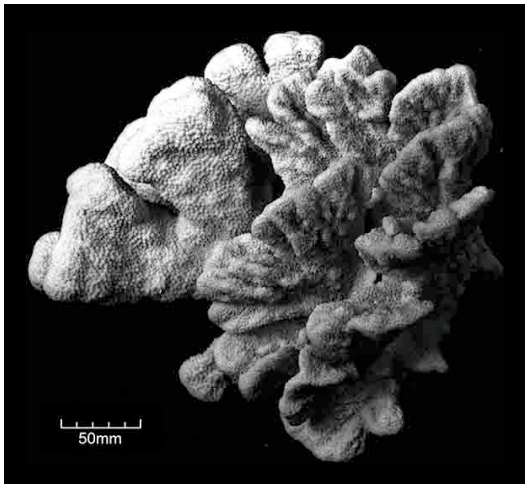


Figure 21. Adjoined skeletons of *Isopora cuneata* (right front) and *I. palifera* (left back) on a semi-protected back reef Chesterfield Reef, Coral Sea. Photograph: J. Veron.

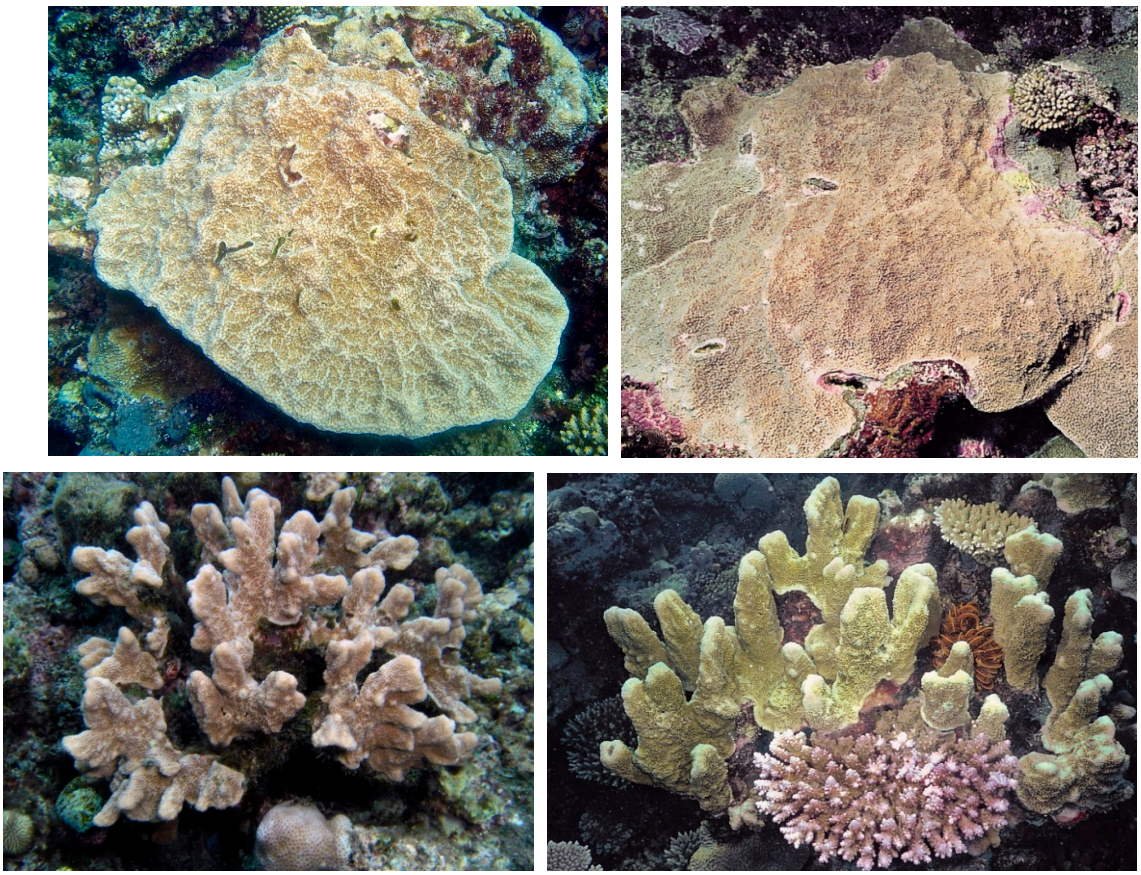


Figure 22. Top row: *Isopora cuneata* (**left**) and *I. palifera* (**right**) on very exposed reef fronts. **Bottom row**: *Isopora cuneata* (**left**) and *I. palifera* (**right**) on back reef slopes, see text. Photographs: R. Kelley (**top left**), J. Veron (**top right** and **bottom left**) and E. Lovell (**bottom right**).

To a large extent, we have moved on from such debates, but we make the point that our understanding of these 'morpho-taxonomic' species is highly dependent on correlations with habitat. This creates challenges for molecular studies for it cannot be presumed that genetic partitioning is not involved (see immediately below for analogous examples). Underwood (2009) [239] provides glimpses of this with a study of genetic variation among reef systems for *Acropora tenuis* in northwest Australia and, more recently, detailed population genetics of a number of other species has begun (e.g., refs. [7,33,100]).

3.4.2. Mesophotic Communities

Mesophotic communities (Figure 65, below) are those where light availability limits the depth range of species and may substantially affect their morphology. Such communities have extensive world-wide occurrences with multiple reports claiming unexpectedly high coral diversity in them (Ref. [240] and a spectrum of publications cited within Loya et al. 2019 [241]). Virtually all species with distributions extending into the mesophotic zone exhibit morphological change with increasing depth, correlated with reduction in both wave energy and light. For some species, these phenotypic changes have a genotypic signature (see below). At such depths in clear oceanic water, changes are commonly below the depth accessible to most scuba divers and as a result the morphology and genetics of deep-water specialists or mesophotic occurrences of predominantly shallow-water species, are poorly known and are under-represented in taxonomic publications. Figures 23 and 24 illustrate extremes. Mesophotic conditions make identifications problematic and molecular results from collected samples potentially misleading.

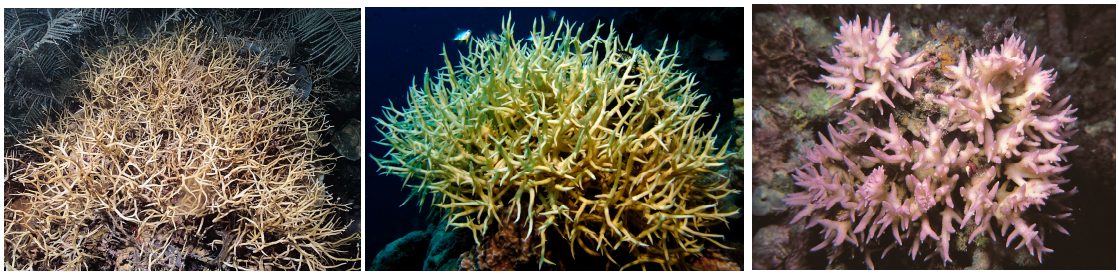


Figure 23. *Seriatopora hystrix* in a mesophotic habitat in the Philippines (**left**), on a back reef slope in Indonesia (**centre**) and on an exposed reef front, Great Barrier Reef (**right**). Photographs: J. Veron (**left** and **right**) and E. Turak (**centre**).



Figure 24. Sequence of growth forms of *Stylophora pistillata* from a mesophotic habitat at 35 m (**top, left**) to exposed reef front (**bottom right**), the bottom row showing a gradation towards the *S. mordax* morphotype. Photographs: Red Sea, H. Nativ (**top left**); Mariana Islands, D. Fenner (**top centre**); Saudi Arabia, Eulalia Banguera (**top right**); Vanuatu, D. Fenner (**bottom left**); Cenderawasih Bay, E. Turak (**bottom centre** and **right**).

As with studies of reproduction (above), we only have limited glimpses of mesophotic populations let alone individual mesophotic species. We note that the many studies of *Stylophora pistillata* we offer in the case study below also extend to mesophotic occurrences, where Malik et al. (2021) [242] provide explanatory correlations between morphological changes, skeletal microstructure and genomics. Also as above, Meziere et al. (2024) [100] have found that Great Barrier Reef colonies of the ecomorph *Stylophora mordax* (Figure 24, bottom row) are in a grey zone of *S. pistillata* speciation.

After studying a large number of samples, Luck et al. (2013) [243] found Hawaii's dominant mesophotic genera, *Leptoseris* and *Pavona* are each polyphyletic and suggest that one *Leptoseris* is an unidentified cryptic lineage. Gijsbers et al. (2023) [244] conclude that reproductive isolation, correlated with depth, has led to diverging molecular clades in five mesophotic *Leptoseris* (*L. mycetoseroides*, *L. hawaiiensis*, *L. explanata* and two that are synonyms of *L. explanata*) and that the same applies to four *Agaricia* (*A. lamarcki*, *A. fragilis*, *A. grahamae* and *A. undata*). Gallery et al. (2025) [245] have found that *Montastraea cavernosa* and *Siderastrea siderea* both have four distinct depth-linked lineages in the Florida Keys. However, given the prevalence of polyphylogeny in the many species noted above, these results are not unexpected. They have led some authors to postulate the existence of cryptic, genetically isolated, species or that deep water corals speciate independently of their shallow water relatives, or

perhaps that morphological norms simply mask divergence at mesophotic depths [246,247]. An alternative is simply that gametes of these corals continue to cross-fertilise with those from colonies in other environments but only suitable crossings survive at mesophotic depths. Resolution of these differing theories awaits further, detailed, population genomic studies.

3.5. Conceptualising Species-Habitat Variability

Following from the above examples, we illustrate these important points conceptually (Figure 25). Consider two taxa, one an established species (left) and another potentially new species (right), both occurring in Habitat 1 and in Habitat 2. In the field, with the myriad of environmental information and numerous corals with which to compare, these two species may be clearly distinct from one another in Habitat 1 and also clearly distinct from one another in Habitat 2. However, if an observer were to take a specimen of an established species unknowingly from Habitat 2 and compare it with a specimen of a potentially new species unknowingly from Habitat 1 it may be difficult to tell these two samples apart if no other information is available.

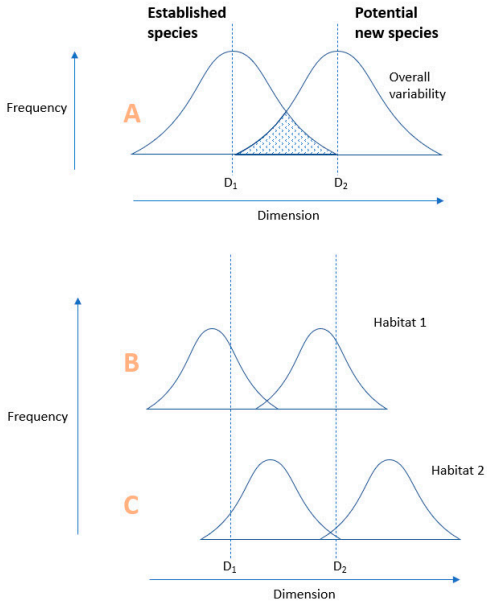


Figure 25. Comparing hypothetical variation in a character or suite of characters of an established species with a potentially new species. (**A**) Full range of variation in this character with moderate to significant overlap between the mean dimensions (D_1 and D_2); (**B**,**C**) showing the actual variability of the same character in two different habitats where overlap in either habitat is very low and the two species are almost always distinct.

Although the above description is hypothetical, this scenario is common. Characters regularly used to identify coral species in both the field and laboratory usually vary in semi-predictable ways. Two species which are distinct underwater and which differ from one another in one or more of these characters may be confused if habitat data are not included. Without these habitat data, investigators may be assessing specimens across the whole spectrum of variability illustrated in Figure 25A where there is substantial overlap between the two species. Significant numbers of samples of the two species from all habitat types would be needed to detect the presence of two separate populations unless the sampling is paired from within the same habitat types.

It is thus crucial to evaluate the relevant range of criteria in situ, not only including morphological characters, but also, as noted above, a wealth of environment-correlated variables. The resulting combination, repeated many times, allows the observer to build up a composite image of the species variation across habitat type and geographic space based

on integration of a range of morphological and environmental criteria across thousands of encounters (e.g., see Supplementary Figure S1).

A different but perhaps even more problematic consequence of this kind of habitat variability is the effect on type specimens (discussed further under Current taxonomic issues below). Holotypes are, by default, single specimens which are taken to represent the species. In reality, the habitats of holotypes are rarely recorded and the specimens may well be unrepresentative of the species, either taken from an unusual habitat or simply an uncommon morphological variation. An understanding of both the relevant habitat and the normal variation in the species is essential to minimise taxonomic confusion (e.g., see Supplementary Figure S2).

The significance of such observations to taxonomy has been well-documented in numerous other animals and plants [248–250] and may seem self-evident to many readers. But because of the relatively recent advent of scuba, limitations of dive time, working in a restrictive foreign environment, as well as expense, weather and ease of access, reef and terrestrial studies are not comparable. As a result, the number of taxonomic experts with broad reef experience is small and most stem from a time when reefs were in much better condition and decades of experience could be gradually acquired.

3.6. Geographic Reticulation

Geographic reticulation raises similar issues to those illustrated above for habitats, albeit with additional complexity. As we have seen, biological entities in a reticulate system have, or are predicted to have, variable genetic, morphological, and geographic boundaries and can therefore be poorly defined. The central issue is not simply that species vary geographically, but rather that they vary geographically in relation to each-other; that is, they are not self-contained but are parts of continua which are interwoven with other biological entities [1,251]. They appear to us to have 'fuzzy' boundaries because humans are not good at envisaging multi-species continua (for example, see Figure 26).

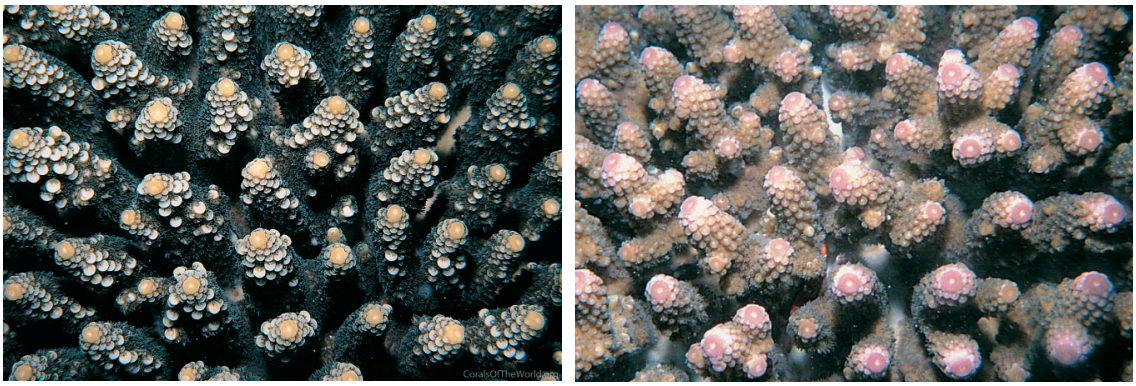


Figure 26. There are significant taxonomic differences in *Acropora digitifera* either side of the Mozambique channel (in Madagascar, **left** and Tanzania, **right**). Even though the geographic distance is <1000 km they are widely separated by surface currents and are not unambiguously the same species. Photographs: J. Veron.

In both theory and practice, geographic reticulate patterns remain obscured behind a veil of taxonomic and nomenclature issues involving a wealth of environmental parameters. However, such matters can be accommodated if it is accepted that corals are parts of continua and are not units. This notion will make no difference in a single place or country but becomes increasingly important in increasingly distant places. For example, a field taxonomist who is very familiar with the corals of the Great Barrier Reef will be comfortably familiar with the corals of Vanuatu as there is little difference between the two faunas. However, if the same observer goes to New Britain in the Bismarck Sea, about the same geographic distance away

but not in any direct surface circulation path, the observer will be less comfortable. This is not because there will be many unfamiliar species (which can be readily accommodated), but because once familiar species are less familiar and, worse, the once clear distinctions between sister species have become less clear. If the observer then makes lists of the corals of the three countries, there will be little difference between the species of the Great Barrier Reef and Vanuatu (about 95% in common) but a larger difference between these countries and New Britain (about 80% in common). However, the discerning observer will be unhappy with these lists because they treat species as units. The observer knows that there are problems of one sort or another in naming at least half the species in New Britain. This is not because of any fault with the taxonomy, it is because the observations are parts of continua where details that distinguish 'sister' species become unendingly complex.

As the observer moves from New Britain northwards to Pohnpei and Yap, northwestwards to the Philippines and westwards to Indonesia, some of the species' complexities become more severe while for others there is greater clarity as understanding of the intra- and inter-species variability is refined. At the same time specialists *within* those countries may have few difficulties because they are seeing and able to distinguish just a subset of the overall variability, whatever they name them.

These are significant matters of concern in making decisions about species boundaries, especially for taxonomic and conservation purposes [252].

3.7. Local Abundance, Isolation and Habitat Marginality

It is an impossible task to describe the taxonomic consequences of local abundance and isolation per se for coral taxonomy as these effects are species-specific and largely unverified. Corals in isolated and/or marginal habitats may have very different molecular signatures from those elsewhere having small populations adapted to local conditions. We only have glimpses of cause and effects.

Continental boundary currents, which transport warm water containing tropical larvae polewards, are predicted to intensify under global warming (excluding the Gulf Stream) [253,254]. Recent and future expansion of species ranges in these currents, with resulting selection and connectivity issues, are difficult to define but are certain to create novel opportunities for genetic mixing and selective survival [1,255–257]. Such expansions will be limited, however, at their high latitude extents by the seasonal reduction in irradiance during winter, aragonite saturation state, temperature anomalies, salinity fluctuations, and competition with macro-algae. At present we only have glimpses of potential impacts from a few studies: (a) poleward dispersal of Great Barrier Reef species is increasing the diversity of more southerly coral communities [1,258], (b) poleward gene flow appears to occur in *Acropora tenuis* and *A. millepora* on the Great Barrier Reef [259] although this is not necessarily correlated with geographic change and (c) cryptic divergence of *Acropora hyacinthus* in Japan is specifically correlated with poleward extension [254]. These last authors (Fifer et al., 2022) propose that range expansion may lead to reduced genetic diversity and increased frequency of deleterious mutations that were rare in core populations [254]. (d) Migration of *Pocillopora damicornis* from southerly locations into temperate Japan may impose a 'migration load' on high-latitude populations with genetic consequences [260].

As examples of extreme geographic isolation, *Catalaphyllia jardinei* in Kabira Bay, Honshu, Japan [261,262] and *Astreopora moretonensis* at the Solitary Islands, eastern Australia, are known from one or very few records [263]. These occurrences may be 'pseudo-populations'—expatriates imported via poleward-flowing currents—although in other high latitude populations local spawning has been documented [264,265].

As an example of ecological isolation, mesophotic mats identified as *Alveopora tizardi* in the northern Red Sea are unlike any tropical counterpart studied so far, an apparent

consequence of depth (Figure 27, left). This identification awaits verification. High to extreme local abundance in many species can also result in taxonomic anomalies. For example, *Diaseris distorta* may reproduce asexually by autotomy [238,266,267] (Figure 27, right) and continue dividing until daughter individuals are <2 mm diameter and have few morphological similarities with mature individuals. In species where fragmentation leads to incomplete or unusual morphologies (e.g., *Diaseris fragilis* [238,268], *Zoopilus echinatus* [269], *Halomitra clavator* [270]), isolated museum specimens or fragments may well be unrecognisable.

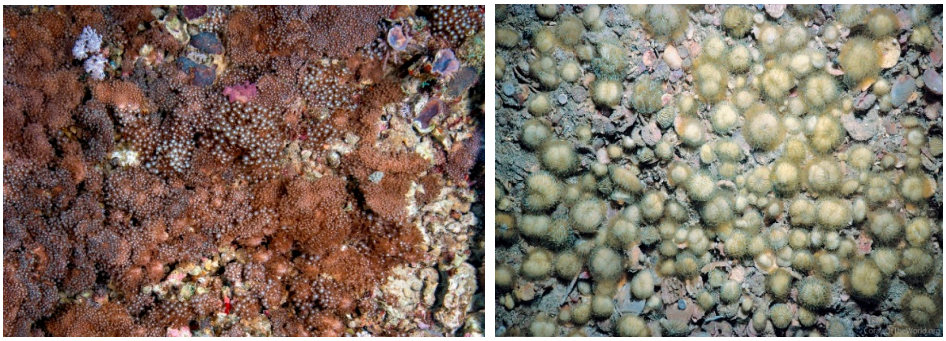


Figure 27. (**Left**) *Alveopora* cf. *tizardi* mesophotic mats at 44 m depth in Eilat, northern Red Sea. (**Right**) *Diaseris distorta* on the Great Barrier Reef. Photographs: H. Nativ (**left**) and E. Lovell (**right**).

3.8. Co-Occurrence

General museum specimens are commonly difficult, often impossible, to identify with any degree of certainty, but not so most collections of co-occurring 'sister' species if they are from the same place and habitat (Figures 28 and 29). Co-occurrence is therefore commonly used aid in modern coral taxonomy, with many species being separable by expert taxonomists only after co-occurrence is established.



Figure 28. Examples where co-occurrence of Indo-Pacific species helps distinguish related or sister species. (**Top left**): *Hydnophora* sp. (left) and *H. rigida* (right) in Indonesia. (**Top right**): *Seriatopora caliendrum* (left) and *S. hystrix* (right) in NW Australia. (**Bottom left**): *Lobophyllia hemprichii* (above)

and *L. robusta* (below) in Fiji. (**Bottom right**): *Dipsastraea danai* (top, centre), *D. favus* (bottom, left) and *D. pallida* (right) on the Great Barrier Reef. These species pairs are readily distinguished in the field where they co-occur but may not be so easily distinguished in museum collections. Photographs: E. Turak (**top left** and **bottom left** and **right**), J. Veron (**top right**).



Figure 29. Examples where co-occurrence of Caribbean species helps distinguish related or sister species. (**Left**)*: Agaricia agaricites* (left) and *A. lamarcki* (right). (**Centre**): *Diploria strigosa* (left) and *Colpophyllia natans* (right). (**Right**): *Orbicella franksi* (left) and *O. faveolata* (right). Photographs M. Vermeij (**left** and **centre**), E. Weil (**right**).

These examples are about co-occurring species, but that is only the start of a more general issue where morphological differences between species which co-occur in one region may become increasingly uncertain with increasing geographic distance. As a result, a substantial proportion of outstanding taxonomic issues are between species which are not sympatric, or which occupy different habitats.

Note that when we use the term co-occurrence, we refer specifically to two colonies occurring as neighbours in the same location, habitat and depth (as illustrated in Figures 28 and 29, above). Co-occurrence is therefore not synonymous with sympatry which refers more broadly to the presence of taxa within the same geographic region at the same time. This distinction is important: both theoretical frameworks (see discussions of reticulate evolution and morphological variation above) and recent molecular studies argue that many distinct genetic signatures may exist within a single biological entity driven by habitat or community-level selection (see Grupstra et al., 2024 [271] for pertinent summaries). As argued throughout this article, such findings should not, by default, lead to new species designations without a thorough understanding of the full inter- and intra-species variability of sibling taxa. Many similar species are readily separated when they co-occur on the reef but may prove challenging to reliably separate as specimens if provenance is unknown (Supplementary Table S1).

4. Species Boundaries and Taxonomic Decisions

Ever since Linnaeus systematised binomial nomenclature, initiating the modern taxonomic framework, classification has relied on unending concepts of 'species' and mechanisms of speciation, many relevant to corals [1,61,272–274]. It is beyond the scope of this review to revisit these concepts. However, we do make the salient point that unlike terrestrial plants and animals on which most concepts were founded and focused, comprehensive in situ observations of corals were not possible until the advent of scuba. Thus, the modern synthesis of neo-Darwinian natural selection as depicted in the Introduction held sway until Veron (1995, Chapters 5, 12 and 13) [1] identified the key role of reticulate evolution and foreshadowed the importance of molecular and reproductive studies in elucidating the increasingly obvious complexity of coral species' origins and relationships.

The burgeoning number of molecular studies since that time has emphasised sympatric speciation with gene flow, effectively (if perhaps unwittingly) de-emphasising biogeographic theories of species origination: centres of origin theories, vicariance, cladistic biogeography, panbiogeography, dispersion biogeography, glacio-eustatic biography, eco-

logical biogeography, paleobiogeography, phylogeography and a host of region-specific mechanisms for species originations (detailed for coral in Veron, 1995 [1]; also see Huang et al., 2025 [275]). Thus, theories of the *origination* of species, *concepts* of species, their *evolution*, their *biogeography* and inevitably, their *taxonomy* are all intertwined and as noted above, share common terminologies, not all of which have the same meaning. To avoid confusion, we review the important concepts below, before examining the species conundrum.

4.1. Syngameons

The term syngameon has had a range of definitions. The term was introduced by Lotsy in the 1920s to describe groups of species (in this case of birch trees) which were interlinked by hybridisation [276]. Most commonly, the term syngameon has been applied to mean a group of taxa which have previously been recognised to be distinct at species level, which nevertheless show a degree of hybridisation leading to genetic exchange between them [277–279]. Some authors have argued or implied that at least three 'species' must be involved for the term syngameon to be invoked [279,280]. In this developmental period, although not always explicitly stated, definitions were couched within a neo-Darwinian context, implying that while distinct species may exhibit a degree of hybridisation and genetic exchange, reticulation of genetic material was limited to species level. Complex evolutionary patterns of reticulation at a generic level were not included. Furthermore, syngameons were not normally associated with sub-species taxon levels. In these, largely non-reticulate scenarios, hybridisation was viewed as rare and species were considered well-defined.

In plants, this assumption was seriously challenged from the 1950s onwards and a new paradigm adopted which saw hybridisation as commonplace. For animals, this has taken longer although, with the explosion of studies of genetics and hybridisation, including of reproductive viability of offspring, interspecific gene flow became widely acknowledged. Nevertheless, the implications for taxonomy are seldom recognised, even today.

In a review of the frequency of hybridisation, Mallet (2005) [281] estimated that 25% of United Kingdom flora hybridise with at least one other species, whereas studies of world birds, European butterflies and European mammals were closer to an average of 10% (ranging from 6 to 12%), but that hotspots could show hybridisation rates as high as plants at 25%. Importantly, Mallet also points out that, although the likely rate of hybridisation for any one individual in a population may be extremely small (generally less than 0.1% in his analysis), even very small probabilities can significantly affect speciation processes if populations are large, hybrids are reproductively viable, and the hybrid provides selective advantages. Some recent studies of corals have found putative hybrids, either among lineages within a species complex or across 'species' within a 'species group', at rates approaching 1% [95,100], well above those discussed by Mallet.

Mallet's summaries did not include any marine animals. In the marine environment, and especially for corals with their mass spawnings, the capacity for hybridisation is multiplied many fold. If the timings are synchronous, and the possibility of hybridisation is not inhibited by physiological or reproductive barriers, we would expect hybridisation to be much more common than the average 10% cross-species capacity for fauna as referred to by Mallet. The constraints will then be whether the resulting hybrid is more or less likely to survive, and whether it is able to back-cross or cross with other hybrids. As noted above, a significant number of coral species are already known to hybridise, and most of those hybrids are able to backcross with parents and/or cross with other hybrids with viable offspring.

At present we have too few data to define syngameons in corals in any rigorous way (Box 4) and, indeed, we may find that corals are so interlinked in a mosaic of hybrid zones

that there are relatively few syngameons each containing a large number of species. If so, we could postulate that this is one reason for their persistence—when times get tough, their capacity to hybridise and adapt is extensive. This can be seen at the peripheries of their distributions even now. We can explicitly state that some species of *Pocillopora*, *Stylophora* and *Seriatopora* are part of a higher level *Pocillopora/Stylophora/Seriatopora* syngameon. We see putative hybrids in the field (e.g., Figures 9, 10 and 16 and see also Supplementary Figure S1, Plate IV), especially in marginal high latitudes such as Lord Howe Island (Figure 16), and there is increasing evidence of poly- and paraphylogeny in molecular studies of many coral species (discussed below). We re-emphasise here that evidence of a lack of reproductive success among species in one region should not be taken as evidence that those species are reproductively isolated everywhere across their ranges. The potential combinations and permutations are complex across both space and time (Figure 1, above).

At the other end of the spectrum there are widespread monospecific genera which show little morphological variation across their entire range and which have no sibling or similar species. As an example, *Diploastrea heliopora* shows almost no morphological variation with habitat or geographical space and can be recognised for many millions of years in the fossil record. *Diploastrea heliopora* is likely to be genetically isolated from all other Indo-Pacific taxa and, being at one extreme of species variability, would provide fascinating insights into genetic variability at that extreme.

Box 4. Characteristics of syngameons.

The syngameon
The term syngameon has had a wide range of definitions but is generally considered to be a group of species-level taxa which are observed to hybridise and exchange genetic material.
To encompass the complexities of reticulation at all levels, in our current context a syngameon is broadened to have the following properties:

- A syngameon is a group of taxa which show detectable or inferred hybridisation and/or gene flow between them;
- Gene flow between members of a syngameon does not need to be direct or frequent (some members may connect with other taxa via intermediates, and hybridisation may be rare or occur only in some habitats or geographic regions and not others);
- The taxa included will commonly be at species level but are not limited to this level;
- Members of a syngameon may come from different genera (and theoretically could come from higher phylogenetic levels although this has not, so far, been demonstrated in corals);
- Genetic lineages forming a syngameon may be part of a single recognised species or belong to more than one species—the defining characteristic being that direct or indirect gene flow must be observable or inferred between them;
- Syngameons could conceptually exist in the past but, since, by definition, they rely on *recognition* of gene flow between organisms, in practice they only exist in the present;
- The number of taxa included in a syngameon is flexible and will generally increase rather than decrease as new gene-flow linkages are discovered;
- Timelines have yet to be well determined but will be a mixture of historical and recent generational genetic exchanges.

4.2. Sister Species, Sub-Species Variants and Cryptic Lineages

Drawing the line between sister species and sub-species variants can be challenging, especially if there is significant gene flow between closely related species. Where these are particularly intransigent we assign the terms 'complex species' and 'species complexes'. A *complex species* is a species-level taxon with morphological complexities which may be hiding cryptic species we have been unable to resolve. *Species complexes* are groups of species which reticulate with one another and thus resolve in different ways in different geographic locations making clear-cut taxonomic delineation uncertain.

These complications aside, the habitat and geographic variability shown by most species has resulted in many synonymised historical names, some of which are being resurrected today. The converse is also true, however, when valid species are incorrectly synonymised. We discuss various aspects of these challenges below.

4.3. Synonyms

The extent of historical and modern nomenclatorial disagreement among taxonomists is readily seen in the synonymies of their species. For many genera, these are chaotic as we have seen in the synonymies of *Pocillopora* (Figure 2, above). Currently, the synonyms of most species, as itemised in various taxonomic publications, remain unstable.

Designation of synonyms is an author-specific process, highly dependent on the experience and perspective of the taxonomist with all the subjectivity that entails. It often relies on comparisons of poorly or mislabelled type specimens, if still found, and usually one or a very few specimens at that, or illustrations dating back centuries (Figure 3, above). Different authors almost always have different opinions, hence unending revisions. It follows that our present synonymies in CoralsOfTheWorld.org (2026 in prep.) [236] may differ, substantially in some cases, from all others.

Published synonymies vary greatly in content and purpose. Some, for example those of Zlatarski and Martínez Estalella (1982) [282] and Hoeksema (1989) [283], are devoted to maximising detail in an assumed taxonomic hierarchy. Others, for example Wells (1954) [284] and Wallace (1999) [285], mostly give names used to establish priority or recent synonymy. Some are taxon-specific as is the case of Hoeksema (1989) [283] and Wallace (1999) [285], which are concerned with mushroom corals and *Acropora/Isopora* (respectively), while most in the scuba era are region- or country-specific. *However, in all cases, the synonyms proposed do not reflect most of the taxonomic issues raised in this article.*

Historical and Modern Synonymies

Throughout the 19th century, most specimens were given different names if they looked different. For example, Dana (1846) [286] described 5 species from skeletons that we currently consider as synonyms of *Acropora muricata*. Milne Edwards and Haime (1849) [287] and Milne Edwards (1857) [288] provided 6 names that are now synonyms of *Lobophyllia corymbosa* and another 5 that are synonyms of *Lobophyllia hemprichii*. Brook (1891, 1892, 1893) [289–291] gave 5 species names now synonymised into *Acropora cytherea*, 4 into *A. humilis*, 2 into *A. nasuta*, 4 into *A. robusta* and 3 into *A. tenuis* (of the latter, see below). There are 10 nominal species described by Bernard (1896, 1897, 1900) [292–294] currently synonymised into *Turbinaria frondens*, 9 into *Montipora digitata* and 7 into *Montipora foliosa*.

At that time, groups of specimens along with their names were described or synonymised with almost no reference to natural occurrences. To be fair, all early workers had little or no field experience or an understanding of coral biology or ecology. They communicated with colleagues internationally at speeds of months rather than seconds, a fact of life in those days. Furthermore, they mostly worked with shallow-water specimens or those dredged from an unrecorded depth, often from unknown locations. Yet, despite these limitations, 546 species (around 63%) described before the widespread uptake of scuba (prior to 1970) remain valid today primarily because most have priority over later descriptions.

When scuba allowed underwater investigation and morphological variation to be recognised, location-specific synonymies which recognised habitat variation were introduced and many previous names were synonymised for the first time. This was a primary focus of the Scleractinia of Eastern Australia series [8,237,295–297] with its strong emphasis on the reality of the reef as opposed to the museum shelf. And so, to molecular studies

where the focus has now turned from the reef to the laboratory and DNA technology which is again providing new insights.

Historical synonyms can act as useful labels for tracking geographic variants of a parent taxon, albeit a species or a syngameon. For example, in our view, *Cyphastrea kausti* Bouwmeester and Benzoni, 2015 [298] from the Red Sea likely defines a subset of Indo-Pacific-wide *C. microphthalma*; *Cyphastrea salae* Baird, Hoogenboom and Huang, 2017 [299] from Lord Howe Island likely defines a subset of Indo-Pacific-wide *C. serailia*; *Leptastrea gibbosa* Benzoni and Arrigoni, 2020 [300] from the western and central Pacific likely defines a geographic variant of *L. inaequalis*; and *Acropora hystrix* (Dana, 1846) [286] from Fiji likely defines a subset of Indo-Pacific-wide *A. cerealis*.

Synonyms of *Acropora tenuis* (*A. kenti*, *A. bifaria* and *A. africana*) recently resurrected by Bridge et al. (2023) [95], most likely define subsets of this widespread species from the Great Barrier Reef, Indonesia and south-east Africa. In such cases, the synonym is usually a geographically restricted part of a more widely spread parent species. If such pairs are subsequently found to co-occur the supposed synonym may prove to be a valid species. Importantly, the species pair may, or may not, be clearly separated in a cladogram of molecular data because genetic exchange has occurred, and may continue to occur, between the paired biological entities, see 'Cladistics' below. One further molecular caveat is that samples collected from different oceans and/or habitats (e.g., shallow slope cf. mesophotic) should be expected to have divergent genetic signatures, reflecting the necessity for sampling intermediate populations across species' geographic and habitat ranges. Further examples are given below, but of course, in all cases, these are matters of opinion. As noted above, all such synonymies are not necessarily stable, as further evidence is brought to bear. Hence, we consider these and some other newly named taxa (see Rassmussen et al., 2025 [81]) as either probably or possibly valid species, pending more detailed study.

Linked geographic subdivisions of a species are likely outcomes of partial or temporary reproductive isolation in widespread continua, a fundamental aspect of reticulation. For example, Arrigoni et al. (2016) [301] divide *Homophyllia australis* into two species with mostly discontinuous distributions calling one *Homophyllia australis* and the other *Micromussa pacifica* with apparent overlap in New Caledonia (their Supplementary Table S1). In the distribution map of Ng et al. (2019, their Figure 3) [302], the range of *Micromussa pacifica* extends into southern Australian waters, citing Arrigoni et al. (2016) [301]. However, southern Australia was not included in the range description for *M. pacifica* (specimens were collected from the Gambier Islands and New Caledonia), but is part of the range of *Homophyllia australis*.

Also, as introduced below, Arrigoni et al. (2016) [301] divide *Micromussa amakusensis* into two: *Micromussa amakusensis* in Japan and *M. indiana* in the western Indian Ocean. In both these cases, the holotypes are semi-distinct but our field studies and associated non-type specimens bridge most character differences (Supplementary Figure S2) that are illustrated as points of differences by these authors. Similarly, *Echinophyllia gallii* Benzoni and Arrigoni, 2016 [303] in the Maldives and Mayotte appears to us to be a likely geographic variant of *Echinophyllia echinoporoides* which was sampled from Papua New Guinea by their team [303]. Despite samples coming from different oceans, both mitochondrial and nuclear molecular analyses place these two nominal species in close proximity (their Figure 3). Again, the taxonomy is a matter of opinion, but these nominal pairs would more likely be considered distinct species if differences between them were found in co-occurring specimens and/or if such molecular studies covered intervening areas with a greater emphasis on habitat variability and replication.

We note that where hybridisation or molecular studies have suggested that two species could be synonymised in one area, but not in another, both results may be valid, reflecting a predicted consequence of reticulation. This highlights the need for caution in synonymising any species pairs on the basis of a small number of samples, particularly if they are widely geographically separated. The converse is, however, also true—the need for caution in designating new species based on a small number of samples, particularly in the absence of extensive fieldwork, notwithstanding challenges on export imposed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) [304]. As an aside, we are not criticising the very worthwhile purpose of the Convention, rather the bureaucratic 'hurdles' that can hinder legitimate export of small numbers of coral specimens for scientific study, while huge numbers of living, usually wild-collected, corals, often with inadequate identification, are exported for the global aquarium trade.

4.4. Misleading Assumptions and Continuing Challenges

As detailed under 'Type specimens' (below), the fact that species are commonly characterised by single, sometimes dubious, specimens can lead to assumptions about the species and their synonymies which are wholly misleading [305]. Here, we highlight one of the most insidious problems resulting from type specimens which has caused multiple valid field entities to be discarded unjustifiably.

Figure 25A (above) shows the hypothetical variation in an established species against the variation of a new species across all habitats. As discussed there, two type specimens, one from each species, could be taken from the shaded section of overlap. A taxonomist who has not seen these two species in the field and observed their differences in similar habitats might consider these two species to be part of the same variation. The potentially new species is synonymised into the established species and the new valid biological entity is incorrectly discarded.

This is a perennial problem. For example, Wallace (1999) [285], in an update of *Acropora* and *Isopora* taxonomy since Veron and Wallace (1984) [237], contained 114 species descriptions. All 114 were included in the 170 *Acropora* and *Isopora* species in Veron (2000) [6]. However, the latter publication also included 43 species that were recognised as valid biological entities following extensive fieldwork, but which Wallace (1999) [285] had synonymised, based on apparent similarities between type specimens. The remaining disparity between Wallace's 114 and Veron's 170 species was made up of 13 new species. All were illustrated with photography of living colonies. Even so, 12 of these new species were not accepted by Wallace, Done and Muir (2012) [306] based on an assessment of type specimens of these species held in the Queensland Museum Tropics (QMT). Furthermore, where type specimens of previously synonymised species were held at QMT, the previous synonyms were re-asserted. Since that time, our fieldwork has determined that two of these synonyms were justified but the remainder (66 species) have been confirmed as distinct biological entities whatever their name. This highlights the importance of separating issues of nomenclature (largely based on the shortcomings of type specimens) from the biological entity (derived from fieldwork). Despite the evidence we have that these field entities exist, the World Register of Marine Species (WoRMS) [307] still has more than two thirds of these species listed as junior synonyms of other species. In other words, if researchers relied only on Wallace (1999) [285] and Wallace et al. (2012) [306] assessments and/or the collated listings of WoRMS, they would not be aware of the existence of up to around 30% of valid and probably valid *Acropora/Isopora* species.

Another recent example is that of *Acropora microclados* (Ehrenberg, 1834). This is an easily recognised, long-standing, valid biological entity which has been unambiguously illustrated and discussed since Veron and Wallace (1984) [237] (and see [6,10,238,285,306],

among many others). Rassmussen et al. (2025) [81] have recently treated the name as a nomen dubium. While their intent may have been purely nomenclatural, the practical outcome is that in WoRMS (as of 20 October 2025) the name is listed as "uncertain > nomen dubium" and no longer appears as an accepted species. For researchers relying solely on WoRMS, the biological entity associated with this long-used name is effectively erased. Detailed investigation of early names will offer numerous examples of dubious descriptions, damaged type specimens and other problematic issues with nomenclature, all of which could similarly remove well-recognised biological entities from accessible taxonomic lists. Whatever the motivation to pursue technical precision to its limits, such changes to long held names linked unambiguously to well established field entities risk unnecessary disruption and are contrary to the core ICZN principle of stability (ICZN, 1999: Preamble and Article 23.2 [2]). The Code offers alternative options in such circumstances, the least destabilising of which is to maintain the name and designate a neotype (Article 75.3). In CoralsOfTheWorld.org (2026 in prep.) [236] we prioritise the biological entity over the name, and circumvent the many nomenclatural idiosyncrasies by (a) retaining those names which have been used unambiguously for many decades while commenting on important nomenclatural issues in the taxonomic and authority notes; or (b) designating the field taxon as an *accepted* biological entity and assigning to it a working moniker for identification, again with explanatory taxonomic notes, pending further taxonomic consideration.

The examples above are offered not as criticisms of individual authors, but to highlight the ways in which the handling of nomenclature, types and synonymies can inadvertently compromise our understanding of the natural world and its diversity. *Field experience and understanding is crucial, not an adjunct.*

4.5. Cryptic Species and Lineages

Cryptic lineages (more or less distinct genetic lineages which the relevant study cannot associate with morphological differences) are being found in many coral species (24 genera spanning the Anthozoa according to Grupstra et al., 2024 [271]), particularly in habitats that require specialised adaptations (such as at mesophotic depths [308]). Such lineages are both predicted by reticulate evolution and postulated from the morphological variability observed within existing coral species. To date, although such lineages have been found, there are few comprehensive studies known to us which conclusively demonstrate that these should be delineated as separate species. One of the more persuasive is that of Bongaerts et al. (2021) [247] on the Indo-Pacific species *Pachyseris speciosa*. From widespread sampling (Red Sea, Japan, PNG, Coral Sea and Great Barrier Reef) these authors reported ecologically divergent lineages that were morphologically indistinguishable occurring sympatrically across shallow and mesophotic habitats. Their observations of spawning of genotyped colonies "highlighted the potential role of temporal reproductive isolation in the limited admixture, with consistent genomic signatures in genes related to morphogenesis and reproduction". As an aside, these authors concluded that morphological crypsis was due to ancient stasis rather than recent divergence. Whether this level of divergence is sufficient to warrant separate species delineation will await (a) a fuller understanding of the temporal stability of reproductive isolation; (b) the intraspecies genomic variability across local and geographic space; and (c) the degree to which hybridisation, even in small numbers, can take place between the lineages.

Further evidence of spawning asynchrony was recently reported by Ricardo et al. (2025) [309] in a local population of the widespread Indo-Pacific *Platygyra daedalea* on a small section of reef on the southern Great Barrier Reef. The high levels of spawning asynchrony were considered, potentially, as indicating distinct genetic clusters, resulting in low fertilisation success (1.5%). Of the fertile eggs, all embryos were self-fertilised, with no

cross-fertilisation. The adult population appeared divided into two genetically distinct sub-populations, with inbreeding. These authors considered that self-fertilisation may provide a reproductive assurance mechanism, with density-dependent localised recruitment.

Wisely in our view, the studies above and several other recent studies have retained the 'parent' species while noting lineage diversity (e.g., *Stylophora pistillata* on the Great Barrier Reef [100], see Case Study below), *Montastraea cavernosa* and *Siderastrea siderea* [245] and the *Madracis* species group [310] in the Caribbean. This is not to imply that there are no cryptic coral species, but rather that reticulate evolutionary processes, aided by complex reproductive systems, indicate that care should be taken before new 'species' are designated, particularly where there are no consistent morphological differences that enable reliable field identification.

Where consistent morphological differences are apparent, however, there may be little or no molecular signal. This, perhaps unintuitive finding, has significant implications for modern taxonomy. For example, major life history and evolutionary differences between corals and fishes notwithstanding, a recent study by Helmkampf et al. (2025) [311] of a radiating group of Caribbean reef fishes *Hypoplectrus* spp. found that phenotypic diversification and reproductive isolation occurred in the "near-absence of a phylogenetic signal, both genome-wide and at the gene-tree level. . . with a large share of the radiation unresolved". For corals, low levels of genetic divergence have been reported among morphologically well-defined species of *Stylophora* in Arabian Seas [312] (see Case Study below).

In these respects, we note, firstly, that no studies have yet evaluated the temporal persistence or spatial gradients of reproductive asynchrony and that these, like so many other features of corals, may vary in ways that allow considerable gene flows across relevant timeframes. Secondly, that studies using a small number of samples in a few widespread locations (assuming accurate identification in unusual habitats) cannot represent the variability expected within a species, and in no way delimits the gene transfer potential between 'new' lineages and the 'parent' species. Such gene transfer potential will differ in both space and time with local population sizes (gamete mating opportunities) and local oceanographic conditions.

Where substantially increased sampling provides growing support for separation of lineages into 'species' that are not morphologically distinguishable, we propose they should be grouped within the morphological parent species until the full suite of habitats and geographic distribution are accounted for and species separation is indisputable. Meanwhile all molecular and morphological variant information can be retained for those specialists who wish to study the detail. In CoralsOfTheWorld.org (2026 in prep.) [236] we have begun this process by providing nested information, references and 'possibly valid species' Factsheets within or linked to the parent species. We may find that once further sampling has been undertaken it will be possible to link specific 'cryptic' lineages with morphological variations in the parent species which will make field identifications less confusing. This was postulated by Meziere et al. (2024) [100] in their study of *Stylophora pistillata* on the Great Barrier Reef, with one lineage displaying the *Stylophora mordax* phenotype (Figure 24).

In summary, the term cryptic 'species' implies a confidence in species level difference which is not yet adequately supported for most, if not all, studies that use this term. It is our view that cryptic 'lineage' or 'variant' should be used until further research unambiguously establishes the degree of molecular difference required to designate species level signatures. These cryptic lineages can be given temporary descriptions and/or monikers and nested into parent species until comprehensive studies are completed. This will help to address the many reports we have had from field workers who are negatively affected by the confusions of premature taxonomic destabilisations.

4.6. Polyphyletic Species

A polyphyletic group or species is one whose members have mixed evolutionary origins. In a reticulate system, if a species is described as polyphyletic, it can indicate historical separation followed by more recent genetic exchange. It does not necessarily indicate that the species has been incorrectly delineated or that separating it into further components is appropriate. Instead, additional study will almost certainly reveal further lineage mixing and highlight the complex influences of reticulation on speciation and evolutionary history.

Setting aside a wealth of technical qualifications, it can reasonably be claimed that at least 70 species (representing some 26 genera from various Scleractinian families), are polyphyletic or probably polyphyletic (Box 5), meaning that molecular studies have shown that they are derived from more than one common ancestor or share an ancestral lineage with other extant species. Most are readily delineated from any other species by an experienced taxonomist (see 'Observing reality' above) at any given location and usually retain their identity over their full geographic range, albeit with the wide range of uncertainties described below.

Box 5. Species for which there is evidence of polyphylogeny.

Evidence of polyphylogeny
The taxonomic spectrum is wide: in this article, we record evidence of polyphylogeny in *Acropora abrotanoides*, *A. aculeus*, *A. aspera*, *A. cerealis*, *A. cervicornis*, *A. cytherea*, *A. divaricata*, *A. florida*, *A. gemmifera*, *A. horrida*, *A. hyacinthus*, *A. intermedia*, *A. millepora*, *A. nasuta*, *A. papillare*, *A. prolifera*, *A. pulchra*, *A. spathulata*, *A. tenuis*, *Agaricia fragilis*, *A. grahamae*, *A. lamarcki*, *A. undata*, *Cyphastrea chalcidicum*, *C. serailia*, *C. microphthalma*, *Cantharellus noumeae*, *Echinopora gemmacea*, *Echinophyllia aspera*, *E. echinoporoides*, *E. orpheensis*, *Fungia fungites*, *Galaxea fascicularis*, *Goniopora columna*, *Homophyllia australis*, *Isopora brueggemanni*, *Leptoseris explanata*, *L. hawaiiensis*, *L. mycetoseroides*, *L. scabra*, *Leptastrea bottae*, *Lobophyllia hemprichii*, *Montipora digitata*, *M. patula*, *M. spumosa*, *M. verrilli*, *M. verrucosa*, *Madracis decactis*, *M. formosa*, *M. pharensis*, *Micromussa amakusensis*, *Montastraea cavernosa*, *Orbicella annularis*, *O. franksi*, *O. faveolata*, *Platygyra daedalea*, *P. lamellina*, *P. pini*, *P. ryukyuensis*, *P. sinensis*, *Pocillopora damicornis*, *Porites compressa*, *P. evermanni*, *P. lobata*, *P. lutea*, *P. rus*, *Pachyseris inattesa*, *Plesiastrea versipora*, *Seriatopora hystrix* and *Stylophora pistillata*.

We note that the list in Box 5 is not a random group of species as they have been deliberately selected for particular molecular analysis. However, as these studies are in their infancy, it seems likely that this list will be greatly extended in coming years and may eventually indicate that most species, however defined, are polyphyletic. They are also likely to reveal complex patterns of reproductive isolation within and between species and that these patterns are likely to vary geographically.

The spectrum of observations about species dynamics we record here highlights the difference between Neo-Darwinian evolution where species are viewed as isolated units, and reticulate evolution where a polyphyletic ancestry is to be expected.

4.7. Stylophora, a Case Study

The following study provides a pertinent example of some of the complexities and apparent conflicts in interpretation of results that can arise from different molecular studies, albeit on one of the best studied of all coral genera, *Stylophora.* Similar issues are likely to arise as molecular studies advance in other genera. We currently recognise seven species of *Stylophora—S. pistillata*, *S. madagascarensis*, *S. danae*, *S. subseriata*, *S. kuelhmanni*, *S. mamillata* and *S. wellsi* in the Red Sea and Gulf of Aden making this region the centre of *Stylophora* diversity (Figure 30).



Figure 30. *Stylophora mamillata* (**top row**, **left**), *S. wellsi* (**top row**, **right**), *S. pistillata* (**centre row**, **left**), *S. danae* (**centre row**, **right**), *S. subseriata* (**bottom row**, **left**), *S. kuehlmanni* (**bottom row**, **centre**) and *S. madagascarensis* (**bottom row**, **right**), all from the Red Sea and/or Gulf of Aden. These species are all readily recognised in situ. Photographs: all J. Veron except **centre row**, **left**: E. Banguera, **bottom row**, **centre**: M. Stafford-Smith.

The most widespread species, *Stylophora pistillata*, has long been recognised as a species complex [6] although there may be little morphological difference between colonies of this species as far apart as the Red Sea and Great Barrier Reef (Figure 18). Stefani et al. (2011) [97] found that *S. pistillata* populations were split into two highly divergent Red Sea/Gulf of Aden and western Pacific lineages, considered 'cryptic species' (meaning, in our view, cryptic genetic lineages) with significant morphological overlap. Flot et al. (2011) [98] found two 'species' in Madagascar, a third in Okinawa, the Philippines and New Caledonia, and also potentially the Great Barrier Reef, Malaysia, South China Sea and Taiwan, and a fourth in the Red Sea. Keshavmurthy et al. (2013) [313] found four deeply divergent clades, corresponding to Pacific–Western Australia (Clade 1), Chagos–Madagascar–South Africa (Clade 2), Gulf of Aden–Zanzibar–Madagascar (Clade 3), and Red Sea–Persian/Arabian Gulf–Kenya (Clade 4).

When combined, these studies illustrate the complexity of reticulate patterns in both phylogeny and distribution. More recently, Meziere et al. (2022) [314] found that Clade 3 was morphologically *Stylophora madagascarensis*, and that most specimens of Clades 1 and 4 were morphologically indistinguishable. These authors concluded that regardless of their

names, the four clades of *S. pistillata* represent distinct lineages with different evolutionary histories and geographic distributions.

Meziere et al. (2024) [100] detailed population genetics study on the Great Barrier Reef indicated that *Stylophora pistillata* comprises five distinct taxa at different stages along a divergence continuum. These taxa have wide geographic ranges and extensive sympatry, being differentially adapted to different environments consistent with niche partitioning. However, these authors also found that some of their samples matched the description of *Stylophora subseriata* (not then recorded from the Great Barrier Reef, but known from the adjacent Coral Sea, E. Turak pers. obs.) and others of *Stylophora mordax* (Figure 24). These results contrast with those of an earlier study by Klueter and Andreakis (2013) [315] that found that molecular diversity in *Stylophora pistillata* from the Central Great Barrier Reef and Coral Sea lacked phylogenetic structure, forming one genetically homogeneous species with highly connected populations.

A comparable result was found in the Red Sea by Arrigoni et al. (2016) [312], presumably working on Clade 4, but also including other Red Sea *Stylophora* 'species'. There, molecular diversity was among the lowest ever documented in corals (<1% in all pairwise comparisons), "which suggested the presence of a single highly connected genetic unit of *Stylophora* in this region". Although these authors found the Arabian endemics *S. mamillata* and *S. wellsi* are easily recognisable, they concluded that extensive gene flow occurs between these species and *S. pistillata* and that *S. pistillata*, *S. danae*, *S. subseriata*, and *S. kuehlmanni* are actually one entity with incomplete evolutionary separation. Conversely, Buitrago-Lōpez et al. (2023) [316] found that *S. pistillata* in the Red Sea exhibited a complex population structure with evidence for within- reef and regional genetic differentiation.

We see these findings against a backdrop where *S. mamillata* and *S. wellsi* are indeed distinctive regional endemics and where the other species also remain distinctive over much wider distribution ranges, showing little or no morphological variation that is not correlated with environment.

Most recently, in the far northern Red Sea, Rachmilovitz et al. (2024) [317] found low gene flow and high levels of inbreeding between most populations of *S. pistillata*, with isolation over distances of several hundred metres to a few kilometres, consistent with its brooding reproductive mode. These authors drew attention to the apparent discrepancy with earlier work by Takabayashi et al. (2003) [318] who documented panmixia between *S. pistillata* populations separated by thousands of kilometres across the Western Pacific. Monroe (2015) [319] also found no distinctive population structures along the length of the Red Sea but reported a greater population structure on a fine scale, suggesting genetic selection based on fine-scale environmental variations.

Although some of the discrepancies among these findings may be explained by the use of different genetic techniques as the molecular tools have developed, collectively they highlight the complexity of reticulate evolutionary patterns across the Indo-Pacific. These patterns can result in discordance between molecular findings from different regions, between reproductive studies in different locations, and between field-based taxonomic studies and molecular phylogenies.

4.8. Integrating Genetics, Reproduction and Biological Entities

The foregoing discussions on reticulation, hybridisation and molecular exchange in its various forms make it clear that distinguishing species across their full geographic extent, separating the variability of an existing species from possible sister species, and identifying the points at which active speciation is taking place, are all issues of great complexity and potential disagreement.

Extensive field studies since the 1970s have broadened the strictly specimen-based morphological species delineations of yesteryear, into a framework of operational taxonomic units that are recognisable in their natural habitat and encompass the wide variations and characteristics of each species. Despite overt and implied commentaries to the contrary in various molecular papers (see, e.g., refs. [60,95,300]), there is little well-supported evidence to date that the taxonomic foundation provided by field assessments of biological entities, backed up by studies of collections, and integration of existing reproductive and molecular studies, is seriously flawed. In fact, considering the potential for disruption, the entities themselves have remained remarkably robust. There is plenty of evidence for infra-entity genetic variability (e.g., refs. [100,245,247,320–326]) as predicted by reticulate evolution [1,6], with a focus on particular species and species complexes in CoralsOfTheWorld.org [10,236] but the entities themselves have not been convincingly challenged (Supplementary Table S2). Rather, the challenges that exist are matters of species definition and the molecular foundation for such discussions is not yet sufficiently developed to be contextualised.

We argue that species delineation should draw on evidence from multiple sources. Reliance on any one field alone risks the omission of essential information. In this context it is valuable to review the strengths and weaknesses of the biological entity in order to see how assessments can help to put modern molecular science into the context of the natural world.

Strengths:

- They represent what is actually observed in nature;
- They are operational taxonomic units below the level of genus but above the level of subspecies or variant which, importantly, can be recognised consistently in the field;
- They have provided a relatively stable taxonomic framework for ecological, reproductive and molecular studies for several decades;
- They have highlighted the inherent environmental variability of taxa and hence provide an important context for design and interpretation of reproductive and molecular studies;
- Their existence and distinctiveness have remained independent of nomenclatural changes, despite potential confusions caused by those name changes (Section 7 below);
- The boundaries of most biological entities are proving robust, notwithstanding the difficulties due to reticulation;
- They offer an important strand of the evidence required for species delineation.

Weaknesses and potential weaknesses:

- Differences in observer knowledge and potential for inter-observer disagreement or bias—agreement depends on geographic experience and whether that is shared or relates to different regions.
- Incomplete knowledge of geographic and habitat variation can lead to limited understanding of the entity, especially with recently described taxa.
- Misalignment of observed field variability with underlying genetic variability:
    - Strong selective conservation of genes controlling phenotypic presentation may obscure deeper molecular divisions (a hybrid may display a single parent's morphology; two sister species may not be recognised);
    - Convergent evolution may, theoretically, lead to similar phenotypic presentation of widely different molecular taxa. Note, however, that (a) the biological entity is identified using many more criteria than just the simple phenotypic morphology of a taxon; and (b) it is unlikely that convergent evolution at genus level or above would be so complete that evolutionarily conserved micromorpholog-

ical elements would also converge (bats and birds may both fly, but they are easily distinguished).

- Recognisable field variability can offer clues to, but cannot, on its own, identify differing genetic signatures.
- While the biological entity reflects the variability that is observed in nature, it can only hint at the significance of that variability to a species' evolutionary history or its reproductive or hybridisation potential. These must be supplied by molecular and reproductive studies.

Reproductive studies are also a crucial element of the species delineation story and, over the past 20 years, they have greatly enhanced our understanding of species propagation, dispersal and hybridisation. The prevalence of hybridisation and generational persistence helps to explain much of the reticulation observed in the natural environment.

Towards the beginning of our investigation into 'Species delineation in a reticulate system' we posit that significant changes to the existing taxonomic foundation requires a thorough understanding of the way in which genetic variability relates to known species variability in the natural environment. Here we consider some recent molecular studies and evaluate their contributions to this understanding.

a Estimates of the natural genetic variance across habitats and geographic range.

Several studies have had a wide geographic focus, including on *Pachyseris speciosa* [247], *Stylophora pistillata* [98,313] and *Pocillopora* spp. [60]. These, and more geographically focused studies, have revealed significant lineage complexity consistent with reticulate patterns.

b The degree of difference in the genetic signatures required for species delineation.

A number of new species descriptions have been published since 2010 based primarily on molecular divergence among samples but also including macro- and micromorphological comparisons of specimens. These include:

Porites fontanesii Benzoni and Stefani, 2012 [327];
Pseudosiderastrea formosa Pichon, Chuang and Chen, 2012 [328];
Pocillopora aliciae Schmidt-Roach, Miller and Andreakis, 2013 [329];
Blastomussa vivida Benzoni, Arrigoni and Hoeksema, 2014 [330];
Pachyseris inattesa Benzoni and Terraneo, 2014 [331];
Pocillopora bairdi Schmidt-Roach, 2014 [332];
Cyphastrea kausti Bouwmeester and Benzoni, 2015 [298];
Echinophyllia bulbosa Arrigoni, Benzoni and Berumen, 2016 [303];
Echinophyllia gallii Benzoni and Arrigoni, 2016 [303];
Micromussa indiana Benzoni and Arrigoni, 2016 [301];
Micromussa pacifica Benzoni and Arrigoni, 2016 [301];
Cyphastrea magna Benzoni and Arrigoni, 2017 [333];
Cyphastrea salae Baird, Hoogenboom and Huang, 2017 [299];
Paraechinophyllia variabilis Arrigoni, Benzoni and Stolarski, 2019 [334];
Porites farasani Benzoni and Terraneo, 2019 [335];
Porites hadramauti Benzoni and Terraneo, 2019 [335];
Leptastrea gibbosa Benzoni and Arrigoni, 2020 [300];
Leptastrea magaloni Benzoni and Arrigoni, 2020 [300];
Acropora rongoi Bridge and Cowman, 2023 [95];
Acropora tenuissima Bonito, Bridge, Fenner and Baird, 2023 [95];
Pocillopora tuahiniensis Johnston and Burgess, 2023 [94];
Paragoniastrea variabilis Kishi, Nomura and Fukami, 2024 [336];
Acropora harriottae Baird and Rassmussen, 2025 [81];
Acropora kalindae Crosbie, Baird, Bridge and Rassmussen, 2025 [81];

Acropora nyinggulu Bridge and Rassmussen, 2025 [81];
Acropora tersa Rassmussen, Bridge and Baird, 2025 [81];
Acropora uogi Randall, Burdick and Bonito, 2025 [81].

Many of the issues we discuss above are not considered by the authors of these new 'species' (see specific commentaries in 'Matters of opinion?' below).

These studies notwithstanding, there is no universal agreement on the degree of molecular difference required for species delineation in corals, nor the level of sampling necessary across habitats and geographic ranges to encompass variability. Recent authors (e.g., Bridge et al., 2023 [95]) have employed the 'unified species concept' [273] which, according to these authors [95], defines species as "independently evolving metapopulation lineages" and permits delineation without requiring species to be distinguishable morphologically or to exhibit intrinsic reproductive isolation. We argue that genetic delineation alone is not sufficient, especially where detailed habitat sampling is omitted and comprehensive genetic variance has not been established. Other studies, most of them focused on population genetics, have examined the degree of net molecular divergence in much larger numbers of samples across lineages, specifically as this relates to 'grey zones' of speciation (e.g., Meziere et al., 2024 [100]). These, more appropriately, begin to build the foundational work necessary to inform molecular decisions.

c The spatial distribution of populations with different signatures.

As noted in 'a' above, only a few studies have examined the geographic distribution of lineages of a species or a species complex. For most corals, such foundational work remains to be done.

d The temporal persistence of different signatures.

At present the persistence of distinct lineages is not well understood, 'molecular clocks' notwithstanding [337], and nor is the persistence of partial spawning asynchrony or other reproductive barriers that may help to maintain divergence.

e Co-occurrence of different signatures (specifically existing in the same vicinity—including habitat and environmental conditions—not just in the same geographic region).

Divergence in molecular signatures in populations within and/or among habitats has been examined in several species, including *Seriatopora hystrix* and *Stylophora pistillata* on the Great Barrier Reef [100,322], and *Montastraea cavernosa* and *Siderastrea siderea* in the Caribbean Sea [245]. These studies have revealed complex, contrasting patterns of divergence within and among habitats. For the latter two Caribbean species, mechanisms maintaining lineage distinctiveness, despite abundant introgression, were considered more likely to be post-zygotic than pre-zygotic [245]. Pre-zygotic mechanisms, such as different spawning times or lack of sperm-egg recognition, were considered likely to cause genome-wide divergence rather than the observed uneven introgression across genomes. On post-zygotic mechanisms, these authors noted that introgression might be reduced at certain loci if they are strongly adaptive for a lineage-specific habitat. However, as all lineages exhibited very similar gene expression responses to any habitat, this was also deemed unlikely. Gallery et al. (2025) [245] concluded that the uneven between-lineage introgression may be driven by the buildup of Bateson–Dobzhansky–Muller incompatibilities in the low-introgressing portions of the genome.

Our main points here are that the coral molecular work conducted to date (noting new studies are published on an almost weekly basis) has shed light on some of the complexities of phylogenetics, adopting different approaches, including in the tools used, the species examined, and the level of detail (sampling) employed. We also note that some of the conclusions, particularly new species descriptions (point 'b' above), have been based on

small sample sizes both at habitat and geographic range scales and that there is usually inadequate habitat characterisation (see below). Wherever possible, species delineations and boundaries should be moderated by reproductive and field evidence, supporting delineations and/or explaining known issues, while also providing insights into new areas. There remain many areas of complexity which are only now beginning to receive detailed molecular study.

5. Current Taxonomic Issues

No taxonomy can hope to capture and entirely resolve the wealth of issues surrounding reticulation, morphological and molecular variability, historical anomalies, and taxonomist preferences surrounding this topic, but awareness of the issues and specific examples (below), will help to avoid some of the preventable complications.

5.1. Historical and Pervasive Issues

5.1.1. Type Specimens

Type specimens are generally more useful for a taxonomist than species descriptions, especially descriptions that predate the scuba era. However, we note that type specimens were not necessarily part of a species description in historical taxonomic publications and were not clearly designated in many taxonomic publications before the 1920s. As a result, at least half of the currently accepted species do not have a clearly designated holotype specimen associated with the original description.

- The type is not the same species as the description

This sometimes resulted from a misplaced label (as with *Acropora fragilis* which was considered to be *A. rambleri* until the type labels were correctly reassigned), but in other cases, notably the holotypes of Verrill, fragments he labelled 'type specimen' were removed from a specimen that was not the specimen used in his original description. Additionally, Verrill sometimes sent specimens so labelled to different museums which were incorrectly assumed to be, or listed as coming from, the described specimen.

- Multiple syntypes belong to different species

This is common and is an issue when a holotype was not originally designated. For example, *Acropora squarrosa* is a long-established species but 7 specimens in the original collection attributed to this species also include *A. forskali* and *A. loripes*. And there may be further anomalies: specimen numbered 898 was listed as the holotype of *Acropora squarrosa* by Wallace (1999) [285] but it came to light later that this specimen number was duplicated for two different specimens representing different species. In the case of *Acropora squarrosa*, it is further complicated by the fact that *Acropora maryae* was synonymised into *A. squarrosa* by Wallace (1999) [285] presumably based on some of these same confusions. Whatever the type issues are, both *Acropora squarrosa* and *A. maryae* are valid biological entities and need to be maintained separately. Analogously, the species group *Acropora convexa*, *A. prostrata*, *A. millepora* and *A. spathulata* involve an array of syntypes which also include *A. selago* and *A. tenuis.* Again, the entities are clearly separable, but the type specimens are not. Syntype issues have especially affected taxonomic decisions of *Acropora* species including *A. pyramidalis*, A. *dendrum*, *A. divaricata*, *A. digitifera*, *A. convexa*, *A. confraga*, *A. excelsa*, and, as above, *A. squarrosa*.

- Type specimen sharing

Early specimens were often interchanged between home institutions, especially the Natural History Museum (UK) and the Museum National d'Historie Naturelle, Paris (by Brook and Bernard) and also the Yale Peabody Museum and the United States National

Museum (by Dana and Verrill) resulting in renaming and labelling errors and other provenance problems.

- The type locality is wrong or details are unrecorded or doubtful

This issue applies almost exclusively to older nominal species and commonly occurs when taxonomic studies are based on museum specimens of uncertain origin or when assumptions are made about all specimens in a collection in the absence of specific collection details. For example, the type locality of *Coelastrea tenuis* Verrill, 1866 is listed as Sandwich Islands ? (=Hawaii) [338], yet this nominal species does not resemble any biological entity or specimen known from Hawaii.

The locality of collections made during historic voyages of discovery usually indicate the country of origin at best and even where the country is recorded, minimal details such as 'on a reef flat' are seldom provided. Yet such details can be essential for the recognition of the species from an isolated specimen. In such instances, no type locality is clearly preferable to a doubtful one. For example, all of Bernard's (1896–1906) [292–294,339–343] and most of Brook's (1891–1893) [289–291] supposedly new species are based on assorted museum collections, many of which have uncertain origins.

One such case, where the absence of a type locality or type series did not seriously confound priority and nomenclatural clarity was the discovery of the type of *Astrea rotulosa* (Ellis and Solander, 1786) by Huang et al. (2014) [344]. Despite its unknown type locality, the almost 240-year-old type specimen was of sufficient integrity to be accepted by us as the senior synonym of *Astrea* (=*Plesiastrea*) *devantieri* (Veron, 2000) [10].

- The holotype does not clearly represent the species

Perhaps the most insidious and underappreciated problem with type specimens relates to replication and representativeness stemming directly from habitat and geographic variability of the species they are meant to exemplify: by definition a holotype has no replicate, and even if there are several additional paratypes the reliance on single or small numbers of specimens to circumscribe a species in the face of its geographic and habitat variability will be adequate for only a tiny fraction of species.

This is common. When a species is first described its full variability is inevitably unknown and the position of the type within this variability is also uncertain. If the species is described from a high latitude, or isolated location, abnormality of a type could be expected or assumed, but uncertainties are also common if the type has an incorrect, or no, habitat description, or if the variability with habitat and geographic space is not well understood by a taxonomist when comparing with other species. Figure 31 illustrates this point.

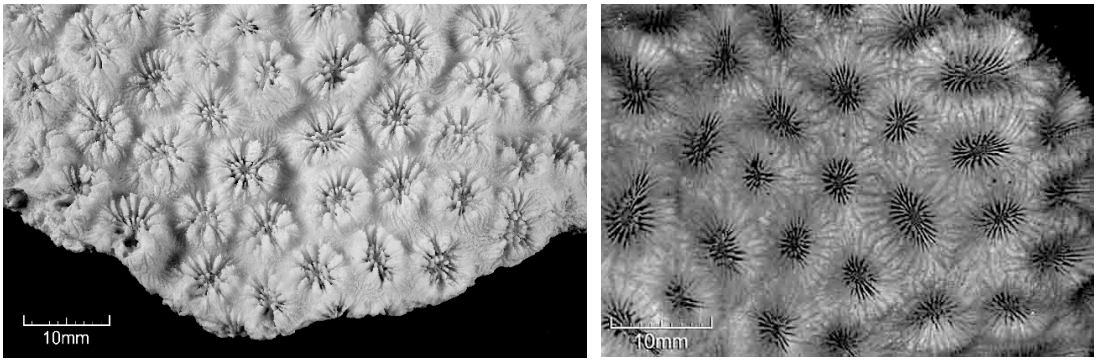


Figure 31. Left: the holotype of *Plesiastrea* (=*Favites*) *russelli* Wells, 1954 from the Marshall Islands was incorrectly recorded as being from a lower reef slope but is actually from an exposed reef front (field study of Veron with John Wells, Enewetak Atoll, Marshall Islands, 1976). Studies at the Marshall Islands,

Australia, and elsewhere reveal a continuous intergradation of specimens from upper reef slopes to mesophotic depths. **Right**: from the Great Barrier Reef. See Figure 36 (below) illustrating the common skeletal appearance of this species. Photographs: J. Veron.

Many other examples are less overt, for example, Dana's holotype of *Montipora digitata*, a common widespread species on reef flats, is not clearly distinct from his *M. tortuosa*, both described in his 1846 monograph [286]. We consider *M. tortuosa* as a possibly valid species.

- Type specimens appear to overlap with another species

We delve into this issue in more detail below because, along with the representativeness of the holotype discussed above, this is one of the principal causes of premature synonymy. It particularly occurs in the larger genera, especially *Acropora* and *Montipora*, where biological field entities are often better separated than are their respective type specimen(s). Figure 25 above explains why single or small numbers of replicates can easily be mistaken for a different species. Some overlaps involve multiple species. For example, type material of *Acropora convexa*, *A. prostrata* and *A. millepora* have led to continuing uncertainty. Although the biological field entities are distinct in all of these cases, the type complexity has precipitated debate as to what name goes with what taxon, with no clear resolution.

- Multiple syntypes or other type specimens come from different locations

Again, this can introduce issues when a holotype has not been designated and geographic variation is significant (e.g., see Section 7.3.6, *Acropora spicifera*). It is clearly advantageous to have multiple specimens illustrating geographic variation in a species description but if the variability is not clearly discussed with commentary on the gradation of form from one region to another, unforeseen issues due to reticulation easily result.

- Nominal species without a specimen or which are unrecognisable

There are many nominal species which cannot be linked to an existing museum specimen or for which the museum specimen is missing, damaged or uncertain. In addition, descriptions may be largely unrecognisable or applicable to more than one field entity, or images or drawings may be poor or ambiguous. These remain 'unresolved' in CoralsOfTheWorld.org [10,236]) for one or other of these reasons.

Type specimens, especially holotypes, certainly aid taxonomists but should always be considered in light of the various issues outlined herein. We note that many similar arguments could be addressed to voucher specimens taken to support molecular studies. These, too, should be collected and considered in the light of the issues highlighted in this review.

5.1.2. Resulting Consequences for Synonymies

The various issues resulting from type specimens all have consequences for synonymies. As discussed above, synonymies are author-specific, can be conflicting and depend heavily on both interpretation of the specimens and understanding of species variability in the field. This is exacerbated by names that are associated with ambiguous or unrepresentative type specimens from unreliable locations and habitats. However, as far as possible, we focus on the biological entity and provide in CoralsOfTheWorld.org (2026 in prep.) [236], for any given species, lists of names and authors of taxonomic publications who use those names, which we believe are likely to be associated with those entities. There are many cases of doubt which are either excluded or are discussed in taxonomic notes. These synonymies are therefore matters of nomenclature, in which they play an important role, but (with the exception of spatial synonyms, see below) they rarely say much about the biological entities they represent.

5.2. Geographic Isolation and Distribution Extremities

As introduced above, these are places where geographically isolated populations can readily form and then be isolated because surface circulation patterns are geographically contained or lead nowhere. The Red Sea has particular relevance where for example, *Acropora horrida* has three uncertain synonyms (*A. tylostoma*, *A. arabica* and *A. microcyathus*), *Acropora gemmifera* has two distinctive but uncertain synonyms (*A. pyramidalis* and *A. pallida*), *Acropora hyacinthus* and *Acropora cytherea* are not as distinctive as they are elsewhere; *Acropora canaliculata* is a Red Sea variant of *A. nasuta*, *Acropora eurystoma* may be a Red Sea variant of *A. tenuis*, *Echinopora mammillosa* may be a Red Sea variant of *E. gemmacea*, *Porites farasani* may be a Red Sea variant of *P. aranetai*. Further, occurrences of *Cantharellus noumeae*, *Goniopora columna* and *Porites rus* are readily distinguished from occurrences of the same biological entity in other places. Hawaii is also an extremity where several biological entities are abnormal: the type series of both *Leptoseris hawaiiensis* and *L. scabra* from Hawaii are significantly different from occurrences elsewhere; populations of *Montipora patula* and *M. verrilli* are not genetically distinct from each-other; *Montipora verrucosa* has three questionable synonyms (*M. tenuicaulis*, *M. bernardi* and *M. studeri* which in combination may indicate a distinct entity); *Porites compressa* has genetic links to *P. lobata*, and occurrences of *Porites rus* have a doubtful status.

With few exceptions, widespread corals at the extremities of their distribution range are significantly different from more central occurrences with which they intergrade. Sometimes this has taxonomic consequences as with, for example, *Homophyllia australis* (which has a complex synonymy including geographically separated *H. australis sensu stricta* and *Micromussa pacifica*), *Plesiastrea versipora* (geographically and taxonomically separated into *Plesiastrea versipora* and *P. peroni*) and *Cyphastrea serailia* (with *C. salae* also taxonomically separated) all occurring in remote temperate south-eastern Australia.

5.3. Taxonomic Complications of Species Complexes and Complex Species

Species complexes and complex species were introduced above in the discussion of species boundaries. Here we briefly focus on the taxonomic complications posed by these groups. Reticulation among these species and species groups is sufficiently complex that even moderately clear boundaries are difficult to assess. Clearly this is an area where molecular studies would be particularly valuable but in this case, identifying the sampled coral may be difficult and attributing the resulting genetic signatures to a given name, supposing that distinct lineages are resolved, will also be difficult. An example of a species complex which could benefit from such a study might be *Acropora abrotanoides*, *A. tutuilensis*, *A. irregularis*, *A. rotumana* and possibly also *A. pinguis.*

5.4. Anomalies and Possible Extinctions

There is a small group of taxa which we recognise as probably valid species for which we have little or no field data and rely on single or minimal specimens or images. We retain these in taxonomic updates because they appear distinctly different to any other recognisable field entity and their details need to be available to other researchers. For example, the validity of *Montigyra kenti* Matthai, 1928 hinges on a single specimen (the holotype) from the Lacepede Islands, north western Australia. The type locality and its surrounds have been extensively searched but no evidence of this species has been found there or anywhere else. It is possible that the specimen was an extreme form of some other known species (though this seems unlikely given its distinctive characteristics), or a hybrid colony, or the species may have been locally endemic and has since become extinct.

In other cases, species are retained because of unique differences but no further records have yet been reported, or source locations have not been comprehensively surveyed.

Recent species designations are expected to have incomplete distribution records but there are a few species which have long been known but remain reported from only one or few ecoregions, based on very few records. Examples include *Simplastrea vesicularis* Umbgrove, 1939 and *Boninastrea boninensis* Yabe and Sugiyama, 1935.

As noted below there are many nominal species which are listed as accepted in WoRMS [307] for which we presently have no evidence of a corresponding field entity despite significant field work at type localities. Many of these nominal species have ambiguities associated with their type specimens but in other cases they may form part of the known variability of a recognised valid species.

5.5. Taxonomic and Nomenclatural Inconsistencies and Disagreements

The difference between nomenclature and taxonomy, frequently referred to above, comes to the fore with WoRMS. According to the site itself, its aim is to "provide an authoritative and comprehensive list of names of marine organisms, including information on synonymy". In so doing, it is a valuable resource, collating publications where names are either "accepted" or "unaccepted".

However, significant problems remain. Along with the numerous species accepted by WoRMS for which we have no evidence of a corresponding biological entity, there are (as discussed above) many species for which we have ample evidence of distinct field entities that are not accepted by WoRMS. These commonly result from one or more of the type specimen issues discussed above. Importantly, these decisions are of necessity based on *names* which, by due process that excludes all alternatives, take no account of the biological information on which an alternative name is based (for example, all *Symphyllia* are listed as *Lobophyllia* based solely on Huang et al. (2016) [345], counter to long-established and useful distinctions in genus morphology, and without confirmatory study, see below). We find that many nomenclatural changes are being made prematurely. To a large extent the reason is a lack of understanding—by both researchers and reviewers—of the issues discussed in this article, which has been a primary impetus for this review. Presumably, WoRMS has an obligation to include all peer-reviewed changes, but where the review process is incomplete or inadequate such inclusions have the potential to promote a high level of information loss or confusion. This is exacerbated when universities and research institutions insist on the exclusive use of WoRMS as a taxonomic source.

Clearly, users are free to draw information from any of the available websites to suit their needs, but care needs to be taken to evaluate the issues we highlight in this paper (e.g., see Section 4.4 above).

Other website compilations of coral species, of which there are several, including Hexacorallians of the World (Fautin, 2013 [346], regrettably not currently operational), the IUCN Red List of Threatened Species [215] as well as regional compilations notably the Atlas of Living Australia [347] and CORDIO [348] datasets, regional field guides to corals and broad-scale compendia (e.g., Reeflex [349]), are all potentially valuable for many purposes, especially conservation. However, it is important to stress that, unlike these publications, CoralsOfTheWorld.org [10,236] does not simply present a compilation of information. Instead, we integrate and actively assess all relevant information available to us from taxonomic and non-taxonomic publications in all relevant fields together with original fieldwork.

6. Issues from Recent Molecular Studies

In the following sections we highlight issues of concern and disagreement in the conclusions of some recent taxonomic studies that rely heavily on molecular technology. We preface this section by noting that most such studies have provided novel insights.

Our concerns lie mainly with methodological inadequacies and related over-reach in interpretations. On the latter, we highlight the serial synonymising of well-established, morphologically distinct genera, confounding the distinguishing characteristics of other genera in the process.

6.1. Sampling

Many of the issues raised in this article stem from the sourcing of corals for study, particularly over wide environmental or distribution ranges. Here we reflect on potential mistakes when habitat variations are not controlled for and/or replication is low. See below for examples of major discrepancies between morphological and molecular taxonomies and their likely causes.

6.1.1. Number of Samples

Of particular concern in forming robust conclusions is the frequently low replication of specimens used in taxonomic studies which precludes capture of geographic and environment-correlated variability. This applies to both molecular and morphological studies and is heavily compounded in instances where researchers have limited field experience. Due to the extent of morphological variation in most corals, it is unrealistic to believe that a sample size of a dozen or less is going to capture a species' variability if this has not been pre-determined in situ.

Field workers usually find many colonies that fall within the known variability of a species and the wealth of environmental and biological information they can collect is orders of magnitude more than anything to be gleaned from museum collections. For taxonomic work, we use photographed voucher specimens wherever possible to record variation in each target species.

How representative a type is and how it fits into the general variability of the species is crucial. Sample number is particularly important when type specimens are nominated, especially holotypes where the sample size is always one. That makes one specimen, with a name attached to it, foundational for an entire species. That species is likely to have a range of environment-correlated variations that far exceeds that seen in the historical synonyms of yesteryear and further, may be linked with geographic variations in other species. There are many issues with holotypes as indicated above: basically, they are often not fit for purpose, especially if not supported by a clear description and, importantly, habitat data and in situ photography. Unfortunately, there are many instances where the holotype is the only available specimen and that includes some new species being described by the present authors [350], usually a result of rarity or CITES-related import regulations imposed by many countries including Australia.

6.1.2. Omission of Gradients of Variability Across Habitats or Geographic Space

Many molecular studies have identified variants and considered the variant a new species without understanding the variation in the potential parent species. The molecular signature may turn out to be distinct, but unless that signature is clearly distinguished from that of a co-occurring parent or sister species, along with other consistent distinguishing characters, such designations are premature. For example, designation of *Pachyseris inattesa* from the Red Sea relied in part on molecular comparisons between shallow water Red Sea species of *Pachyseris* and *Leptoseris* with GenBank [351] samples of *Leptoseris* from the mesophotic zone of the central Pacific [331]). Other examples are given below.

6.1.3. Omission of Key Species

It is not appropriate to either designate new species, or synonymise existing species, when a key sister species or potential senior synonym has been excluded from a molecular

analysis, see for example, discussions of *Acropora tenuissima*, *A rongoi*, *A. uogi* and *A. kalindae* below.

6.2. Misidentification

An increasing number of disagreements between morphological and molecular taxonomies, including several referred to above, originate from field misidentifications, see below. Voucher specimens and topotypes may be helpful, although these are rarely, if ever, examined by anyone other than the authors and possibly, where photos are provided, by reviewers, particularly in pre-publication. In the case of topotypes, these can pose additional risks of adding further confusion. The overarching issue of accurate identification is obviously not new. Indeed, it has long affected coral research including both taxonomic and non-taxonomic publications. A recent example is a detailed and highly technical study comparing interesting aspects of the genome of "*Montipora foliosa*" and "*Montipora capricornis*" by Han et al. (2023) [352]. Two images are included in their Supplementary Materials (Image 1.pdf) as examples of their *M. foliosa* and *M. capricornis*. Although it is not possible to definitively identify the illustrated corals from the photos, it is clear that their *M. foliosa* does not exhibit characteristics of the species—it is much closer to *M. grisea*. Their *M. capricornis*, however, shows the characteristics of *M. foliosa*. Given the ease by which supposedly accurate molecular identification has become readily obtainable, notably from GenBank [351], we emphasise the need for credible field verification. Certainly, some of the more recent taxonomic publications that include both molecular and morphometric or other morphological data, have recognised the need for such verifications by nominating voucher specimens, but clearly, voucher specimens need to be assessed carefully as they can suffer the same issues.

6.3. Information Processing

This review is not intended to include a detailed discussion of molecular technologies, for that is neither our purpose nor our area of expertise. Rather, we highlight issues with methodology, sample replication and scope of conclusions within the context of the variability we observe in nature.

6.3.1. Cladistics

There is little recognition of the fact that the wide use of cladistics to analyse molecular data is potentially misleading. The subject has deep roots in the history of evolutionary theory. In 1950, Willi Hennig's treatise "phylogenetic systematics", set the foundation for cladistics in a strictly neo-Darwinian context [353,354]. Mayr (1982) [355] criticised Hennig's theory for assuming that speciation is always dichotomous and that the stem species always goes extinct when its lineage splits into two daughter species (discussed by Rieppel, 2011 [356]). McDade (1992) [357] subsequently proposed that cladograms would not be disrupted unless hybridisation occurred between distantly related species. At that time, these matters attracted a deluge of opinions which are summarised as far as cladistics is concerned by Hull (1979) [358] who found (somewhat unhelpfully) that "cladograms and classifications cannot represent everything about phylogeny".

At that time, hybridisation was thought to be an unusual occurrence, limited in both space and time. And so the debate went on, engaging in large part with the role of hybridisation (reticulation) versus bifurcating evolutionary trees in data analysis [359] and evolutionary theory [360], with the latter authors (Degnan and Rosenberg, 2009) expanding on the notion that "gene tree discordance [is] so widespread that no single tree topology predominates". And so we move on to Mallet et al. (2016) [361] question, "how reticulated are species? and their answer that "many groups of insects, vertebrates, microbes and plants" show "introgression and reticulation" so that "our understanding of adaptive

evolution, speciation, phylogenetics and comparative biology must adapt to these mostly recent findings". A decade on, we still look in vain for widespread acceptance of this rather obvious view as far as corals are concerned.

For corals, assessments of gene tree discordance require a thorough understanding that reticulation is evident in all aspects of their biology. This is not to say that cladograms indicating the phylogeny of coral species are wrong, just that they can be mistaken, misleading, or may have multiple interpretations. Stable phylogenetic trees require careful selection of target species and variants for inclusion, a suitable spread of habitat and geographic variability within those targets, analytical methods that allow gene trees to have different topologies and adequate replication to ensure that gene tree discordance is minimised and results can be relied upon (e.g., refs. [357,359,360]). We would argue too, that many potentially problematic gene tree results can be identified by a greater understanding of the variability of field entities. At the very least, if gene trees do not make sense with reference to what is observed in nature it is wise to avoid taxonomic destabilisation prior to comprehensive confirmation from additional studies which are completely independent.

6.3.2. Bayesian Inference

This is an analytical process that allows new information to be combined with existing information [362]. In taxonomy, it allows morphological and molecular data to be numerically combined on the basis of probabilities. This process was used by Gittenberger et al. (2011) [363] in their analysis of mushroom corals and has since been used in other studies as indicated below. This is a potentially useful procedure but without sufficient sampling and appropriate replication, can give misleading results.

Bayesian topologies used by different authors sometimes yield the same morphologically questionable findings indicating its use may have been between shared rather than independent datasets. For example, the findings of Arrigoni et al. (2014) [364] and Arrigoni et al. (2016) [301] concerning the taxonomic juxtaposition of *Micromussa amakusensis* (or *M. indiana*) and *Phymastrea multipunctata* suggests datasets that are not independent. When we refer to the need to have additional supporting data to confirm unusual or morphologically controversial results, it is important that such supporting data should come from entirely independent sources.

6.3.3. DNA Methodology

Most accounts of the technology used in individual coral molecular taxonomic publications are obviously well understood by at least some of the authors, but not so by most readers including, sometimes, other molecular taxonomists. This is because these accounts are, for good reason, of a specialist nature. Consequently, most stakeholders in this field are better informed about results than they are about methods and as they do not understand the methods in detail, the results commonly go unquestioned.

The availability of expertise, funding for field and laboratory work and equipment does not remotely meet present demands, a shortfall that is usually countered by shortcuts in methodology. One result has been the premature publication of questionable outcomes as noted in 'Major discrepancies between molecular and morphological taxonomy' below. Most methods currently in use seek to provide a balance between frequently changing, ecologically relevant, parts of the genome, and highly conserved parts which are more meaningful in taxonomic (evolutionary) timeframes. Thus, sequences associated with population dynamics may be separated from sequences used to determine species differences. This separation involves a multitude of decision-making processes, many of which are specific to individual author groups or host institutions. For example, the technique of 'target bait capture' (Bridge et al., 2023 [95]) assumes that the data obtained are phy-

logenetically informative at a species level. However, this has not been well tested for corals and promotes the assumption that different sequences represent potentially different, 'cryptic', species. Indeed, adoption of a 'unified species concept' definition (e.g., Bridge et al., 2023 [95]) with its lack of reliance on morphological and/or reproductive supporting evidence, underpins this approach. It may well result in premature conclusions particularly when local and geographic genetic variations (which have been shown to exist in studied species, see above) are not thoroughly assessed. This process is usually associated with 'data cleansing' and 'maximum likelihood' presentations as seen in Oku et al. (2017) [365] (their Figure 8) or Bridge et al. (2023) [95] (their Figure 2), see below. As introduced above, there are more appropriate approaches to investigating coral genomics and speciation, which include extensive sampling (e.g., refs. [33,100]).

6.3.4. Morphometrics

Morphometrics can offer important insights into the skeletal structure of particular species and species groups. However, it is not uncommon for morphometrics to be undertaken on a small number of replicates which may be from unknown or poorly known habitats and in which morphological variability may not be considered. Under these circumstances, detailed measurements of morphological features can create an illusion of scientific rigour which is unlikely to be justified. Furthermore, the use of morphometrics after the fact to support otherwise dubious findings can lead to confirmation bias. We cannot stress enough that to distinguish variation within and between species (a) the group of species in question should be well understood in situ prior to any study; (b) sampling should be replicated across habitats and depths, and across the relevant geographic space for the study's scientific purpose; and (c) care needs to be taken that inferences from the results do not extend outside the scope of the experimental design. We have seen above (Cladistics) that gene tree discordance is not uncommon and this will be exacerbated if known variabilities are ignored. The same will apply to any amount of detailed morphometrics if the species' habitat and geographic variability is not taken into account as part of the assessment. Conversely, we also caution that significant, consistent morphological differences among species in, for example, corallite structure, should not be ignored where these conflict with molecular results, as this can lead to inappropriate synonymy, an issue addressed below.

6.3.5. Microstructure

As revealed in thin sections, microstructure has played a significant role in diverse aspects of coral palaeontology, primarily stemming from Wells [366] and Chevalier [367,368]. For example, recent studies have provided insights into the Palaeozoic origins of the Scleractinia [369] and have provided proxy records of past ocean carbonate chemistry from *Acropora* as far back as the Eocene [370]. Ontological changes have also been seen in centres of rapid skeletal accretion in extant *Stylophora pistillata* over wide depth ranges in the northern Red Sea which have a partly genetic causality [242].

However, if microstructure is deemed relevant it would seem incumbent on the author(s) to explain why and provide relevant information including microstructural variations due to ontology and changes along geographic and environmental gradients. It would indeed be an extraordinary revelation if sister species were found to have different microstructural elements of any kind, given that these are fundamental skeletal building-blocks at the family level.

7. Discrepancies Between Molecular and Morphological Taxonomies

Here, we provide examples that highlight the issues stemming from molecular studies referred to above. These examples are far from comprehensive; less illustrative occurrences of the same issues apply to details of a wide range of other studies. Although this section deals with discrepancies, we note that we have accepted some of the recent shuffles of species across genera (see CoralsOfTheWorld.org (2026 in prep.) [236]) where these are warranted from both molecular and morphological viewpoints. We also note, however, that overt conflicts between morphology and molecular results require careful review.

In almost all cases, the authors of molecular studies introduce their work with an axiomatic 'out with the old' (meaning morphological taxonomy) and 'in with the new' (meaning molecular taxonomy) and usually go on to claim that such changes are important for conservation and sometimes biogeography. As this has almost become a mantra, the accuracy of these introductions and what follows clearly warrants careful reflection, especially as what usually follows goes far beyond taxonomy per se; it can affect conservation [252] and our knowledge of coral distributions and diversity.

7.1. Shuffles Between Genera

Increasingly over the past two decades, there has been substantial shuffling of species, in some cases repeatedly, across genera as the various findings of different studies, driven by the rapid development of molecular technology, has dominated the literature. These developments can involve internal inconsistencies, contradictory molecular findings from other authors, and can also lack support from field and associated morphological studies. We stress that it is the field entity that is of primary importance, not its name. Nevertheless, if the signpost—the name—is changed, there are inevitable consequences as taxonomy is not just for name-savvy taxonomists.

We seek to avoid destabilisation of well-established genera, as also strongly advocated by other authors. For example, Nicolle et al. (2024) [371] specifically stated that "If a genus is found to be non-monophyletic, then actions to render it monophyletic should minimise current and future taxonomic disruption" and "Genera should have distinctive and identifiable field traits that distinguish them from one another." Our approach is thus contrary to several recent taxonomic decisions that have destabilised well and long-established genera [305]. The replacement of genus *Favia*, a name used unambiguously for 32 Indo-Pacific coral species in several thousand publications, by *Dipsastraea*, a name not used since its original publication in 1830, is an extreme, avoidable, example (Veron, 2015) [305].

7.1.1. *Lithophyllon mokai*, *Psammocora explanulata* and *Coscinaraea wellsi*

We note the moving, by Benzoni et al. (2012) [372], subsequently followed by Oku, (2017) [365], of the three colonial species *Lithophyllon mokai*, *Psammocora explanulata* and *Coscinaraea wellsi* into the genus *Cycloseris*, otherwise composed of solitary, unattached, non-colonial species (Figure 32). This decision expanded on the initial proposal by Gittenberger et al. (2011) [363] that *L. mokai* was related more closely to *Cycloseris* than to *Lithophyllon*. In the mitochondrial tree of Benzoni et al. (2012, their Figure 3) [372], the 12 widespread samples of *Coscinaraea wellsi* and *Psammocora explanulata* are grouped closely together, then with one sample each of *Lithophyllon mokai* and *Cycloseris cyclolites*. Their nuclear tree (their Figure 4) is less clear-cut although 14 samples of *P. explanulata* and *C. wellsi* are still closely linked along with one sample each of *Cycloseris sinensis* and *C. costulata*. Oku et al. (2017) [365] included two samples of each ("referred from DNA databank", which presumably were derived from the earlier study) of these three species in their assessment of *Cycloseris hexagonalis* (see below). These authors also found that these three species are

grouped with *Cycloseris* (their Figures 7 and 8) then grouped more closely with different *Cycloseris* species than with each other (their Figure 8).

We are not concerned here with the taxonomy of the three colonial species, as these are each well-defined entities, but rather their inclusion in *Cycloseris*. This move would create a genus with no distinguishing macro- or micro-morphological characters and containing micro-morphological characters that were once used to help define four separate families [366]. Furthermore, *Cycloseris* has an unbroken fossil record extending back to the Cretaceous [366]. The first three species have several morphological characters and molecular signatures in common but have no morphological similarity with *Cycloseris*. Consequently, we unreservedly reject these generic changes.



Figure 32. *Lithophyllon mokai* (**top left**, on the Great Barrier Reef), *Psammocora explanulata* (**top right**, on the Great Barrier reef) and *Coscinaraea wellsi* (**bottom left**, in Hawaii), with *Cycloseris cyclolites* (**lower right**, in Brunei), see text. Photographs: E. Turak (**top left**, **bottom right**), J. Veron (**top right**), and K. Stender (**bottom left**).

7.1.2. *Fungia concinna*, *F. repanda*, *F. scabra* and *F. spinifer*

The moving of four *Fungia species* (*F. concinna*, *F. repanda*, *F. scabra* and *F. spinifer*) to genus *Lithophyllon* (the genus of *Lithophyllon mokai*, Figure 32, top left) by Gittenberger et al. (2011) [363] has no morphological congruence (their Figure 8) and there are internal conflicts in their molecular analyses (7 specimens in all) between their nuclear (their Figures 2 and 3) and mitochondrial trees (their Figures 4 and 5). In the nuclear tree (their Figure 2) *Fungia scabra* grouped with *F. spinifer*, then with *Lithophyllon undulatum* and more distantly with *Podabacia kunzmanni*. Much more distant from this group, *Fungia concinna* is grouped with *F. fralinae*, then with *Pleuractis* (=*Fungia*) *scutaria*. In their mitochondrial tree (their Figures 4 and 5), *Fungia scabra* grouped with *Lithophyllon undulatum*, then with *F. spinifer* and more distantly with *F. concinna* and *F. repanda.* The combined tree (their Figure 6, with intraspecific variation) placed *Fungia concinna* closest to a large group of species from

various genera, including *Heliofungia* and *Halomitra*. *Fungia scabra* again grouped with *Lithophyllon undulatum*, and more distantly with *F. spinifer*. *Fungia repanda* was not included.

A subsequent study in Okinawa (Oku et al. 2017, their Figures 7 and 8 [365]), included one local sample each of *Fungia concinna* and *F. repanda*, and two of *F. scabra*. It also included, from the "DNA data bank", two samples each of *F. scabra* and *F. concinna* and one of *F. repanda* and *F. spinifer*, along with two samples of *Lithophyllon undulatum*. Their mitochondrial tree (their Figure 7) grouped samples of *F. concinna* and *F. repanda* together, then with *F. scabra*, *F. horrida*, *F. spinifer* and *Lithophyllon undulatum*. Their second tree (their Figure 8), which did not include samples of *F. repanda*, separated *Fungia concinna* and grouped *Fungia spinifer* with *F. scabra*, and one sample of the latter with *Lithophyllon undulatum*. Quite apart from the small sample sizes, re-use of GenBank [351] samples and apparent molecular ambiguities, these changes would turn *Lithophyllon* from a well-defined genus into one without any defining characters and also confounds the genus *Fungia*. Consequently, we retain these four species in *Fungia*.

7.1.3. *Fungia fralinae*

The moving of *Fungia fralinae* to genus *Heliofungia* (Figure 33) by Gittenberger et al. (2011) [363] has little, if any, morphological congruence (their Figure 8). *Heliofungia actiniformis* is a highly distinctive species, with large extended tentacles unique among Fungiidae (see relevant Factsheets in CoralsOfTheWorld.org [10,236]). The molecular analyses, which included one specimen of *Fungia fralinae* from Sulawesi, Indonesia, produced conflicting results (their Figures 2–5). In their nuclear analysis, *F. fralinae* clustered with *F. concinna* (their Figure 2) and was widely separated from other taxa (their Figure 3). In their mitochondrial analyses, *F. fralinae* did group with *Heliofungia actiniformis*. The subsequent study by Oku et al. (2017) [365], which included the same GenBank [351] sample used by Gittenberger et al. (2011) [363], placed it closer, in their mitochondrial tree, to a group including *Pleuractis* (=*Fungia*) *scutaria*, *F. fungites*, *F. scruposa* and species of *Halomitra* than to *Heliofungia actiniformis* (their Figure 7). It did, however, group with *Heliofungia actiniformis* in the nuclear tree, albeit among a larger group of different species (their Figure 8). For these multiple reasons, we retain *F. fralinae* in *Fungia.*

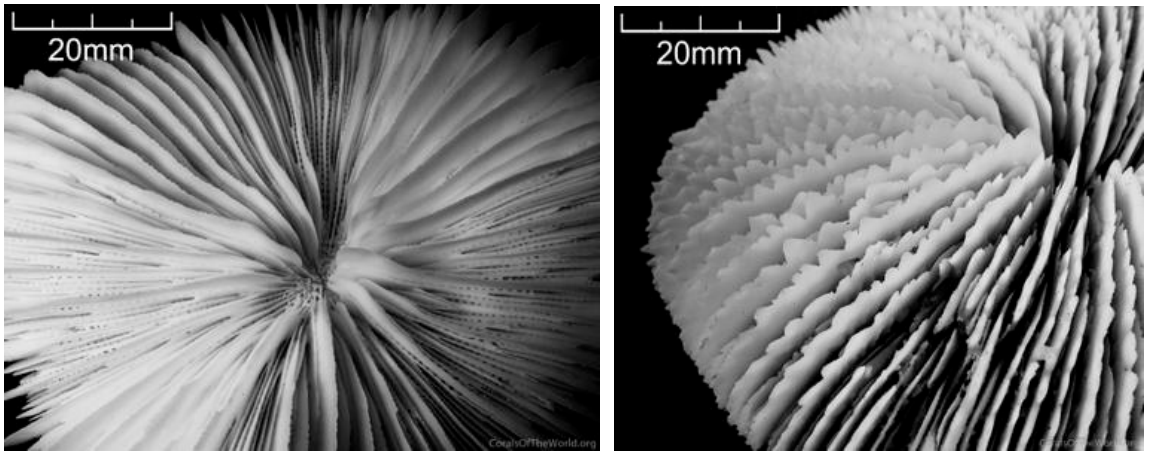


Figure 33. *Fungia fralinae* (**left**, from the Philippines) and *Heliofungia actiniformis* (**right**, from Brunei), see text. Photographs: J. Veron (**left**) and E. Turak (**right**).

7.1.4. *Cycloseris hexagonalis*

The creation of a separate genus, *Sinuorota*, for *Cycloseris hexagonalis* by Oku et al. (2017) [365] based on a study of 20 specimens from one location, Iriomote Island, Okinawa, is insufficiently supported. This species, well-defined both morphologically and genetically (18 samples), clusters with two DNA data bank samples of *Heliofungia actiniformis* in one

clade (mitochondrial tree, their Figure 7) and is very distant in another (nuclear tree, their Figure 8, one sample of *H. actiniformis*). Given that this species closely resembles other *Cycloseris* (Figure 34) and their study included only a very small part of its distribution range, we retain it in *Cycloseris*.

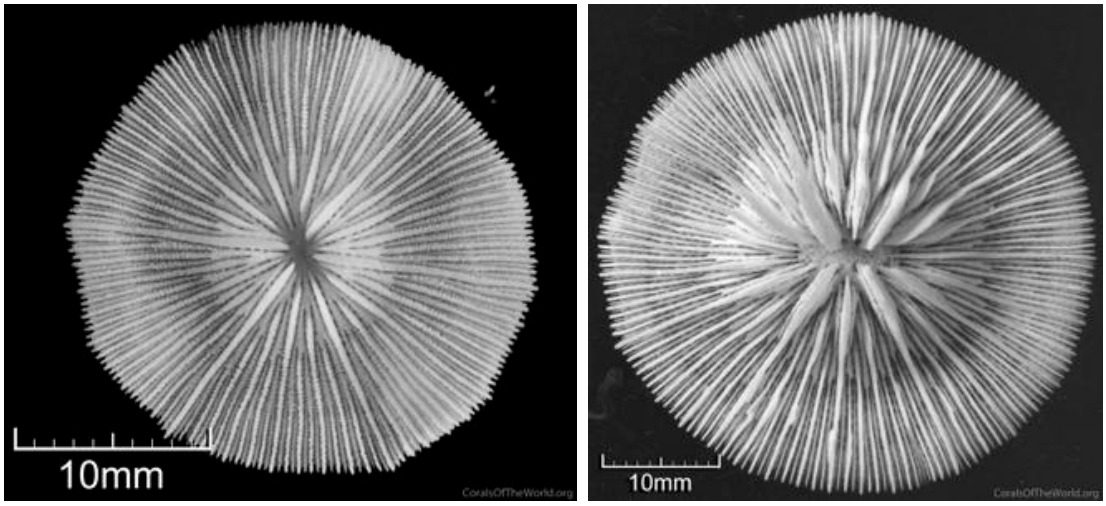


Figure 34. *Cycloseris* (=*Sinuorota*) *hexagonalis* (**left**, from the Ryukyu Islands, Japan) closely resembles *Cycloseris patelliformis* (**right**, from the Great Barrier Reef) along with all other *Cycloseris*, see text. Photographs: E. Turak (**left**) and J. Veron (**right**).

7.1.5. *Phymastrea*, *Favites*, *Goniastrea* and *Paragoniastrea*

This group of genera, part of the 'Bigmessidae' of Huang et al. (2011) [373], has proven particularly intractable for molecular taxonomy. We briefly review taxonomic and nomenclatural changes since 2011, when the above authors first provided "a robust molecular phylogeny". At that time, this grouping was derived from five DNA sequence markers. Despite few if any issues regarding the identity of the biological entities involved, studies since 2011 have shuffled species, in some cases repeatedly, across genera, a classic example of serial taxonomic destabilisation. From the Supplementary Tables of these studies, it appears that the shuffling, in many cases, was based on very few samples of each species, in some cases just one. For example, Huang et al. (2011) [373] analysed 124 specimens representing some 83 species, of which approximately 60 species (including cf.'s and aff.'s) were represented by a single specimen, with a further 16 species represented by two specimens.

In 2012, Budd et al. [374] resurrected *Phymastrea* to include eight species (*P. valenciennesi*, *P. magnistellata P. curta*, *P. serageldini*, *P. salebrosa*, *P. colemani*, *P. annuligera* and *P. multipunctata*) while also noting that these species "most likely belong to more than one genus and require further investigation" (a strong hint that these changes might have been premature). In 2014, Huang et al. [344] found that their molecular topologies divided the newly resurrected genus into three genera: *Favites*, their newly resurrected *Astrea* and newly created *Paramontastraea* Huang and Budd, 2014 [344]. Huang et al. also split species of *Goniastrea* among three genera, including the newly resurrected *Coelastrea* and *Dipsastraea*. Their Figure 1 [344] is illustrative of the significant shuffling to that point.

Although we accepted several of these decisions in the 2016 version of CoralsOfTheWorld.org [10], we disputed others, including the shifting of all *Phymastrea* species to *Favites*, *Astrea* and *Paramontastraea* by Huang et al. (2014) [344], in conflict with Budd et al. (2012) [374]. For *Favites*, the Supplementary Table S1 of Huang et al. (2014) [344] lists a total of 42 specimens from 12 included species. Most or all of these were analysed morpho-

metrically and a subset (possibly of 13 specimens collected by D. Huang) molecularly. Of the latter, most were represented by a single specimen.

As highlighted previously, morphometrics, however detailed, on only one or two specimens of a species has little meaning, and molecular studies with similar replication are proving contradictory (see also 'Underlying issues', below). This is clearly insufficient evidence for the loss of *Phymastrea*, resurrected as noted above, by a group including several of the same authors just two years previously. Accordingly, we retain three of the *'Favites'* species in *Phymastrea* (*P. colemani*, *P. magnistellata* and *P. valenciennesi*). These are morphologically congruent with significant corallite differences from the 13 *Favites* species (Figure 35).



Figure 35. *Phymastrea colemani* (**left**, in Brunei) and *Favites abdita* (**right**, in Fiji). These species do not belong in the same genus, see text. Photographs: E. Turak (**left**) and R. Kelley (**right**).

Favites (=*Plesiastrea*) *russelli* was moved from *Plesiastrea* to *Favites* by Veron et al. (1977) [295] and thence to *Paragoniastrea* by Huang et al. (2014) [375], the last move based on three molecular markers. According to the latter authors, genus *Paragoniastrea* includes *Goniastrea australensis*, *Paragoniastrea deformis*, and *Favites* (=*Plesiastrea*) *russelli* (Figure 36). More recently a fourth species has been added, *Paragoniastrea variabilis* Kishi, Nomura and Fukami, 2024 [336].

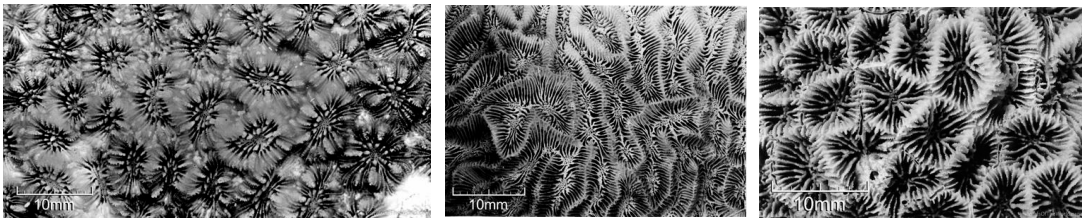


Figure 36. *Favites* (=*Plesiastrea*) *russelli* (**left**, from the Great Barrier Reef), *Goniastrea australensis* (**centre**, from the Great Barrier Reef) and *Paragoniastrea* (=*Goniastrea*) *deformis* (**right**, from Japan), see text. Photographs: J. Veron.

In the analysis of Huang et al. (2014, their Figure 2) [375], their *Paragoniastrea* (as *'Favites'*) *russelli* (with 2 nuclear, 3 mitochondrial samples) grouped with *Favites* sp. (2 samples) and *Goniastrea deformis*, and then with *Goniastrea australensis*. These authors noted that *Paragoniastrea* Huang, Benzoni and Budd, 2014 [375], is "morphologically similar to *Goniastrea* and *Favites* with members being formerly classified in these genera". However, in the second study (3 nuclear and 2 mitochondrial markers), published the same year, Huang et al. (2014) [344] found that *Paragoniastrea russelli* (1 sample) formed a grade with a group that included several species of *Astrea*, and "together they are part of a peculiar clade with *Goniastrea australensis* supported by molecular data (Huang et al., 2011) [373]." These

authors also noted that the "relationship needs further study as it is currently supported by very few morphological characters, particularly with *Goniastrea australensis* and *Favites russelli* switching places between the trees." Given these multiple conflicts and minimal replication of known variation, we retain *Favites russelli* in *Favites* (see Figure 31, illustrating environment-correlated morphological variation in this species, and Figure 36).

For similar reasons, we do not accept the moving of *Goniastrea australensis* (Figure 36, centre) to *Paragoniastrea* by Huang et al. (2014) [375]. These authors stated:

> "The recovery of the clade comprising *G. australensis*, *G. deformis* and *F. russelli* is a fascinating result, first and foremost because it is well supported in all three gene trees. None of the previous reconstructions have recovered this grouping—the five-gene phylogeny of Huang et al. (2011) [373] showed *G. australensis* and *F. russelli* as a paraphyly with *A. curta* nested within them, while Arrigoni et al. (2012) [376] supported the sister relationship between *F. russelli* and *A. curta*."

Huang et al. (2011) [373] also noted that their samples of *Goniastrea australensis* from different regions occurred in two clades, and that another *Goniastrea*, *G. pectinata* was paraphyletic, nested with *G. australensis* and *G. favulus* (their Figure 2).

In the nuclear and mitochondrial trees of Huang et al. (2014, their Figure 2) [375], *Goniastrea australensis* is distinct, albeit linked to other *Paragoniastrea* and more distantly, in their mitochondrial clade, to what was most recently renamed as *Goniastrea* (=*Orbicella* = *Favia*, =*Dipsastraea*) *stelligera* (Figure 59, below), *Goniastrea minuta* and *G. retiformis*. In addition, Huang et al. (2014, p. 298) [344] found that *Goniastrea australensis* "has been recovered as the sister taxon to *Astrea curta* + *Favites russelli* in one instance (Huang et al., 2011) [373]; but see Arrigoni et al., 2012) [376]." These authors retained this species as a *Goniastrea*, while also noting that "*Goniastrea australensis* and *Goniastrea deformis* are not nested within other *Goniastrea* spp. but have been recovered near the main *Goniastrea* clade to varying degrees ([their] Figure 2; Fukami et al., 2008 [377]; Huang et al., 2011 [373]; Arrigoni et al., 2012 [376])." However, in both the nuclear and mitochondrial trees of Huang et al. (2014, their Figure 2) [375], the other *Goniastrea* spp. do not group coherently. In their mitochondrial tree, *Goniastrea edwardsi*, *G. favulus* and *G. pectinata* were placed in a separate sub-clade which also included *Merulina* species, with the other sub-clade also including *Goniastrea stelligera* (see below), *Goniastrea minuta* and *G. retiformis*. In both trees, *Goniastrea retiformis* and *G. edwardsi*, which are morphologically sister species, were placed in different sub-clades whilst the latter was placed in the same sub-clade as *Merulina* species which have few relevant morphological characters in common (Figure 37).

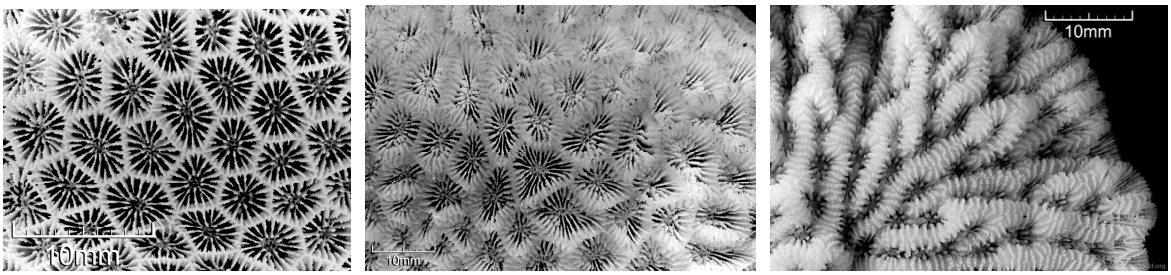


Figure 37. *Goniastrea retiformis* (**left**) and *G. edwardsi* (**centre**) are sister species yet were placed in different sub-clades by Huang et al. (2014) [375]. *Goniastrea edwardsi* was then placed in the same sub-clade as *Merulina ampliata* (**right**), although the latter species has little in common with the others at a generic level, see text. Photographs: from the Great Barrier Reef, E. Turak, courtesy QMT (**left**) and J. Veron (**centre** and **right**).

We also note the incongruous grouping of *Goniastrea aspera* (as *Coelastrea*) and *Goniastrea palauensis* with *Trachyphyllia geoffroyi* (Figure 38) by Huang et al. (2014) [344] on

both molecular and morphological criteria. Although it is difficult to verify (see their Appendix S1 [344]), it seems that their molecular analysis included one sample each of *T. geoffroyi* (from Japan), *C. aspera* and *G. palauensis* (both from Singapore). Needless to say, *T. geoffroyi* bears no similarity with the others. Given this level of discrepancy, we expect that additional work may well find different affinities among these species.



Figure 38. *Goniastrea aspera* (**left**, in Guam) and *Trachyphyllia geoffroyi* (**right**, on the Great Barrier Reef), see text. Photographs: G. Paulay (**left**) and R. Steene (**right**).

Further, the generic change from *Goniastrea* to *Coelastrea* has long-standing issues.

The type species of *Coelastrea* is *Coelastrea tenuis*. This species and *Platygyra verweyi* were considered as probable synonyms in 2016 [10] and further study supports this synonymy. The type locality of *C. tenuis* is listed by Verrill (1866) [338] as "Sandwich Islands ?" (=Hawaii), which is almost certainly incorrect (see Type specimens above). The name *Coelastrea tenuis* appears in sporadic early taxonomic literature (based only on the original specimen: [378,379] or cited briefly, without description: [380,381]) and in one later publication [382]. Huang et al. (2014) [344], who are the only other authors to have reviewed this species recently, were "unable to verify the species status of *Coelastrea tenuis*" believing that it might have been identified as *Goniastrea aspera* by recent authors. However, it in no way resembles *G. aspera*. Notably, Verrill, himself, described both *Coelastrea tenuis* and *Goniastrea aspera* in his 1866 monograph, distinguishing the two species as belonging in separate genera.

Platygyra verweyi has been in stable usage in numerous publications since it was described in 1976 [383]; it has a clear type locality and diagnostically unambiguous specimens. For this reason, along with the *C. tenuis* inadequacies, we are retaining the junior synonym for the species (see Veron et al. [350]). An important consequence of this synonymy (independent of the species seniority issue) is that, because *C. tenuis* is the type species of *Coelastrea*, and *Platygyra* is the senior genus, *Coelastrea* cannot be used for other species.

For all of these various reasons, we retain both *Goniastrea* species and *Trachyphyllia geoffroyi* in their respective genera.

We also note the comment by Huang et al. (2014) [344] "Unexpectedly, sequences from Saudi Arabian specimens putatively identified as *Coelastrea* (=*Goniastrea*) *aspera* [3 specimens] and *C.* (=*Goniastrea*) *palauensis* [1 specimen] are distinct from those derived from the central Indo-Pacific [for *G. aspera* 1 specimen from Singapore, 3 from the Great Barrier Reef; for *G. palauensis* 1 specimen from Singapore]". Our current distribution for *Goniastrea* (=*Coelastrea*) *aspera* does include the Red Sea, whereas that for *G. palauensis* does not. The Red Sea and central Indo-Pacific populations are, literally, oceans apart, and hence significant molecular differentiations are to be expected, despite retention of clear, unambiguous morphological structure. Adding complexity, Mitsuki et al. (2021) [384] found that their collections of *Goniastrea aspera* in Japan were divisible into two clades,

one from reef environments and the other from both reef and non-reef environments, which they called *Coelastrea* (=*Goniastrea*) *incrustans* (Duncan, 1886). This latter species, previously considered a junior synonym of *G. aspera*, was initially described from the Mergui Archipelago of the Andaman Sea, while the illustrated Japanese species bears similarities with a rarely encountered *G. aspera*-like entity from the Great Barrier Reef (L. DeVantier pers. obs.). The morphological, molecular and reproductive differences in the Japanese populations provide support for species delineation in this case.

It seems that the "Bigmessidae" was well named and to a large extent remains so.

7.1.6. *Caulastraea* and *Astraeosmilia*

There is clear morphological gradation among some species of *Dipsastraea*, *Astraeosmilia* and *Caulastraea*. This was alluded to in Arrigoni et al. (2021) [385] placement of the former *Dipsastraea maxima* in *Astraeosmilia*. In our present taxonomy, we also include the former *Dipsastraea vietnamensis* in *Astraeosmilia*. However, the shuffling of different species of *Caulastraea* by Arrigoni et al. (2021) [385] requires review. In their study, two species, *C. echinulata* (1 sample) and *C. furcata* (19 samples) were grouped closest to two species of *Mycedium*, four species of *Pectinia* and four species attributed to *Oulophyllia* than they were to *Caulastraea curvata* (6 samples), placed in genus *Astraeosmilia* (Arrigoni et al., 2021, their Figure 3 [385]) (Figure 39). The three *Caulastraea* species (*C. curvata*, *C. echinulata* and *C. furcata*) are a well-defined group morphologically. The *Astraeosmilia* species group (*A. connata*, *A. tumida*, *A. vietnamensis* and *A. maxima*) is less well-defined, evidenced by the various shuffles undertaken to date. However, as each of these species is well-defined in the field and skeletally, the conflict between the molecular results and morphology of *C. curvata* requires resolution.



Figure 39. *Astraeosmilia connata* (**top left**, in Tanzania), *Caulastraea curvata* (**top right** in the Dampier Archipelago, Western Australia), *Caulastraea echinulata* (**bottom left** in the Philippines) and *Caulastraea furcata* (**bottom right** in the Philippines), see text. Photographs: **Bottom right**, E. Turak, the others J. Veron.

7.1.7. *Erythrastrea* and *Oulophyllia*

Concerning *Erythrastrea*, firstly we agree with the "detective work" noted in Arrigoni et al. (2021) [385] that showed that two broken pieces of the type specimen of *Lobophyllia wellsi* Ma, 1959 had been designated as the paratypes of *E. flabellata* Pichon, Scheer and Pillai, 1983 [386] (discussed by Pichon, Scheer and Pillai in Scheer and Pillai, 1983 [386]). Huang et al. (2014) [344] had designated a lectotype of *E. flabellata* which was the same specimen as Pichon et al. [386] (WA 75b, USNM 78094). That specimen clearly appears to be a broken piece of Ma's (1959) [387] holotype of *Lobophyllia wellsi*. Hence, we are in agreement that the two nominal names relate to the same species and that 'wellsi' has precedence. However, we do not accept the moving of *Erythrastrea wellsi* (Figure 40) to genus *Oulophyllia* (Figure 41) by Arrigoni et al. (2021) [385]. Their molecular analyses found that eight specimens from the Red Sea of *E. flabellata* grouped closely with two specimens of *O. levis* and 26 of *O. crispa*, and more distantly with 7 specimens of *O. bennettae*. We disagree that "all macromorphological, micromorphological and microstructural characters of *Erythrastrea wellsi* (=*E. flabellata*) are identical to those of the other three species of *Oulophyllia*". Previously, based on the type of *Erythrastrea*, Huang et al. (2014) [344] had diagnosed *Erythrastrea* as matching in all but one character each with *Caulastraea* (discrete instead of uniserial) and *Oulophyllia* (fused walls instead of phaceloid) (Figures 40 and 41). However, following their reassignment, Arrigoni et al. (2021) [385] concluded that "a remarkable consequence of the inclusion of *O. wellsi* within *Oulophyllia* is that fused walls can no longer be considered a synapomorphy of the genus". This is analogous to the combining of *Lobophyllia* with *Symphyllia* (see below). Given their clear genus-level morphological differences this curious shuffle is not accepted and we retain *Erythrastrea* as a distinct monotypic genus.

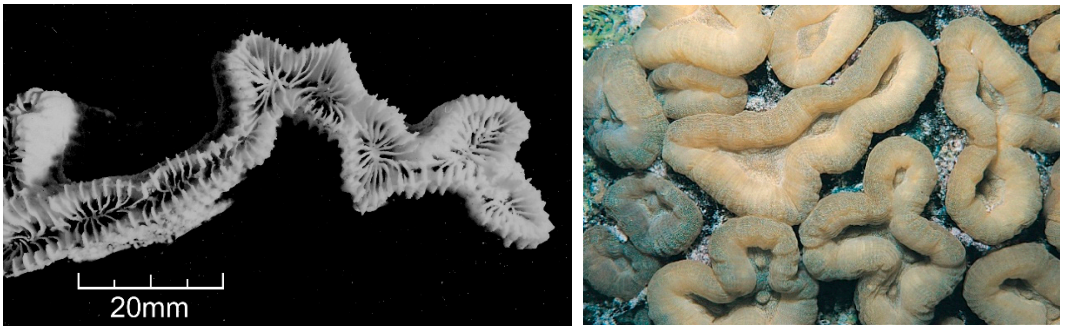


Figure 40. *Erythrastrea* (=*Lobophyllia*) *wellsi* Ma, 1959 part of the holotype (**left**) and living colony (**right**) from the Red Sea. Colonies of this species have separated valleys (are flabello-meandroid), see text. Photographs: J. Veron.

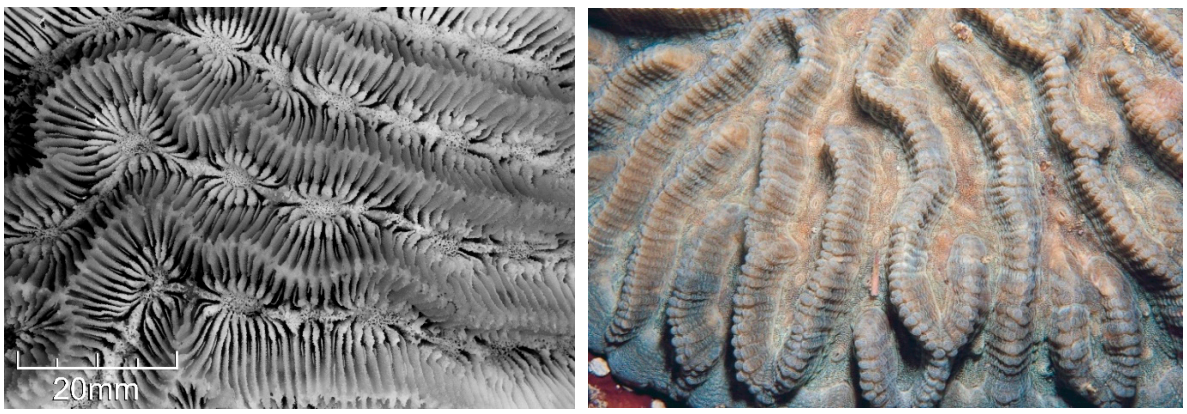


Figure 41. *Oulophyllia crispa* from The Great Barrier Reef (**left**) and Japan (**right**). Colonies of this species and all other *Oulophyllia* do not have separated valleys (are meandroid), see text. Photographs: J. Veron.

Despite apparent progress, these various taxonomic issues are not resolved at present, demonstrating the need for more work unravelling the 'Bigmessidae', early and continuing assurances of 'robust phylogenies' notwithstanding. The sampling in some studies does not, in our view, provide adequate support for the taxonomic changes on which they are based.

These considerations are not unique to the 'Bigmessidae' of course, as the following examples demonstrate.

7.1.8. *Turbinaria* and *Duncanopsammia*

The moving of *Turbinaria peltata* to the formerly monospecific genus *Duncanopsammia* by Arrigoni et al. (2014) [388] was based on molecular analysis (one nuclear and two mitochondrial regions) of two samples of each species. These species were not independently sampled in Mehrotra et al. (2023) [389] subsequent study of Dendrophylliidae. Rather, the prior samples from Genbank [351] of *D. axifuga*, *T. peltata* and *T. patula* were used which consequently mirrored the 2014 study. Although these are neighbouring genera, *Duncanopsammia axifuga* has Pourtalès plan of septal insertion not seen in any *Turbinaria* (Figure 42). This difference was not considered an important character by Arrigoni et al. (2014) [388] in their decision to move *T. peltata* to *Duncanopsammia*. There are other anomalous results, notably the wide molecular separation between *Turbinaria peltata* and its sister species, *T. patula*. We therefore consider this nomenclatural change inadequately supported.

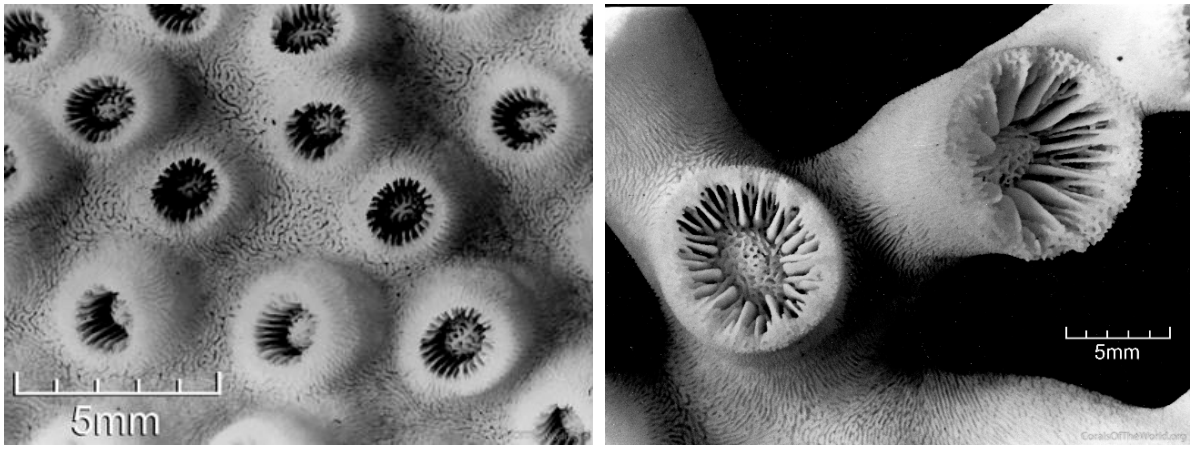


Figure 42. Corallites of *Turbinaria peltata* (**left**) and *Duncanopsammia axifuga* (**right**), both from The Great Barrier Reef. These species do not belong in the same genus, see text. Photographs: J. Veron.

7.1.9. *Poritipora*

Kitano et al. (2014) [390] found that *Poritipora paliformis* "may be a morphological variant of *Goniopora minor*" based on molecular similarity between *P. paliformis* (two samples from Japan) and two species of *Goniopora* (*G. columna* and *G. minor*, their Figures 4 and 5). Their gene trees grouped other samples of *G. columna* and *G. minor* with a diverse array of other *Goniopora*. Morphologically, in contrast to *G. minor* (and all other *Goniopora*), *P. paliformis* corallites have two distinct orders of 12 septa each and no columella (Figure 43). Despite the apparent inability to separate these genera genetically, the results are not well supported as they are based on few molecular markers from a small number of specimens with strong morphological characters to the contrary.

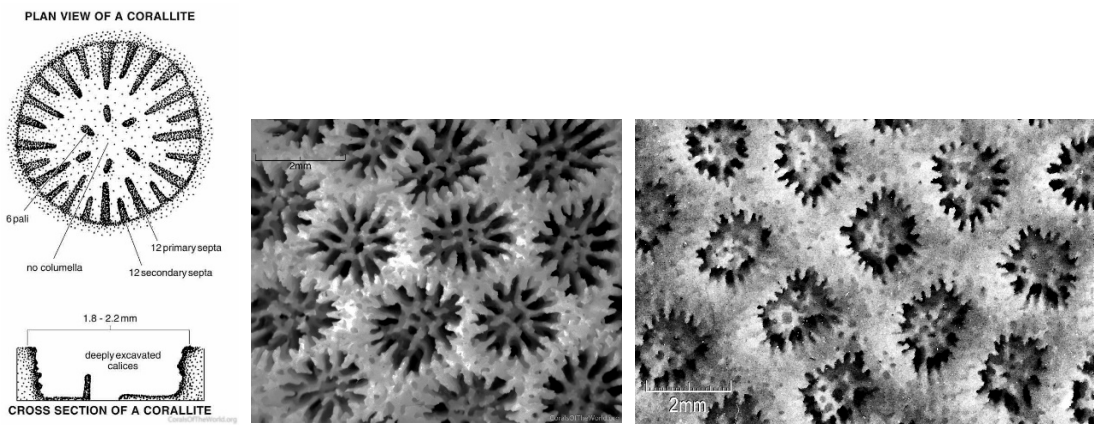


Figure 43. Calice characters of *Poritipora paliformis* (**left** and **centre**) and *Goniopora minor* (**right**), see text. Drawing: Veron (2000) [6]. Photographs J. Veron.

7.1.10. *Calathiscus*

Kitano et al. (2014) [390] finding that *Calathiscus tantillus* is a sister species of *Goniopora somaliensis* was based on four samples of the former and seven or eight of the latter. This is in stark contrast with their morphological dissimilarity (Figure 44). Further, their mitochondrial gene tree (their Figure 4) grouped *C. tantillus* with one sample of *G.* cf. *somaliensis*, then with a sample of *G. somaliensis*. Other samples grouped *G. somaliensis* with four other *Goniopora*. Their nuclear tree (their Figure 5) grouped *Calathiscus tantillus* with three species of *Goniopora*. As with *Poritipora*, and despite the apparent inability to separate the genera genetically, their results, based on few molecular markers from a small number of specimens, are not accepted. We therefore retain genus *Calathiscus* in agreement with Claereboudt and Al-Amri (2004) [391].

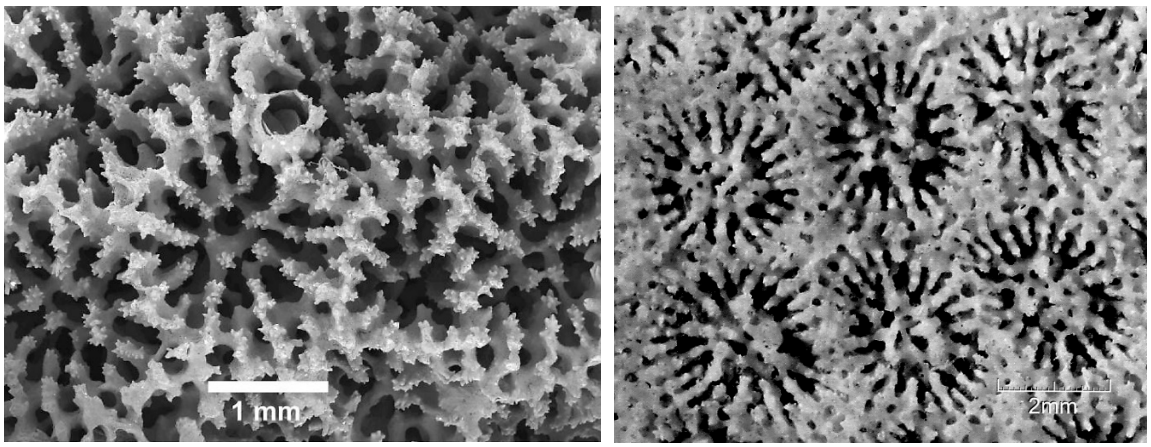


Figure 44. *Calathiscus tantillus* type specimen (**left**) and *Goniopora somaliensis* type specimen (**right**), see text. Photographs M. Claereboudt (**left**) and J. Veron, courtesy NMNH (**right**).

7.1.11. *Paraclavarina*

The monospecific genus *Paraclavarina* was made a synonym of *Merulina* by Huang et al. (2014) [375], on molecular evidence and that "there are no diagnosable morphological differences" between them. The molecular analyses included two samples of *P. triangularis* from Papua New Guinea. Both nuclear and mitochondrial gene trees grouped those samples with the *Merulina* clade (Huang et al., 2014 [375]: their Figure 2). Morphologically, *P. triangularis* and all *Merulina* species have little in common: *P. triangularis* is a purely branching species, whereas all *Merulina* are encrusting to foliaceous, with or without digitate upgrowths and micro-morphological structures are equally dissimilar (Figure 45).

Given the small number of samples and the morphological incongruence, there is no persuasive evidence for the loss of *Paraclavarina* as a distinctive monotypic genus.

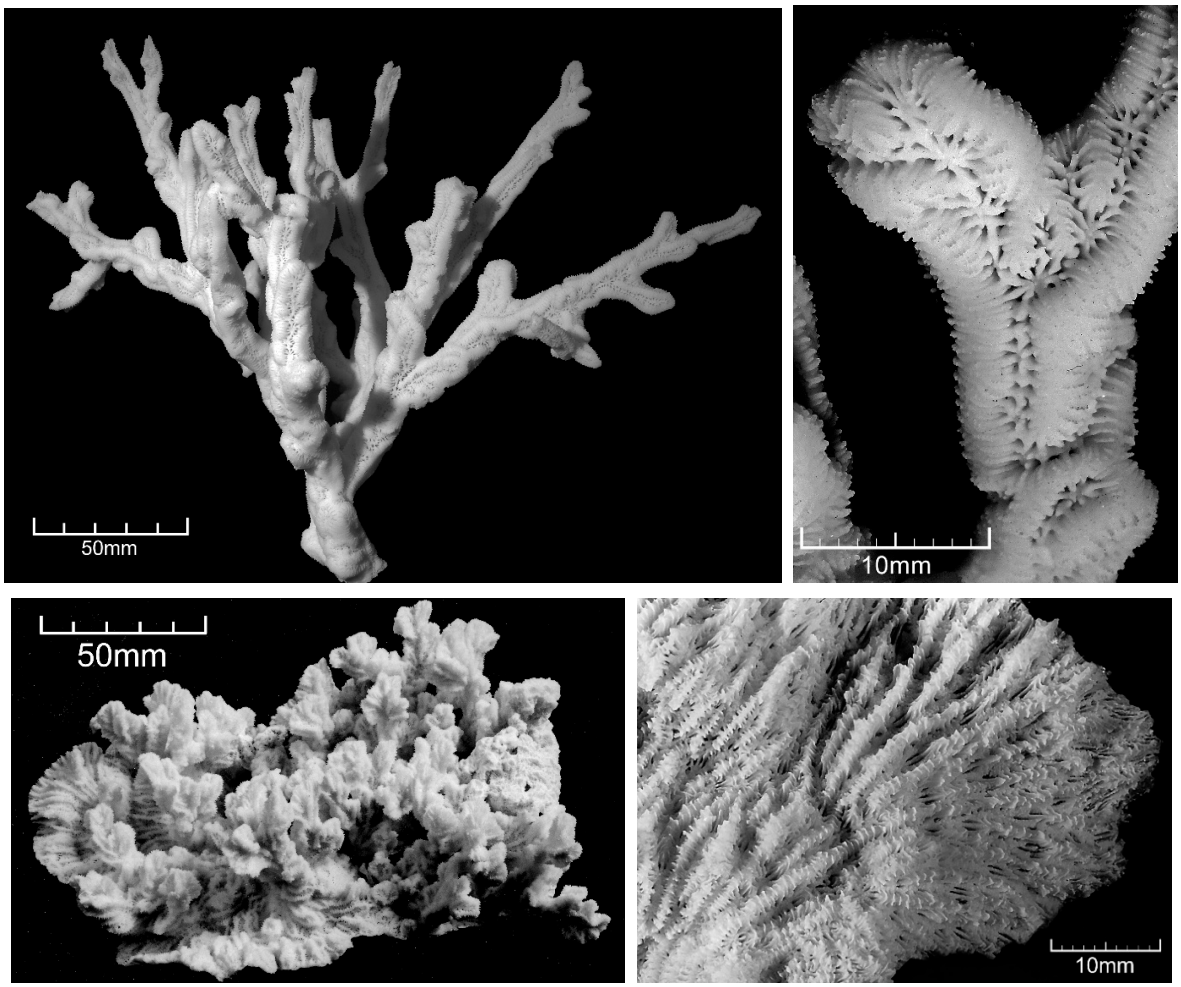


Figure 45. *Paraclavarina triangularis* colony and skeletal detail (**top row**) and *Merulina scabricula* colony and skeletal detail (**bottom row**), both from the Great Barrier Reef, see text. Photographs: E. Turak, courtesy QMT (**top row**), J. Veron (**bottom row**).

7.1.12. *Symphyllia*, *Australomussa* and *Parascolymia*

As with the aforementioned 'Bigmessidae', there has been major recent shuffling, again in some cases repeatedly, among species and genera in what used to be the Indo-Pacific family Mussidae (Huang et al., 2016, their Figure 1 [345]), which these and other authors split into several families, notably Lobophylliidae and Merulinidae.

Within Lobophylliidae, the moving of most *Symphyllia* species, as well as *Parascolymia* and *Australomussa*, to *Lobophyllia* by Huang et al. (2016) [345] foreshadowed by the Bayesian topology of Arrigoni et al. (2014, their Figure 9) [364] appears supported by molecular data of the former authors (their Figure 2), but has no morphological congruence (Figure 46). On the molecular analyses, which used three markers, most sequences were derived from prior published data [301,364,373,376,392,393]. Huang et al. (2016) [345] Appendix Table S1 lists a total of 14 voucher specimens of '*Lobophyllia*', one sample for each species analysed, of which three samples were from the present study, and 11 samples from prior work. Locations of collection ranged widely: *Lobophyllia corymbosa*, *L.* (=*Symphyllia*) *erythraea* and *L. hemprichii* (each from the Red Sea), *L. diminuta* (Mayotte), *L. flabelliformis* and *L. robusta* (Papua New Guinea), *L. costata* (French Polynesia), *L.* (=*Acanthastrea*) *ishigakiensis* (New Caledonia), *L.* (=*Australomussa*)

rowleyensis (Australia) and *L.* (=*Parascolymia*) *vitiensis* (Papua New Guinea). For the other species of *Symphyllia*, one voucher specimen each was analysed, for *S. agaricia* (Papua New Guinea), *S. recta*, *S. radians* and *S. valenciennesi* (New Caledonia or Australia), also from the earlier studies.

Huang et al. (2016) [345] reported that all their subclades were well supported, but also commented that only a few contained stably resolved relationships. They also reported that *Australomussa*, *Parascolymia*, and *Symphyllia* (sensu Veron, 2000 [6]) were indistinguishable genetically (citing Arrigoni et al., 2014 [364]) and that integration of morphological data "unequivocally" supported the placement of these genera under the senior synonym, *Lobophyllia*, along with *Acanthastrea ishigakiensis*.

There are several relevant points of contention in this major revision. Firstly, the species names used refer to well-defined field entities, long-established and accepted. The above authors' assertion of unequivocal support from their morphological data is not supported by their own tree (their Figure 2) where *Symphyllia* and *Lobophyllia* are clearly distinct. In addition, the small number of samples, lack of habitat and geographic replication and markers employed, make consideration of any synonymy premature. Results from one sample of each species are not, in our view, sufficient evidence on which to make major nomenclatural changes. These two genera are clearly distinct in the field and skeletal specimens and have been considered so by a formidable array of authors.

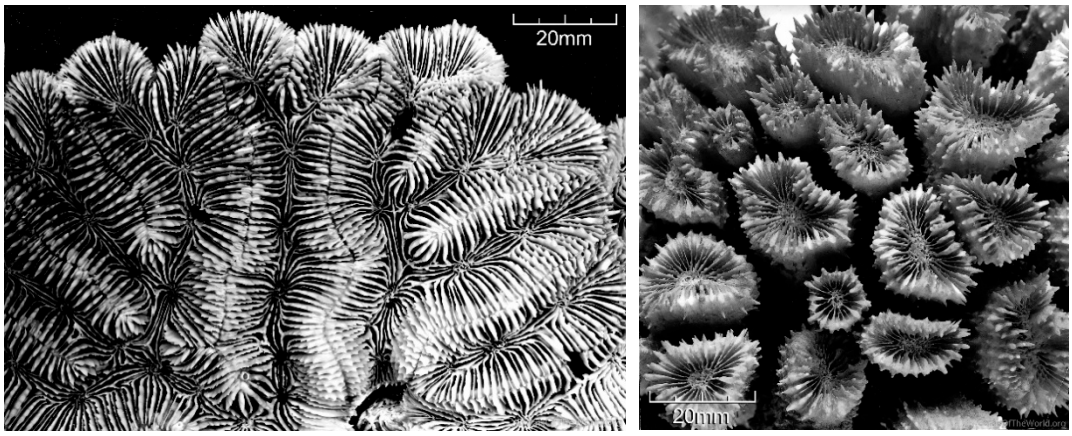


Figure 46. *Symphyllia radians* (**left**) and *Lobophyllia corymbosa* (**right**) from the Great Barrier Reef. These species, which were included in Arrigoni et al. (2014) [364] study, are representative of their respective genera. They do not belong in the same genus. Photographs: J. Veron.

Arrigoni et al. (2014) [364] finding from three molecular markers that the distinctive monotypic genera *Australomussa* and *Parascolymia* are synonyms appears to be supported by their data (their Figure 9). However, these are morphologically very distinct. *Australomussa*, represented by *A. rowleyensis* is colonial; *Parascolymia*, represented by *P. vitiensis*, with rare exceptions, is solitary. Juveniles of both species have some skeletal details in common, but not so mature colonies/individuals especially as *A. rowleyensis* has most corallites < 15 mm diameter and mature *P. vitiensis* has most corallites > 50 mm diameter (Figure 47). Subsequently, both genera have been synonymised into *Lobophyllia* [345] along with *Symphyllia*, confounding multiple long-standing generic distinctions in the process.

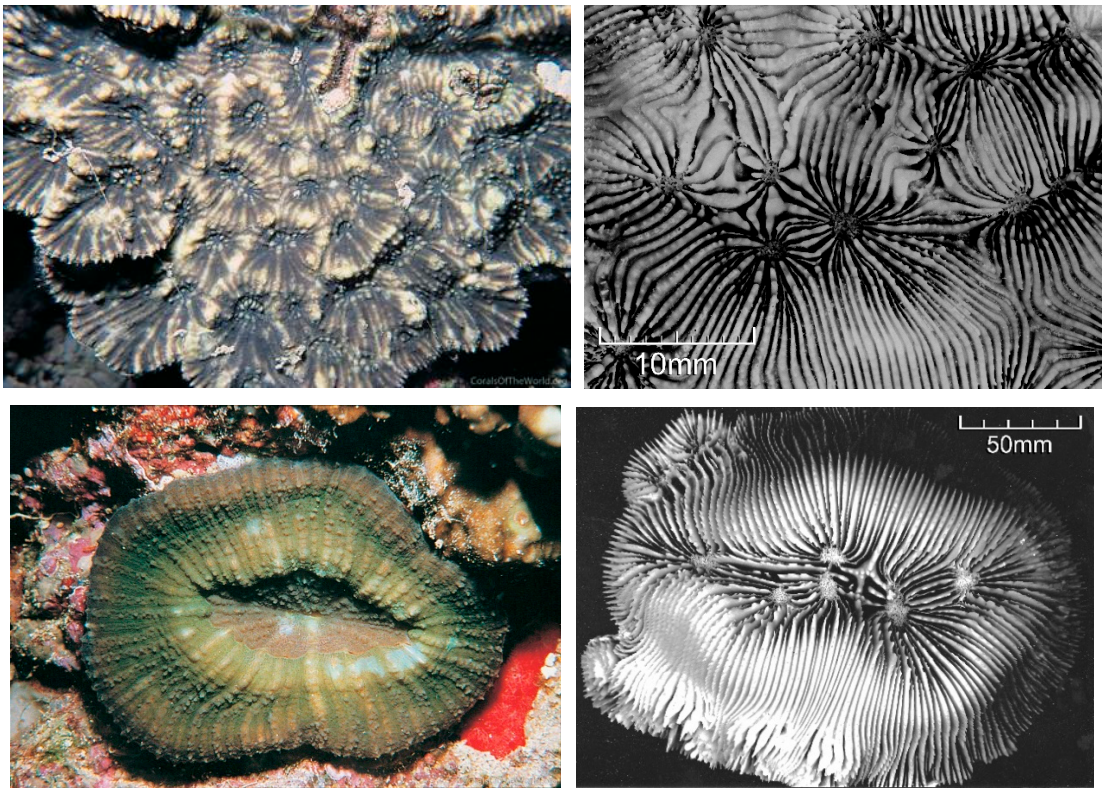


Figure 47. *Australomussa rowleyensis* in the Mergui Archipelago (**top left**) and from the Rowley Shoals, Western Australia (**top right**) and *Parascolymia vitiensis* on the Great Barrier Reef (**bottom row**) see text. Photographs: V. Taylor (**top left**) and J. Veron (the others).

Given that all these taxa have been used unambiguously in hundreds of taxonomic and non-taxonomic publications with clear morphological separations, such synonymies would require comprehensive independent support showing genetic overlap across habitats and space and demonstrated reproductive compatibility. Consequently, we retain all four genera.

7.1.13. *Porites*

Before moving on to species-level issues, we briefly mention a recent publication by Terraneo et al. (2025) [394] that endeavours to further promote the dogma of 'out with the old and in with the new' with a "genomic approach" to *Porites*. Citing Veron (2000) [6], these authors found that "making species identification based solely on morphology inherently complex". In reality, while the taxonomy of *Porites* may seem complex at first, with a little perseverance and a hand lens, *Porites* becomes the least problematic of all the major genera simply because their corallites have a wealth of reliable characters which are diagnostic for each of the 63 species we recognise. To make identification easier, these characters were summarised in a diagram for each species in Veron (2000) [6] and in CoralsOfTheWorld.org [10,236]. And to make it easier still a simple key to all species was provided. The only significant exception to these comments is where corallites vary substantially with position on massive colonies. This primarily occurs with *Porites lobata* and *P. lutea*, growing on reef flats (Figure 48).

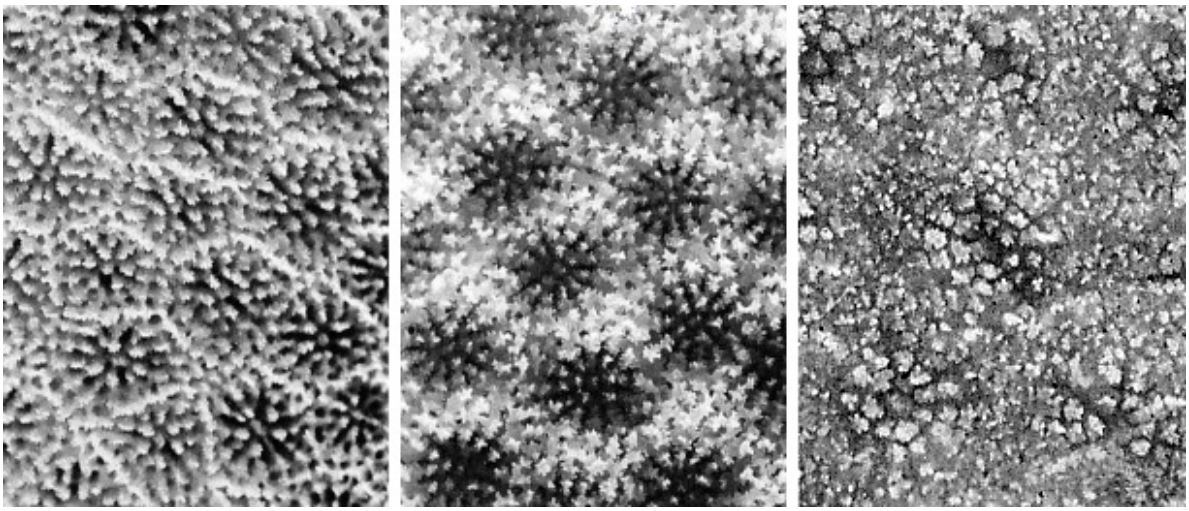


Figure 48. Changing corallite structure around the rim of bell-shaped *Porites lutea* colony on a reef flat. Corallites are approximately 1–1.5 mm in diameter. Photographs: J. Veron.

7.2. Summary of Generic Shuffles

In briefest summary of the unaccepted examples of genus-level changes stemming from molecular studies (Box 6), we find that all are due to a combination of (a) inappropriate or superseded (but still cited) technology, (b) low replication of samples, (c) non-inclusiveness of geographic and environment-correlated variation (commonly both), (d) gene tree discordance in cladistics (see above) and (e) failure to maintain clear morphological distinctions among well- and long-established genera. These have resulted in substantial premature taxonomic destabilisations. Many authors have acknowledged the uncertainty posed by some of these issues but have made the changes regardless.

Box 6. Brief summaries of unaccepted genus level changes stemming from molecular taxonomy.

Examples of unaccepted genus-level changes stemming from molecular taxonomy
See above and below for further details of these brief summaries.

1. The moving of *Lithophyllon mokai*, *Psammocora explanulata* and *Coscinaraea wellsi* to genus *Cycloseris* [365,372].
2. The moving of four *Fungia* species (*F. concinna*, *F. repanda*, *F. scabra* and *F. spinifer*) to genus *Lithophyllon* [363,365].
3. The moving of *Fungia fralinae* to genus *Heliofungia* [363,365].
4. The creation of a separate genus, *Sinuorota*, for *Cycloseris hexagonalis* [365].
5. The shuffling of *Phymastrea*, *Favites*, *Goniastrea* and *Paragoniastrea* [373].
6. The moving of *Favites russelli* to *Paragoniastrea* [375].
7. The moving of *Goniastrea australensis* to *Paragoniastrea* [375]; citing [373,376,377].
8. The shuffling of some *Caulastraea* and *Astraeosmilia* spp. [385].
9. The placement of *Erythrastrea* in genus *Oulophyllia* [385].
10. The moving of *Turbinaria peltata* to the formerly monospecific genus *Duncanopsammia* [388].
11. The placement of *Poritipora paliformis* as a morphological variant of *Goniopora minor* [390].
12. The placement of *Calathiscus tantillus* as a sister species of *Goniopora somaliensis* [390].
13. The synonymy of *Paraclavarina* with *Merulina* [375].
14. The placement of *Australomussa* and *Parascolymia* as synonyms [364].
15. The moving of *Symphyllia* species, as well as *Parascolymia* and *Australomussa*, to *Lobophyllia* [345]; foreshadowed by [364].
16. The grouping of *Acanthastrea ishigakiensis* with *Symphyllia* species (as *Lobophyllia*) [345].
17. The moving of *Lobophyllia pachysepta* to *Acanthastrea* [345].
18. The moving of *Montastrea multipunctata* to *Phymastrea* [364,374]; and then to *Micromussa* [301].

7.3. Issues with Species

We reflect here on several examples of anomalous species-level issues highlighted in recent publications, likely reasons for them, and our solutions to them.

7.3.1. *Leptastrea magaloni/L. pruinosa*

The species of *Leptastrea* are usually readily separated once geographic variations are determined. Be that as it may, Arrigoni et al. (2020) [300] synonymised the long-established *Leptastrea pruinosa* with *L. purpurea*. The molecular evidence for this was apparently based on three samples identified as *L. pruinosa* from French Polynesia and New Caledonia (their Supplementary Table S1). These authors then identified another genetic lineage apparently restricted to a small region of the southwestern Indian Ocean (their Figure 6) which they named *Leptastrea magaloni* Benzoni and Arrigoni, 2020 [300], with illustrations which fall into the known morphological variability of *L. pruinosa* (see Figure 49 from NW Australia). Indeed, these authors illustrate this (Ref. [300], their Figure 7) where their *L. magaloni* specimens grouped morphometrically with those of *L. purpurea* (presumably also including their synonymised *L. pruinosa*).

The two species we identify as *L. purpurea* and *L. pruinosa* regularly co-occur and have variabilities in the field which are distinct from one another and these differences include their respective type specimens. This enables these species to be readily identified and named (Figure 49).



Figure 49. *Leptastrea purpurea* (left) and *L. pruinosa* (=*magaloni*) (right) on Ashmore Reef, north-western Australia. These species are readily separated. Photograph: J. Veron.

A somewhat similar set of circumstances surrounds the likely validity of their Pacific *Leptastrea gibbosa*, which probably defines a geographic variant of *L. inaequalis*, which the authors consider to be restricted to the western Indian Ocean (see their Figures 6 and 7). Indeed, the three species that clustered closest in the gene trees (their Figure 5) were all from the Western Indian Ocean region, with the six specimens identified as *L. bottae* from the Red Sea, the six specimens identified as *L. magaloni* from Madagascar and Mayotte, and the nine specimens identified as *L. inaequalis* from the Red Sea, Gulf of Aden and Socotra (their Supplementary Table S1). The radical re-drawing of the distribution range for *L. inaequalis* disregards the fact that this species is readily identifiable from the Red Sea, throughout the central Indo-Pacific and northern Australia, to the central Pacific. As noted widely throughout this review, molecular signatures in samples are expected to reflect geography (and habitat). *Comprehensive sampling across intervening areas could radically change the relationships between lineages and species clusters in gene trees.*

This illustrates the fundamental role of widespread fieldwork and field identification and the necessity for its integration into molecular and morphological taxonomy alike.

7.3.2. *Goniastrea* (=*Paramontastraea* = *Favites*) *peresi*

To address long-standing confusion surrounding the generic placement of this species (also noted by Huang et al., 2014 [344]) a new genus name will be assigned to this species (see [350]). The other two species of *Paramontastraea* (*P. salebrosa* and *P. serageldini*) (Figure 50), currently retained by us in *Paramontastraea*, await further consideration as, morphologically, there are genus-level differences between them. No molecular analyses of *P. serageldini* or *P. peresi* were undertaken in the 2014 study. Although Huang et al. (2014, p. 333) [344] found *Goniastrea peresi* to be morphologically similar and a close relative to *P. salebrosa* and *P. serageldini*, there are clearly fundamental differences between these species (Figure 50).



Figure 50. *Goniastrea* (=*Paramontastraea*, =*Favites*) *peresi* (**left**, in the Red Sea), *Paramontastraea salebrosa* (**centre**, in Vanuatu) and *Paramontastraea serageldini* (**right**, in Tanzania), see text. Photographs: J. Veron.

7.3.3. *Paraechinophyllia variabilis*

Paraechinophyllia variabilis Arrigoni, Benzoni and Stolarski, 2019 [334] was described from the molecular signature of 13 specimens from the western Indian Ocean and Red Sea. These authors and their co-workers [334] found that this 'species' had a molecular signature revealing "a deep separation" (their Figure 4) from two other entities, *Echinophyllia orpheensis* and *Echinophyllia aspera*, sister species according to the Bayesian topology of Arrigoni et al. (2014, their Figure 1) [392]). We conclude that this enigmatic finding is likely the outcome of inadequate sample replication as their molecular analysis included just one sample identified as *Echinophyllia aspera* (from Gulf of Aden) and one of *E. orpheensis* (from Australia).

7.3.4. *Micromussa indiana/M. amakusensis*

Molecular analysis of specimens from different oceans (Japan and the Arabian Sea) by Arrigoni et al. (2016) [301] and with subsequent inclusion of Singapore (Ng et al., 2019 [302]), together with our extensive collections from Japan and the Western Pacific, the Coral Triangle, Indian Ocean and Red Sea, indicates that *M. amakusensis*, like many other species, is composed of geographic continua rather than discrete units. This reticulate pattern was alluded to by Arrigoni et al. (2016) [301] who initially called their Gulf of Aden 'species' *Micromussa* cf. *amakusensis* (their Figure 3). Several specimens of *M. amakusensis* (Figure 51 and Supplementary Figure S2) in our collection are very similar to the holotype of *M. indiana*. Other specimens show the range in skeletal form. *M. indiana* might be considered a valid species should it be found to co-occur as a distinct entity in sympatry with *M. amakusensis*, but this appears not to be the case from their molecular analysis. As it is likely that morphological criteria and molecular signatures will vary in tandem, we consider that *M. indiana* is a probable synonym of *M. amakusensis*. Notably, two Singapore samples of *M. amakusensis* analysed by Ng et al. (2019) [302] showed a degree of molecular separation (their Figure 2) with one positioned in their gene tree towards the Genbank [351] samples of '*M. indiana*' from the north-western Indian Ocean. These authors concluded that *M. amakusensis* formed a paraphyly. Furthermore, the claim by Ng et al. (2019) [302] that their discovery of *Micromussa amakusensis* in Singapore represents the southern-most occurrence of the species in the Indo-Pacific is incorrect. This species is much more widespread.

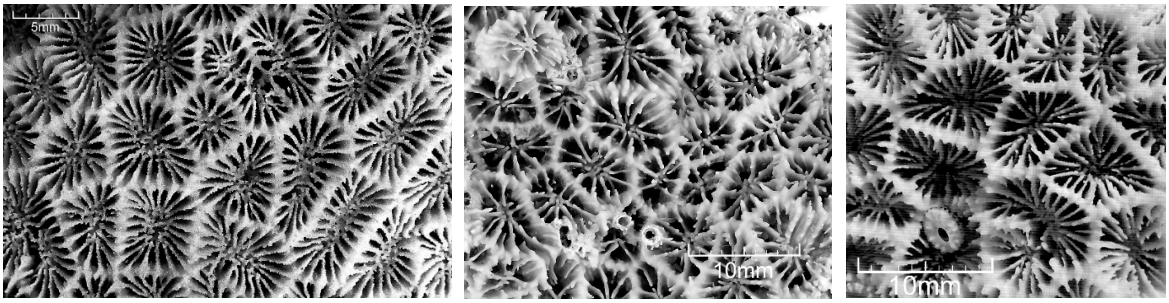


Figure 51. Holotype of *Micromussa amakusensis* from the Amakusa Islands, Japan (**left**), holotype of *M. indiana* from the Gulf of Aden (**centre**) and *M. amakusensis* from Oman (**right**), see text. Photographs: J. Veron, courtesy QMT (**left**), E. Turak, courtesy MNHN (**centre**) and M. Claereboudt (**right**).

7.3.5. *Acropora tenuissima* and *Acropora rongoi*

Bridge et al. (2023) [95], along with their division of *Acropora tenuis* into smaller taxa (*A. kenti*, *A. bifaria* and *A. africana*, see below), also described two new species, *Acropora tenuissima* Bonito, Bridge, Fenner and Baird, 2023 [95] and *A. rongoi* Bridge and Cowman, 2023 [95]. This study raises multiple issues. In summary:

For *Acropora tenuissima*, molecular analyses were of one specimen from Fiji and one from the Great Barrier Reef. As these authors note, their *Acropora tenuissima* is closest, morphologically, to *A. nana*, for which no molecular comparisons were undertaken. Minor microstructural differences between types notwithstanding, there are no taxonomically significant points of distinction between these species (Figure 52).

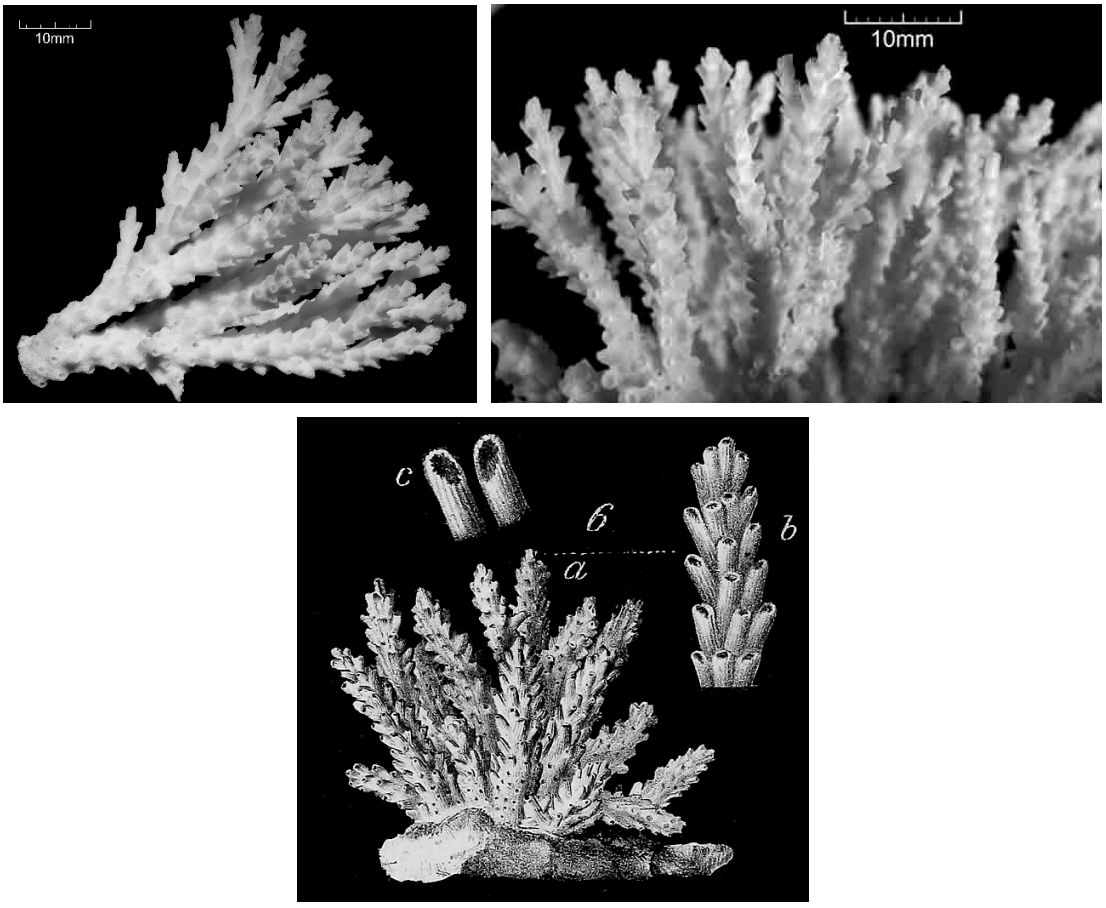


Figure 52. Paratype of *Acropora tenuissima* (**top left**) a specimen of *A. nana* from the Great Barrier Reef (**top right**), and illustration of the type of *Acropora nana* (**bottom centre, '6a–c'**) see text. Photographs: E. Turak, courtesy of QMT (**top row),** from Studer (1878) [395] (**bottom centre**).

Two samples from the Cook Islands described as *Acropora rongoi* by Bridge and Cowman [95] are morphologically very similar to A. *striata*, (Figure 53) for which four putative molecular comparisons (of *A*. aff. *striata* from Pohnpei and Japan) were undertaken by Bridge et al. (2023) [95]. The authors claimed (their p. 16):

> "Specimens of *A. rongoi* in the collection at QMT were previously identified as *A. striata* (Verrill, 1866), *Acropora elseyi* (Brook, 1892) and *Acropora florida* (Dana, 1846), attributable to the variability in gross morphology of *A. rongoi* in different habitats. Verrill's holotype of *A. striata* from the Ryukyu Islands has similar radial corallite shape but is clearly distinguished from *A. rongoi* on the basis of molecular and biogeographical evidence. Furthermore, the interpretation of *A. striata* as hispidose (Shirai, 1980 [396]; Veron and Wallace, 1984 [237]; Wallace, 1999) [285]) is likely to be incorrect because the holotype lacks tertiary branching."

There are several issues here. Contrary to these assertions, the *Acropora striata* type, a sub-branch, does have secondary and tertiary branching. The study placed great reliance on minor morphological differences between types (see 'Type specimens' above). However, the *A. rongoi* type not only closely resembles the *A. striata* type but also falls with the range of variation in the species in the field. As a result of these reservations, we hold concerns on the re-identification and re-labelling of specimens at QMT. Further, given the wide geographic separation among their samples (from the Southern and Northern hemispheres), it is not surprising that molecular differences were found. Indeed, the cladogram (their Figure 2) highlights the molecular complexity of the group.

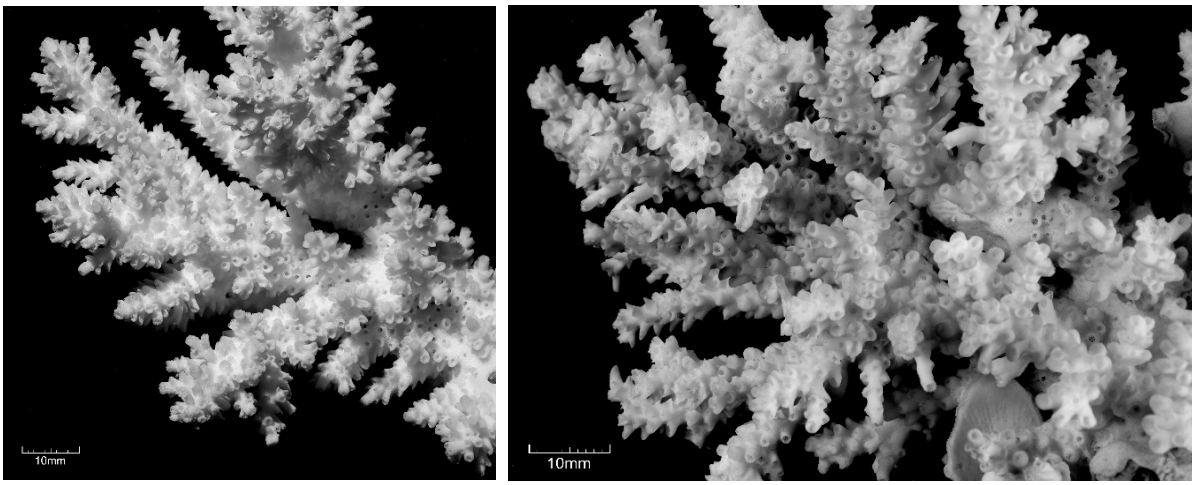


Figure 53. Holotype of *Acropora rongoi* (**left**) and *Acropora striata* syntype USNM 371 (**right**). See text. Photographs: E. Turak, courtesy QMT (**left**), J. Veron, courtesy USNM (**right**).

The delineation of *Acropora rongoi* has thus been based on small sample size, lack of appropriate molecular comparisons and a focus on fine scale morphological differences among types rather than on a broad assessment of morphological and molecular variability.

7.3.6. *Acropora bifaria*, *A. kenti* and *A. africana*

Bridge et al. (2023) [95] also resurrected *Acropora bifaria*, *A. kenti* and *A. africana* from junior synonymy with *A. tenuis* (synonymy according to Veron and Wallace, 1984 [237]) radically altering the distribution range of *A. tenuis* in the process. These authors stated (their p. 18): "*Acropora tenuis* is currently known only from Fiji and Tonga in the South Pacific . . . all other *tenuis*-like specimens from other regions are likely to represent distinct species that require additional taxonomic investigation."

For *A. bifaria* and *A. africana*, along with *A. macrostoma* (a species we have long accepted), no molecular analyses were undertaken, the resurrections relying on comparisons of type specimens. The authors noted (their p. 14):

> "The other three nominal species are . . . resurrected because: (1) they have type localities a long distance from Fiji; and (2) they show morphological differences from the holotype of *A. tenuis* . . . This biogeographical and morphological evidence, combined with the strong geographical variation in numerous other studies of '*A. tenuis*', warrants resurrection of these nominal species. . . . [However] . . . additional sampling, particularly in the Indian Ocean, will be required to confirm their taxonomic boundaries."

Reliance on geographic distance between locations of type specimens as a criterion for designating species when the parent species varies in a gradual and predictable way across intervening regions is not appropriate. Thus, conclusions based on minor morphological differences among one or several type specimens, without additional consideration of the range of variation both locally and regionally, are not adequately compelling.

Further, in the presentation of "maximum likelihood" results (their Figure 2) A. *tenuis* is linked with *A.* aff. *striata*, *A. echinata* and *A. kenti*, thence, more remotely, between *Acropora* aff. *echinata*, *A.* sp(p.) and *A. yongei*. The apparent disagreement among different molecular studies of the grouping of *A. tenuis*, *Acropora echinata* and *A. yongei* requires consideration. These were placed in the same clade by Bridge et al. (2023) [95], based on the prior analysis of Cowman et al. (2020) [397], (see 'DNA methodology'). This was not supported by Quek et al. (2023) [398] who instead placed *A. tenuis* in the same clade (Acroporidae I) as a different group of species including *A. austera*, and placed *A. echinata* and *A. longicyathus* as sister taxa in clade VI (their Figure 1). These authors also emphasised the direct experimental, molecular or genetic evidence for hybridisation, polyploidy and gene duplication events, which may interact with other processes to confound interpretations of evolutionary history. These are all relevant points, for, obviously, the apparent cladistic relationships among these various well-defined species are also not supported by morphology (Figure 54).



Figure 54. *Acropora echinata* in the Philippines (**left**), *A. yongei* on the Great Barrier Reef (**centre**) and *A. tenuis* on the Great Barrier Reef (**right**), see text. Photographs: J Veron (**left** and **right**), E. Lovell (**centre**).

Clearly there are many conflicting lines of evidence here which argue that conclusions are premature and await further, more comprehensive, studies. For these multiple reasons, at present we consider the various cladistic designations and other nomenclatural decisions, insufficiently supported and retain *Acropora kenti*, *A. bifaria* and *A. africana* as possibly valid species/probable synonyms of *A. tenuis*, pending further confirmation.

7.3.7. *Acropora hyacinthus* Complex

A similar set of circumstances surrounds the more recent reassessment of the *Acropora hyacinthus* species complex by Rassmussen et al. (2025) [81]. From 139 samples collected

from various Indo-Pacific locations, 16 molecular lineages were considered to represent distinct species. This led the authors to resurrect nine nominal species and describe five new species, two of the latter apparently based on two and three molecular samples and morphological comparisons with type material.

We have long considered *Acropora hyacinthus* a species complex [6,10], warranting comprehensive study. This work adds to our knowledge of the taxon/taxa involved and provides valuable additional data. However, as with previous cases, we have significant reservations about some of the newly published decisions, given extensive evidence for morphological plasticity and complex reticulate patterns of gene flow among *Acropora*, and the identification of 'grey zones' of speciation among other coral taxa (see *Stylophora* case study above). Rassmussen et al. [81] reported evidence of hybridisation between species across their clades, with interspecific admixture among multiple lineages. They suggested this could reflect uneven sampling or introgression from a recent hybridising ancestor. These authors also noted that "further phylogenomic analysis specifically investigating hybridisation, combined with other evidence such as breeding trials, are required to better understand the prevalence and also pre and post-zygotic barriers to hybridisation in synchronous broadcast-spawning *Acropora*". Despite these important caveats, they proceeded to make major taxonomic and nomenclatural changes, as discussed below.

Firstly, we agree with the renaming of *Acropora pectinatus* Veron, 2000 (via *Acropora pectinata*, see [399]) to *Acropora floresensis*, as this resolves the earlier nomenclatural issue with the nominal species *Acropora pectinata* Brook, 1893.

Acropora bifurcata is a species long recognised [6,10]. Ongoing field studies since 2016 have confirmed that *Acropora surculosa* is distinct from *A. hyacinthus* and is thus considered a valid species in CoralsOfTheWorld.org (2026 in prep.) [236]. This position has recently received molecular support [400].

Regarding the new species, *Acropora harriottae* was separated molecularly from *A. hyacinthus* in a high latitude, marginal environment in Eastern Australia, as was *Acropora tersa* from *A. hyacinthus*, occurring sympatrically across the Great Barrier Reef and a broader region of the Indo-west Pacific. Although there is apparent wide molecular separation of both nominal species from *A. hyacinthus*, samples of *Acropora tersa* clustered closest to those identified as *A. spicifera*, while those of *Acropora harriottae* clustered with a broader group of 'species' (their Figure 3), in both cases requiring further resolution.

Acropora kalindae was described based on three samples from the central Great Barrier Reef, apparently absent molecular comparison with its likely senior synonym *A. anthocercis* (Brook, 1893), the lectotype of which is also from the central GBR. Morphological differences between type specimens were apparently considered sufficient evidence, without due consideration of inherent morphological variability (see Section 5.1). Further assessment that includes a thorough analysis of *Acropora anthocercis* is required. Indeed, given that two nominal species are both from the same region, we question why *A. anthocercis* was not sampled. With only three samples and without thorough comparisons to key species, support for a new species is unconvincing. The three *A. kalindae* sequences may instead correspond to *A. anthocercis*.

We have similar reservations surrounding designation of *Acropora uogi* (from two molecular samples) and reinstatement of *Acropora turbinata*, considered a form of *A. surculosa* by Dana (1846) [286] in his original descriptions. No sequencing of *A. surculosa* for molecular study was undertaken, with two type specimens the only material examined.

Rassmussen et al. (2025) [81] provide the following description of the *A. uogi* holotype (their p. 23): "Radial corallites: labellate **with round openings**" and paratypes (also their p. 23): "Variations shown in paratypes G84925 and G79945: both paratypes

share similar features; radial corallites labellate **with flaring lips**, radial corallites at almost 90° angle to the final branch; . . .” [Our bolding]. However, in their later Remarks on *Acropora uogi* (their p. 24) these authors conclude: “. . . the radial corallites of *A. uogi* are larger and labellate with a round opening, whereas those of *A. surculosa* are labellate **with flaring lips**.”

There is clear conflict (and conflation) in these descriptions, which depict the shape of the radial corallites of *A. uogi* as being both different from *A. surculosa* in the *A. uogi* holotype, and the same as *A. surculosa* in the *A. uogi* paratypes.

Such minor differences between radial corallites of specimens of the same species are not uncommon. This demonstrates both the inherent minor variability exhibited by most corals, and by extension, the likely issues that can occur between type specimens of synonyms (Section 5.1.1). Thus the two molecular sequences attributed to *A. uogi* could, in our view, be better assigned to *A. surculosa*, pending additional work across its range. Indeed, in their remarks on *Acropora surculosa*, Rassmussen et al. (2025, p. 30) [81] noted the necessity of collection and sequencing (of a topotype) for *A. surculosa* to resolve the status of both *A. turbinata* and *A. surculosa*.

For comparison, Torrado et al. (2025) [400] had previously analysed molecular samples of *Acropora surculosa sensu* Randall and Myers (1983) [401] in Guam. Rassmussen et al. (2025) [81] consider this nominal species to be their new *Acropora uogi*, of which two samples from Pohnpei were sequenced. Unfortunately, the latter authors did not discuss or compare their molecular results with the previous work by Torrado et al. (2025) [400]. It seems likely that these studies represent genetic variations in what may be a single entity, *Acropora surculosa* –more comprehensive sampling is required.

The molecular lineage attributed to 17 samples of *Acropora nyinggulu* has a very broad geographic distribution, from the northern Ryukyu Islands through the Coral Triangle south to the Houtman Abrolhos Islands of Western Australia. In their analysis, it appears genetically distinct from the four samples identified as *A. spicifera*; much less so from the four identified as *A.* cf. *tanegashimensis* (their Figure 3). The paucity of samples of the latter two species, and the apparent lack of regular co-occurrence, indicate that further work is required, particularly considering that prior taxonomists had studied this species (identified as *A. spicifera*) from its type location at Ningaloo Reef, and elsewhere [6,285]. From their molecular comparisons, Rassmussen et al. (2025) [81] claim that the earlier work conflated the two species. However, the evidence presented in this case, and several others, including the apparent molecular relationships and lack of clear morphological separations, among the various nominal species, raised additional questions, and is far from definitive.

A related issue surrounds the type material of *Acropora spicifera*, a point acknowledged by Rassmussen et al. (2025) [81]. The lectotype colony (USNM 244) is not illustrated by Dana (1846, plate 33, Figures 4a,b and 5, plate 31, Figure 6). The main illustrated specimen (his Figure 4) from Fiji, is housed in the Peabody Museum (Registration number IZ002007.CN). It is the one on which Dana’s original description was largely based ([286] p. 442), although Dana highlighted morphological variability of his Fiji and Singapore specimens (the latter listed as fragments). The differences among these syntypes, and the new comparisons by Rassmussen et al. (2025) [81], (reliant on the Singapore lectotype), provide another example of the type issues raised above (Section 5.1).

Furthermore, Rassmussen et al. (2025) [81] new distribution range for *A. spicifera* (their Supplementary Figure S10) restricts this species to the central western Indo-Pacific, despite the fact that Dana’s main illustrated type (IZ002007.CN) was from Fiji, and that numerous records well to the east in the central Pacific have come from many different

researchers. The considerable uncertainty that remains surrounding these various issues requires resolution.

Further on distribution ranges, Rassmussen et al. (2025) [81] also noted that their sampling across the Indian Ocean (Christmas Island, the Cocos Keeling Islands, Seychelles and Red Sea) failed to find specimens from the *A. hyacinthus* complex, in part leading to their major restriction of the distribution range of *Acropora hyacinthus* to the southwest Pacific. However, table corals, including *Acropora hyacinthus*, are very widespread across the central and Western Indian Ocean, as reported by numerous authors (Supplementary Table S2). We find the apparent dismissal of all prior work, much of it undertaken by dedicated workers who had spent years to decades in the region, to be premature. Clearly far more comprehensive studies are required before, as these authors claimed in their provocative title, 'The tables are turned'.

Indeed, this work, the prior paper (Bridge et al., 2023 [95]) on *Acropora tenuis* by several of the same authors, and that on *Leptastrea* (Arrigoni et al., 2020 [300]), are emblematic of significant recurring issues. These include undue focus on comparisons of minor differences and similarities among type specimens absent a thorough understanding of variability in nature, leading to unwarranted or premature splitting or synonymy and significant taxonomic destabilisation. These also include assignment of molecular sequences to newly described (or resurrected) species when they may well be those of 'unsequenced' senior synonyms (also see Section 8.2).

As discussed throughout this review, reticulate theory predicts, and direct evidence from studies support, detectable lineage divergence based on environmental factors, habitat type, depth and spatial separation, while also highlighting the prevalence of hybridisation allowing frequent recombinations to occur. We re-stress that species delineations based on single or small numbers of types and samples, which do not include key species, or which are based on studies which do not adequately control for the known variations across habitats, depth and geographic space, are premature. These should await (a) a more complete understanding of the genetic variability of populations, sister species, and hybrids across all of these different environmental conditions; (b) some consensus, following such foundational studies, of the degree of genetic variability required for separate species designation; and (c) a clear understanding of the connection between the genetic lineages and biological field entities.

We recognise and acknowledge that some conclusions from recent studies may ultimately prove to be valid. However, our principal contention is that, at present, most such conclusions are premature and require substantially more supporting evidence derived from well-designed foundational studies of morphological and genetic variability. The *Stylophora* case study illustrates the many complexities involved.

7.4. Generic Solutions

The above considerations notwithstanding, a number of species have long been considered 'misfits' in their respective genera, several of which have been the subject of recent molecular analyses that have also highlighted anomalies. As foreshadowed above, new generic placements are being finalised for formal taxonomic submission (see [350]). The following is hence a brief introduction, highlighting, again, that genera should be both morphologically and genetically distinct [371].

7.4.1. *Acanthastrea ishigakiensis* and *Symphyllia erythraea*

Acanthastrea ishigakiensis (Figure 55) groups with *Symphyllia* species (all lumped as *Lobophyllia* according to the molecular findings of Huang et al., 2016 [345]). *Acanthastrea ishigakiensis* has cerioid corallites < 15 mm diameter, typically covered with thick fleshy

Acanthastrea- like tissue, whilst *Lobophyllia* are phaceloid and *Symphyllia* are meandroid with a thin tissue layer (Figure 55). In this case, the similarities between *A. ishigakiensis* and *Symphyllia erythraea* and their multiple differences with all three abovementioned genera, requires creation of a separate genus (see [350]).

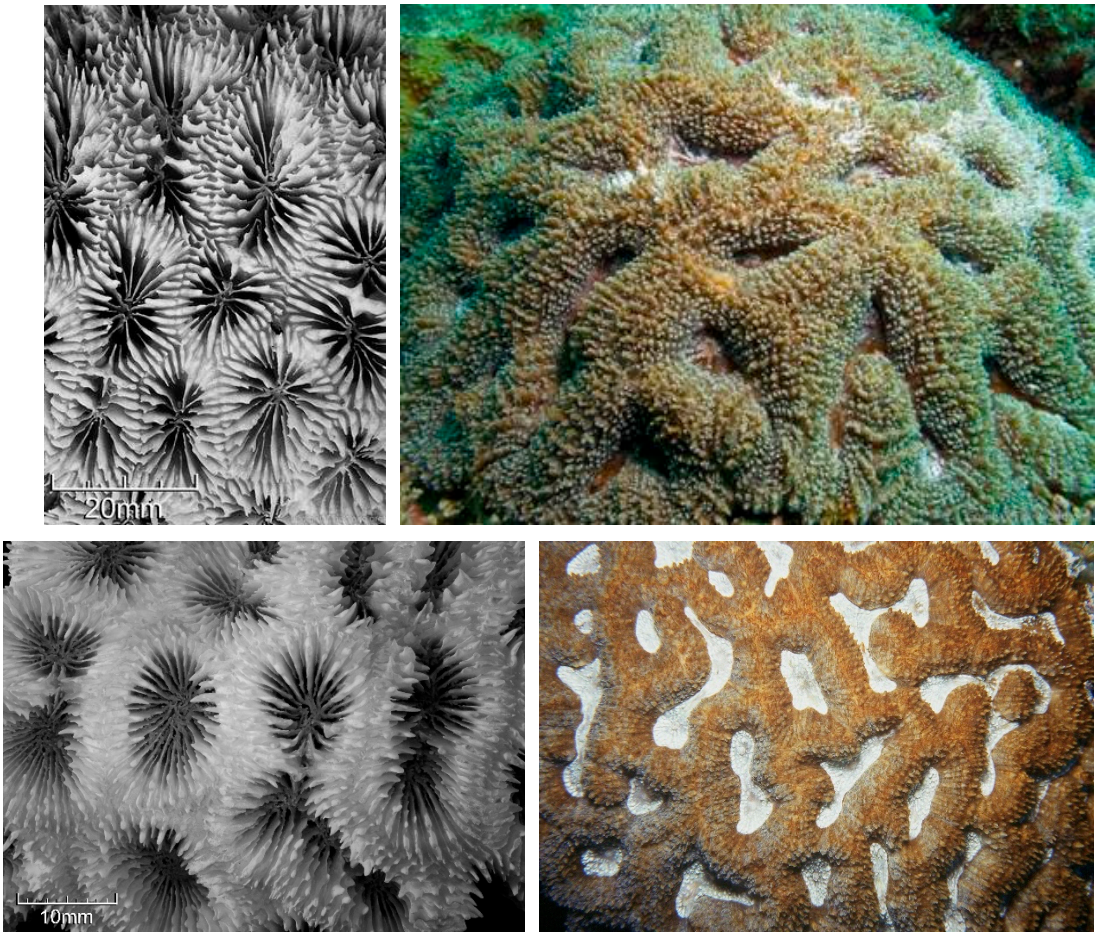


Figure 55. *Acanthastrea ishigakiensis* corallum (**top left**, from the Cook Islands) and in situ (**top right**, in Brunei) and *Symphyllia erythraea* (**lower left** and **right** from the Red Sea). The characters of these distinctive species warrant a new genus, see text. Photographs: J. Veron (**top** and **bottom left**), E. Turak (**top** and **bottom right**).

7.4.2. *Favia leptophylla*

Favia leptophylla Verrill, 1868 was transferred to genus *Mussismilia* by Nunes et al. (2008) [402] followed by Budd et al. (2012) [374]. The major morphological differences between this species and *Mussismillia* (Figure 56), and its apparent molecular differentiation from *Favia fragum* indicate that this may require the creation of a new genus (see [350]).

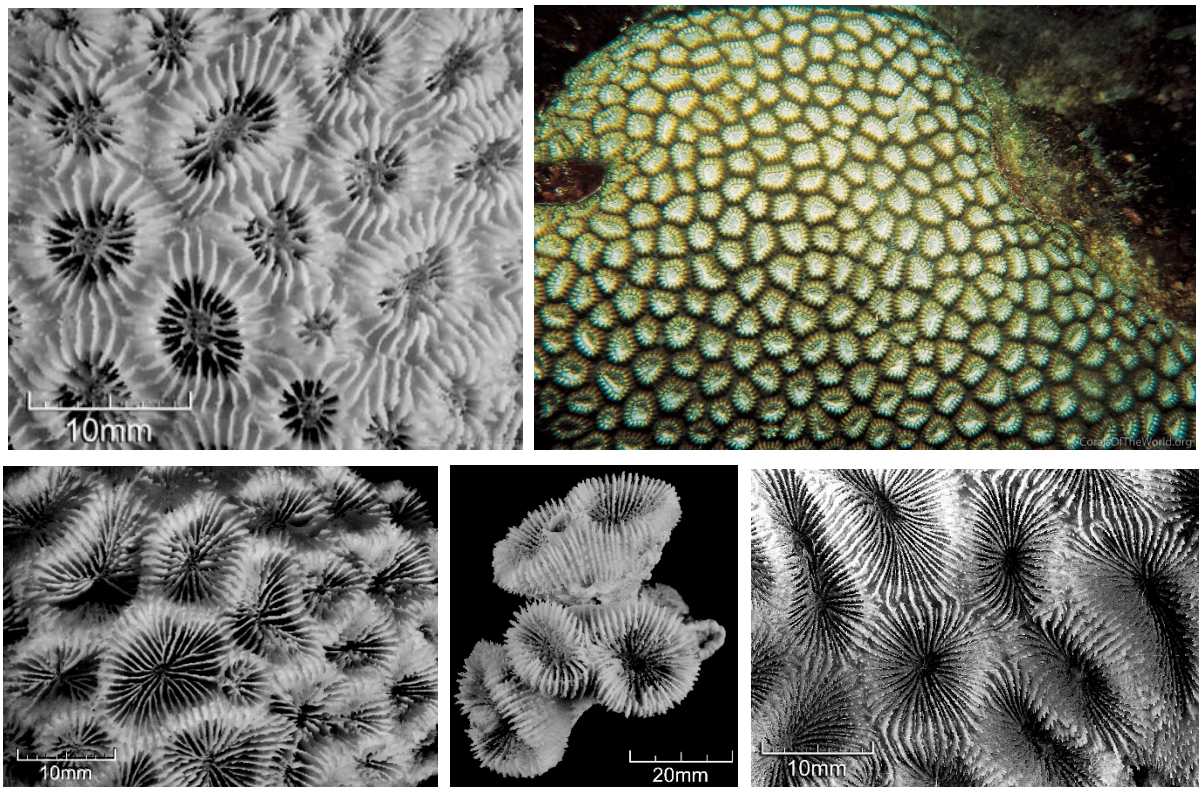


Figure 56. *Favia* (=*Mussismilia*) *leptophylla* skeleton and colony (**top row**) and the three species of *Mussismilia* (*M. braziliensis*, *M. harttii* and *M. hispida*) (**bottom row**), all from Brazil. The three *Mussismilia* species have similar corallite detail unlike that of *Favia leptophylla*. Photographs: J. Veron (**top right**), the remainder E. Turak and J. Veron.

7.4.3. *Acanthastrea* (=*Lobophyllia*) *pachysepta*

Lobophyllia pachysepta was moved to *Acanthastrea* by Huang et al. (2016) [345] (Figure 57) based on one sample from New Caledonia, and despite molecular-morphological incongruence with *Acanthastrea* was considered a "rogue species" by the authors. This move was followed by Arrigoni et al. (2019) [334] apparently without additional sampling. Given its clear morphological differences from all *Acanthastrea*, its suggested molecular separation from other *Lobophyllia*, requires further study. It may warrant creation of a new genus (see [350]).



Figure 57. *Lobophyllia pachysepta* (**left**, in Micronesia) has corallites that are phaceloid or partly flabello-meandroid, and *Acanthastrea echinata* (**right**, in Brunei) are cerioid, rarely sub-plocoid. These species do not belong in the same genus. Photographs: P. Colin (**left**) and L. DeVantier (**right**).

7.4.4. *Micromussa* (=*Phymastrea*, =*Montastrea*) *multipunctata*

Another well-defined species that has resisted stable generic placement is *Montastrea multipunctata* Hodgson, 1985 (Figure 58), described initially from the Philippines [403]. This species was moved to *Phymastrea* by Budd et al. (2012) [374], subsequently supported by Arrigoni et al. (2014) [364]. It was then moved to *Micromussa* by Arrigoni et al. (2016) [301] based on molecular analysis of three samples from Malaysia and one from the Philippines (their Supplementary Table S1). According to the Bayesian topology of the latter authors, *Micromussa amakusensis* (or *M. indiana*, see Figures 51 and 58) and *M. multipunctata* are sister species. As all these generic placings are highly questionable, creation of a new genus is warranted for this species (see [350]).

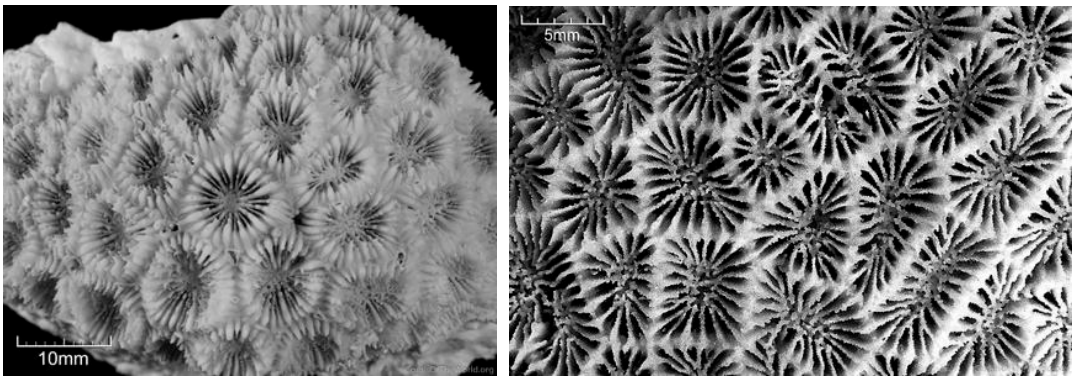


Figure 58. *Montastrea* (=*Phymastrea*, = *Micromussa*) *multipunctata* from the Philippines (**left**) and *Micromussa amakusensis* from Japan (**right**, as above). These species do not belong in the same genus. Photographs: J. Veron.

7.4.5. *Goniastrea* (=*Dipsastraea*, = *Favia*, =*Orbicella* (*Astrea*)) *stelligera*

As with others above, this well-defined species has a complex taxonomy. Originally described as an *Orbicella* (*Astraea*) by Dana (1846) [286], it was placed in *Favia* by Veron et al. (1977) [295]. It was then moved to *Dipsastraea* by Budd et al. (2012) [374] and thence to *Goniastrea* by Huang et al. (2014) [344]. The latter move was supported by the molecular data of Huang et al. (2014) [375], with eight samples (4 from Fiji, 1 from Philippines and 3 from Red Sea) grouping this species with *G. retiformis* and *G. minuta.* This surprising result has no morphological congruence (Figure 59). Furthermore, the molecular analyses (their Figure 2) showed a degree of separation from the two *Goniastrea* in both mitochondrial and nuclear trees. Given these multiple generic changes together with more recent disagreements, and the clear morphological differences, creation of a new genus is warranted for this species (see [350]).



Figure 59. '*Goniastrea*' *stelligera* (**left**) and *Goniastrea aspera* (**right**), both in the Great Barrier Reef, do not belong in the same genus, see text. Photographs: J. Veron (**left**) and N. Coleman (**right**).

7.5. Agreements

The foregoing discussion, highlighting the notion 'out with the old, in with the new', which appears like a mantra in most introductions to molecular taxonomic publications, may well suggest that there is little agreement between the two taxonomies, but this is not the case. To emphasise this important point, molecular studies conducted to date also use the species names we recognise [6,10,236], albeit with several species therein shuffled across different genera, as noted above (Supplementary Table S3). We also note that most coral species have yet to receive molecular analysis. We make no assumptions concerning agreements or disagreements about these species except to note that they have all been recognised and used by molecular taxonomy specialists.

8. Why the Discrepancies?

And so, contrary to popular beliefs, there is widespread species recognition between morphological and molecular taxonomy. There is plenty to agree about including most straightforward generic changes, for this is about binomial nomenclature, very much the domain of molecular phylogenies. Also, many authors have specifically endeavoured to combine morphological and molecular results and have highlighted the need to do so (e.g., Benzoni et al., 2010 [404]). A recent case in point is the unambiguous restoration of *Pocillopora favosa* in the Red Sea and Arabian Peninsula by Oury et al. (2025) [405], formerly considered unresolved in CoralsOfTheWorld.org (2016) [10]. This species forms part of the *Pocillopora* syngameon in Arabia, co-occurring with *P. damicornis* and *P. verrucosa* (Figure 60). We retain all three species, consistent with the results of earlier work that showed very low genetic diversity among Arabian pocilloporid species [312,316] (and see *Stylophora* Case Study above), while also noting that phenotypic diversification and reproductive isolation can occur in the near-absence of a phylogenetic signal (as recently demonstrated for reef fishes by Helmkampf et al., 2025 [311]).



Figure 60. Co-occurring *Pocillopora* spp., Gulf of Aden. *Pocillopora verrucosa* (left) and *P. favosa* (right). Photograph: L. DeVantier.

8.1. Author-Related Explanations

Some readers may ponder the reasons why the examples of generic shuffles illustrated above have been published when, seemingly, there are clear conflicts. These include known patterns of species variation, evidence of potential reticulation, habitat specialisations likely to promote lineage sorting without evidence of reproductive incompatibility, and above

all, such stark morphological differences. We surmise that one or more of the following explanations could be applicable:

(1) The author believes that their findings do not need to relate to morphology. However, since most molecular studies broadly support existing species delineations, such conflicts should, at the very least, 'raise a red flag' and require additional confirmation.
(2) The results were derived from a superseded technology, commonly in GenBank [351] data, and would be different using modern methods and/or more comprehensive samples.
(3) The results are not nested in a broader consideration of the molecular composition of the species studied, and the molecular consequences of environmental and biogeographic variations and thus the scope of conclusions were not supported by the sampling design.
(4) Misunderstanding the risks of relying on unreplicated cladistic trees in reticulate systems, leading to unwarranted confidence in phylogenetic conclusions. This issue can be compounded by post hoc examination of specimens in search of morphological distinctions, a process that can introduce or reinforce confirmation bias.
(5) A collecting error.
(6) Omission of one or more key species which skewed the results.
(7) The authors were unaware how their results (such as summarised by a cladogram) would map onto what is seen in nature, and might have modified their conclusions or awaited further confirmation had they understood.
(8) The authors were fully aware of overt conflicts with morphology but considered that their results were nevertheless correct.

We find that each of these explanations appears to be applicable to at least one of the cases presented in 'Discrepancies between molecular and morphological taxonomies' (above), which is not a trivial matter especially as our cited cases are only selected because they are visually obvious. Given the overwhelming prevalence of molecular taxonomy today, this repeatedly calls for close scrutiny, the essential point being, of course, that any sort of taxonomy is only as meaningful, or as accurate, as its depiction of what occurs in nature. And that requires extensive, detailed, fieldwork.

8.2. Underlying Issues

The ways and means of authors say less about underlying issues than the basics of the biology involved.

(1) Inadequate fieldwork, in both sample collecting and seeing the living reality of molecular results, is a common cause of biological incongruence. By analogy, satellite imagery swept to prominence in studies of reef morphology and coral community distribution, initially providing highly erroneous results with mixtures of uniquely useful data (e.g., broad-scale surveys) and misleading, unsupported, claims (e.g., analyses of biodiversity), the latter leading to many premature publications.
(2) We emphasise the importance of an adequate number of samples taken from an appropriate range of locations. Small sample numbers may produce strongly supported but misleading phylogenies due to stochastic effects. Without broad geographic and ecological sampling, results may be misleading if used prematurely to justify species delineation. Pertinent examples which support the need for such broad sampling are provided by detailed studies with much higher replication, for example, *Acropora spathulata* [33] (with geographic distance); *Montastraea cavernosa* [323], *Stylophora pistillata* [100], *Seriatopora hystrix* [322], and *Pachyseris speciosa* [247] (with depth); and the review (not about coral) of Ahrens et al. (2016) [406].
(3) Some authors of what we believe are clearly incongruent results appear to assume that an alternative explanation for their molecular findings *cannot* exist. Considering the range of

molecular complexities continually being revealed in all living organisms, this is a bold assumption. These cases are especially pertinent because the species involved (and we illustrate above) are morphologically readily recognised, suggesting that similar but less recognisable occurrences may be common for similar reasons in other molecular studies.

(4) Species, however defined, are not isolated units to be shuffled repeatedly among genera with every new molecular result. This has created significant unnecessary destabilisation. If there is a perceived case for a generic change, it is pertinent to ensure that (a) the change reflects reality in nature; (b) that alternative views (including those based on other molecular studies) are addressed and if there is disagreement explain why; and (c) potentially related species are included in the study.

(5) The 'splitting versus lumping' debate, as old as taxonomy, has a modern twist where molecular studies have again brought it to the fore, especially where geographically widespread species are split into regional species based on molecular differences, sometimes augmented by observations about type specimens. Clearly, populations of widespread species in different oceans cannot directly interbreed over such distances and molecular differences are therefore to be expected. However, for many species including those referred to in 'Geographic Reticulation' (above), a multitude of intermediate populations exist which potentially facilitate unlimited gene flow between distant regions over timescales of decades to centuries. Species splitting, taken to a logical endpoint, would mean that every coral population on a semi-isolated reef tract is open to being deemed a new species if their molecular signature reflects their isolation. Our alternative view is that many of such nominal species are geographic variants of a widespread parent in grey zones of speciation. A second cause of runaway splitting may occur with polyphyletic species which, as discussed above, potentially includes most species irrespective of their distribution. Again, taken to a logical endpoint, such splitting could be a source of thousands of supposedly 'new species'.

9. Reticulate Patterns

If reticulate patterns are seen in coral evolution, morphology and distributions—and by now it should be clear that there is overwhelming evidence that they are—some very basic questions remain largely unanswered:

(1) Are morphological and molecular variations in lock-step? This is a critical question, both for its own sake but also because it profoundly affects the number and variety of samples required for molecular studies. Until foundational studies are made, perhaps it is reasonable to assume that a small number of well-authenticated samples are representative of a species at a single location if several samples are taken from each of the more benign environments, but as we have seen, these samples would not be representative of the same entity in mesophotic or exposed reef flat environments.

(2) Is polyphylogeny the norm or the exception? Again, this is a question on which taxonomic decisions are repeatedly made. Reticulation predicts a dominance of the former, supported by the multitude of studies listed in 'Species for which there is evidence of polyphylogeny' (Box 5 above). However, there must be a spectrum which separates these species (of which *Pocillopora damicornis* is an extreme example according to the frequent referrals to it throughout this article) from those that seem clearly monophyletic such as the monospecific *Diploastrea heliopora*, *Coeloseris mayeri*, *Gardineroseris planulata*, or *Oulastrea crispata*. Knowing where individual species fit on this spectrum is essential for clarifying their taxonomic position.

(3) To what degree are mesophotic corals genetically independent from their shallow-water neighbours? If they are largely independent, can these corals act as lifeboats when their shallow-water neighbours are bleached to extinction?

(4) Is there an objective measure of molecular distinction between entities that form a continuum and those which do not? This question goes to the foundation of what, operationally, we should or should not deem to be a species.
(5) Is there any molecular basis for determining levels of geographic variation in an entity and, if so, can these groupings be given an operational name? This question has particular relevance to conservation decisions.

10. The Need for Foundational Studies

Molecular science is building on the theoretical predictions of reticulate evolution, offering insights into the phylogeny of species and unravelling some of the species complexes that have been highlighted by us and other taxonomists. But, as we have seen, molecular studies have not yet fully addressed species variability—indeed, the relationship of variability to species delineation remains in its infancy.

Despite advances over the past decade, the most significant problem we face to date is the lack of comprehensive foundational molecular studies to provide context for interpretation of both our existing understanding and the burgeoning flow of new data. Whatever the quality of the molecular methods themselves, it is commonplace for claims about results to go far beyond the scope of sampling design and replication.

Consider, for example, the image of morphological variation in *Pocillopora damicornis* in Figure 4 and its implications. In the pre-scuba days of taxonomy, all or most of these variants would be considered different species. The diagram is a reminder of the variability of corals down a reef slope, across habitats and, by extension, between neighbouring locations and across geographic space. Yet these basic questions remain largely unstudied, reviewed for *Pocillopora* by Johnston et al. (2022) [407].

Do all such variations have individual molecular signatures? If so, where do they lie on the speciation spectrum supposing they should be on the spectrum at all? As we have seen, substantial molecular variability has been established with different habitat types and environmental drivers (e.g., refs. [100,245,247,320–326]).

However, before any genetic lineages should be defined as cryptic 'species' as is commonly proposed (rather than cryptic lineages or variants), it is incumbent on the proponent to understand the full molecular variation in the species. This cannot be done with a few replicates from a small number of habitats. Only a few of the most recent papers have sampled widely enough with sufficient replication to begin to answer these questions.

Instead, we have 'new species' based on comparisons of one to a few molecular samples from one area with one to a few molecular samples from another without any knowledge of the full molecular variability of that species across habitats within a single region. The molecular and morphological differences are hardly a surprise—they are seen across a wide range of species which are predicted in a variable reticulate world.

11. The Future

We endorse a change to the notion '*out with the old and in with the new*' to '*in with the old combined with the new*' as some authors have suggested, for that would capture both taxonomies. But how much better it would be if we could make a further change to '*. . .in with the old combined with the new and the dynamic processes of reticulate evolution*' for that would integrate morphology, molecular data, environmental and geographic data, reproductive biology and population dynamics. We submit that this change, albeit imaginatively summarised here, is the gateway to the future.

The tools available to investigate the morphological and genetic aspects of coral taxonomy, at local, regional and metapopulation levels, continue to develop rapidly. These will increasingly inform understanding but must always be founded in the reality of the reef—

the many complexities arising from the interactions of habitat, geography, oceanography, reticulation and selection.

However labelled, there are no alternatives if our goal is effective conservation. In such a scenario, coral taxonomy would retain its role as a universal signpost that links together all reef studies, surely needed as never before in a world where coral reefs far outweigh all other marine ecosystems in supporting marine biodiversity—not just the diversity of the corals that build reefs, but that of all the life reefs protect at some stage in their life cycle. That is the keystone role that reefs have, and it must be taken seriously for not much is standing between functionally diverse reefs and those destroyed by mass bleaching. Scientists and conservationists alike must make the best use of what they have and that means keeping the signpost that links reef sciences up to the task, a far cry from what coral taxonomy used to be.

More than any other major group of marine invertebrates, the taxonomy of reef corals has had a long and tortuous history and seems certain to have a long and interesting future. But whatever that future turns out to be, it must stem from what occurs in nature and that requires fieldworkers with extensive experience working in different environments and in different countries. That is no small ask, for it demands that taxonomists must work in the enormous range of reef environments a few of which we illustrate below (Figures 61–73).



Figure 61. Reef flat community, Great Barrier Reef. These shallow-water communities were the main source of specimens collected during historic expeditions of discovery and thus became the specimens most taxonomists of the time worked with. This has had unfortunate consequences for coral taxonomy because the characters that distinguish similar species are poorly developed at such sites. Photograph: Ed Lovell.



Figure 62. A shallow semi-protected *Acropora* community, Great Barrier Reef. In contrast to reef flat habitats, these are usually good places to study differences between similar species. Photograph: J. Veron.

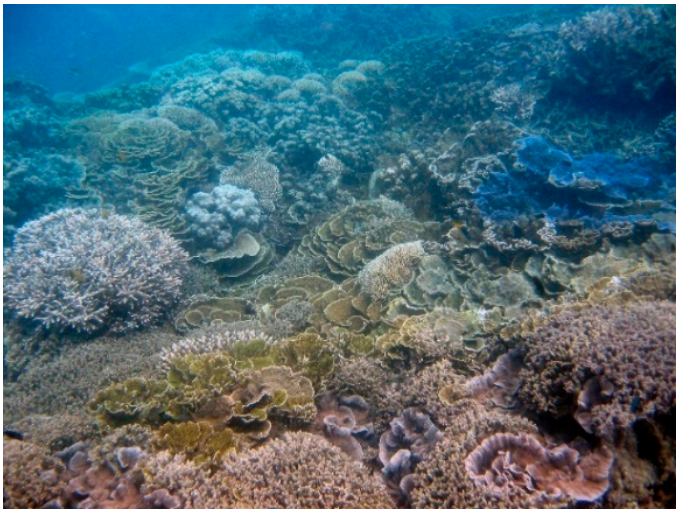


Figure 63. A normally turbid water community, Princess Charlotte Bay, Great Barrier Reef. Most species in these habitats have their distinctive characters well developed making them valuable places for detailed study. Photograph: K. Fabricius.

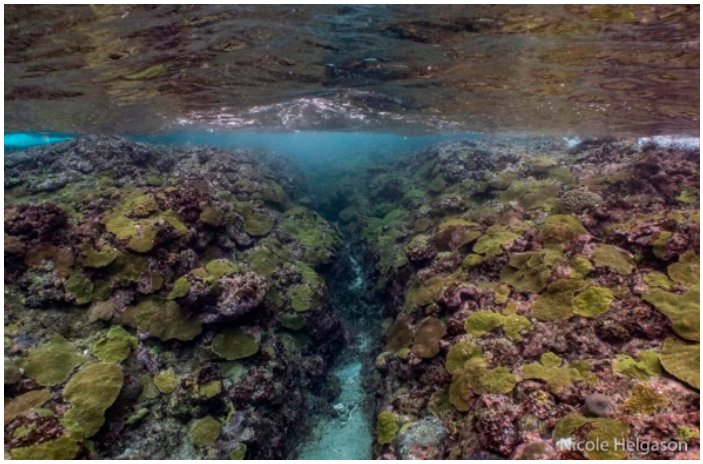


Figure 64. A shallow, very exposed reef front community, Indonesia. Differences between similar species in these environments are least developed. For example, *Isopora palifera*, *I. cuneata* and *I. crateriformis* are difficult to separate in such habitats but they are good sites to find fundamental differences. Photograph: N. Helgason.



Figure 65. Most mesophotic communities commonly occur at depths which are challenging for scuba divers. For this reason, mesophotic corals are relatively poorly studied. Tahiti. Photograph: A. Rosenfeld.



Figure 66. Corals growing in extreme environments are usually particularly difficult to identify. These corals occur on a reef flat of the Kimberley Coast, Western Australia where the tidal range sometimes exceeds 10 m leaving them exposed to full tropical sun for up to 3 h [408]. Photograph: J. Veron.



Figure 67. Reef slope community, Chumbe Island, Tanzania, showing a diversity of growth forms. These communities are attractive to taxonomists because they are not dominated by *Acropora*, allowing the characters of other taxa to become fully expressed in large colonies. Photograph: J. Veron.



Figure 68. A staghorn *Acropora* community, Ryukyu Islands, Japan. Differences between four finely branched species were readily determined here, where they occur together, but could never be derived just from study of museum specimens. Photograph: J. Veron.

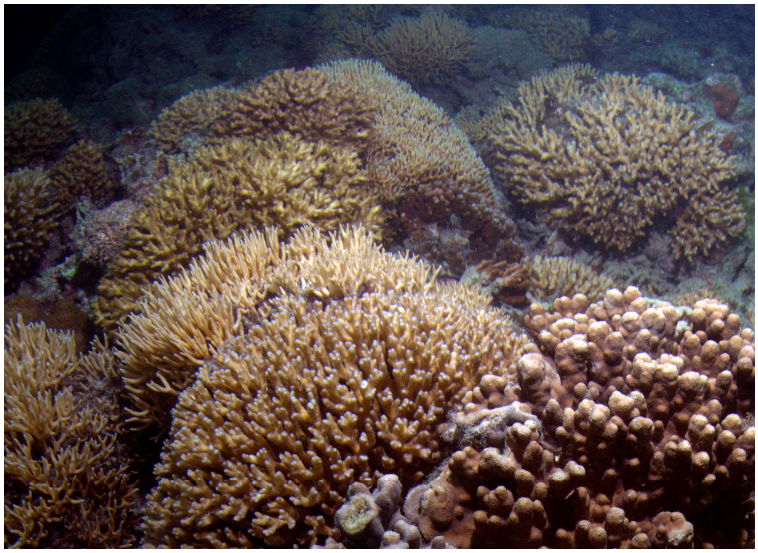


Figure 69. Large mound -like colonies of *Pocillopora damicornis* and *Stylophora pistillata* (excluding a colony of *Porites heronensis*, front right) together with a continuous mixture of these species at Comet's Hole, Lord Howe Island. Extreme (mounding) growth forms of *Seriatopora caliendrum* can also be seen. It is unlikely but possible that these colonies are chimaeras as seen in *Pocillopora damicornis* from the Red Sea [201]. Photograph: Reef Life Survey.

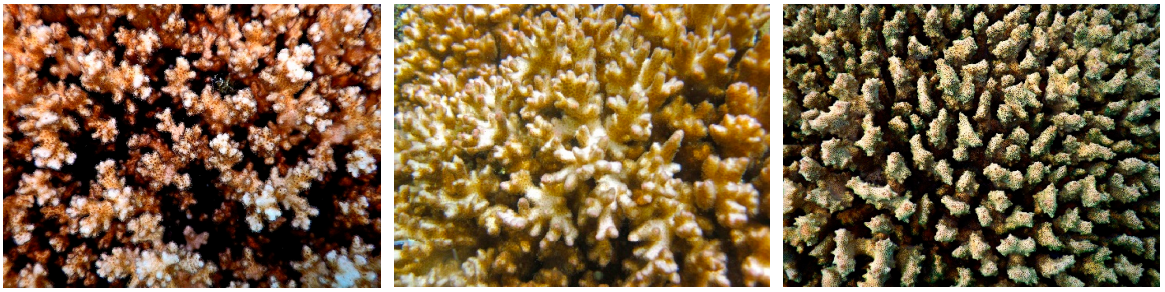


Figure 70. 'Normal' *Pocillopora damicornis* (**left)**, a common regional variant (**centre**)**,** and what could be an extreme variant (**right**), all in the far eastern Pacific. The nominal species '*Pocillopora inflata*' Glynn, 1999 is also part of this complex. Photographs: M. Olán González (**left** and **right**); D. Paz-Garcia (**centre**).



Figure 71. Branching *Montipora* community, Ryukyu Islands, Japan, where eight species occur in close proximity. Such communities are invaluable as they allow differences between taxonomically similar species to be studied in detail. Photograph: J. Veron.



Figure 72. Mushroom coral community, Indonesia. There are usually many species in these communities making them particularly valuable places to study differences between species. Photograph: R. Steene.

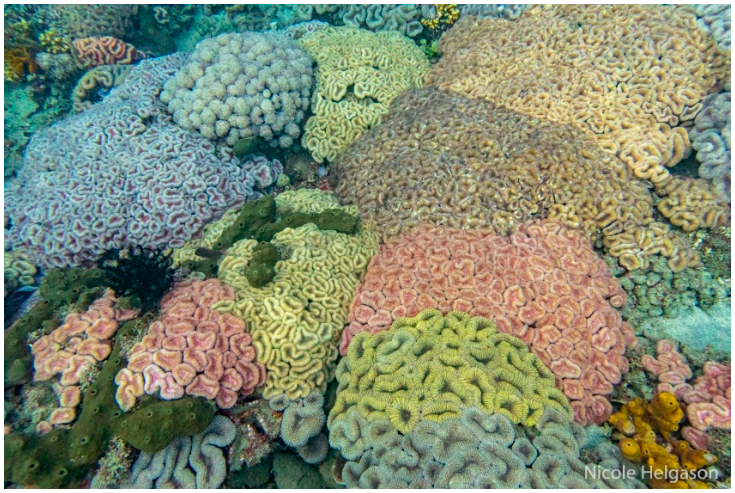


Figure 73. *Lobophyllia hemprichii* exhibiting a bewildering array of corallite variation. Sulawesi, Indonesia. Photograph: N. Helgason.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17120823/s1, Figure S1: Plate I, Illustrations of a range of colony morphologies exhibited by *Acropora florida*. (A) Philippines; (B,D) Palau; (C) Solomon Islands; (E,G) Bali; (F,H) Brunei. Photographs: E. Turak, (F) L. DeVantier. Despite the broad range in colony forms, corallites are characteristic of *A. florida*. Plate II, Illustrations of a range of stout upward branching colony morphologies exhibited by *Acropora florida*. These colony forms often, although not exclusively, occur on shallow reef slopes. (A,B) Philippines; (C) Palau; (D) Coral Sea; (E) Indonesia; (F,G) Solomon Islands. Photographs: E. Turak. Plate III, Illustrations of a range of flattened branching colony morphologies exhibited by *Acropora florida*. (A,F) Philippines; (B–E,G–I) Brunei. The flattened forms often, although not exclusively, occur in biotopes of low illumination, as for example with increasing depth, turbidity or chlorophyll. Photographs: E. Turak. Plate IV, Illustrations of colony morphologies exhibited by putative *Acropora florida* hybrids. (A,B) Brunei; (C) Coral Sea. Corallite form appears intermediate between *A. florida* and (A) *A. plumosa*, (B) *A. samoensis*, and (C) *A. intermedia*. Photographs: (A) L. DeVantier; (B,C) E. Turak. Figure S2: *Micromussa amakusensis* specimens from widespread locations across its Indo-west Pacific distribution range, illustrating the wide variety in corallite form. Some of the illustrated variation is also found within individual colonies. Despite skeletal variability, living corals are readily identifiable. The holotype and paratype of *Micromussa*

indiana and holotype of *Micromussa amakusensis* are included. Photographs: *M. indiana* holotype courtesy MNHN, *M. indiana* paratype modified from Arrigoni et al. (2016) [301]. *M. amakusensis* holotype J. Veron; Brunei image E. Turak; all other photographs E. Turak, courtesy QMT. Scale bar 10mm. For additional illustrations, see CoralsOfTheWorld.org (2016, 2026 in prep.) [10,236]. Table S1: Species which are readily separated where they co-occur but may not be otherwise; Table S2: Records of *Acropora hyacinthus* from the Western and central Indian Ocean. Table S3: Species in CoralsOfTheWorld.org (2016, 2026 in prep.). which are also used, albeit several with different generic names, in molecular studies. Names of each genus are given at first occurrence.

Author Contributions: J.E.N.V.: Conceptualisation, writing—original draft, review and editing, resources and design. M.G.S.-S.: Conceptualisation, writing—review and editing, resources and design. L.M.D.: Writing—review and editing, resources and design. E.T.: Review and editing, resources and design. All authors have read and agreed to the published version of the manuscript.

Funding: This review is part of a major production about the reef-building corals of the world (CoralsOfTheWorld.org (2026 in prep.) [236]), funded by the Australian Institute of Marine Science, Townsville, with additional support from Gaia Resources, Perth.

Data Availability Statement: All data and commentaries referred to in this review are either integrated or interpreted by us from the cited papers, or appear as discussions of the relevant species in CoralsOfTheWorld.org (2026 in prep.) [236].

Acknowledgments: This work synthesises, collectively for the authors, more than 20,000 h of scuba-based study of corals on most reef regions of the world. In this work, we have been aided by far too many people to list here (but see CoralsOfTheWorld.org [10,236]). To all, we express our heartfelt gratitude. We have also been very privileged to have received many thousands of photographs of corals sent to us by hundreds of people around the world. Those included in this article are all individually acknowledged. Clearly, these photos are an essential component of this review, so we give heartfelt thanks to all the photographers concerned. This has been a difficult article to structure and write, especially because so many publications have had to be compressed into single sentences and whole subjects into single paragraphs—all to be as accurate as the current state of our rapidly developing science permits, and to make sense, in context, for a wide range of readers. In both these respects we especially thank the anonymous Diversity reviewers who took the time to critically comment on this submission. We also thank Madeleine van Oppen, Katharina Fabricius, Zoe Meziere, Richard Pearson, Iva Popovic, Cynthia Riginos, Mark Stafford Smith and Rob van Woesik for their time and effort to help with this, in earlier iterations. We acknowledge that areas of uncertainty and disagreement will continue to arise among the many scientists working on this complex, multi-faceted topic. We hope that this work provides a well-supported foundation upon which such uncertainties can be contextualised and assessed. This review is part of a major production about the reef-building corals of the world (CoralsOfTheWorld.org, 2026 [236]), funded by the Australian Institute of Marine Science, Townsville, with additional support from Gaia Resources, Perth. We also acknowledge the 7700+ registered users and many thousands more unregistered users from 147 countries who rely on CoralsOfTheWorld.org for identification and taxonomic assistance. Our aim with this contribution is to provide clarity to users on many pertinent taxonomic issues and apparent conflicts.

Conflicts of Interest: The authors declare no conflicts of interest.

Glossary

Terms used in this article may have different meanings in other publications. To avoid confusion, the terms we use have the meaning indicated here:

Admixture	A process where individuals from two or more previously isolated populations interbreed. The previously isolated populations are ancestral or parental and the newly formed population admixed (also see hybridisation).
Algorithm	A process or set of rules to be followed in calculations or other problem-solving operations, especially by a computer.

Amphitropical distribution	The same biological entity has disjunct populations, one in the tropical northern hemisphere and another in the tropical southern hemisphere.
Assisted evolution	Human mediated interventions designed to accelerate the adaptation of organisms to environmental stressors with the aim of enhancing resilience and persistence. Principal mechanisms include: *induced acclimatisation*, such as environmental preconditioning or modulation of epigenetic mechanisms; *selective breeding*, including intraspecific and interspecific hybridisation for stress-tolerant traits; *holobiont community manipulation*, changes to host-associated microbial or symbiont communities, through shuffling, switching, or inoculation with naturally tolerant strains; *genetic modifications* of either host or symbiont genomes to enhance tolerance or performance under stress.
Assortative mating	A form of non-random mating in which individuals select mates based on certain similar (positive assortative mating) or dissimilar (negative assortative mating) traits. It can have significant consequences for genetic divergence and speciation (positive assortative mating) or mixing (negative assortative mating).
Autotomy	(in corals) a means of asexual reproduction due to break-up of a parent corallite. Seen commonly in *Diaseris*.
Backcrossing	Cross of a hybrid with one of its parent species.
Bayesian inference	A method of statistical inference used to update information as new data become available, specifically by providing more readily interpretable confidence intervals.
Biogeographic boundaries	Distribution boundaries of species.
Biological entity	A discrete 'species-level' taxonomic unit (whether named or unnamed, formally described or not) which has an identifiable suite of variability in the field and is recognised across different environmental and spatial scales. Depending on the degree of confidence, a biological entity may be considered a 'valid entity', a 'probably valid entity' or 'possibly valid entity'. In CoralsOfTheWorld.org, observations made in the field have, as far as possible, been combined with genetic, reproductive and physiological studies to develop a taxonomic framework of biological entities integrating all of these sources. Where these can be associated with existing descriptions and names these become 'valid species'. The boundaries of biological entities may become modified where new information from molecular studies, reproduction and physiology make sense with what is observed in the natural world.
Biological Species Concept	A concept of a species defined as a group of individuals living in one or more populations that can potentially interbreed to produce fertile offspring and which are reproductively isolated from other such groups.
Cenozoic	The Earth's current geological era representing 66 million years of Earth's history.
Chimaeras	Genetically mixed taxa formed by the fusion of spat from two or more parent colonies.
Cladistics	A numerical classification procedure that attempts to reconstruct the evolutionary history of taxa by focusing on shared derived characters (synapomorphies) deduced to have originated from a recent common ancestor. The process groups taxa into 'clades' which are monophyletic groups that include the recent ancestor and all its descendants. While cladistics is a useful tool, it has limitations in reticulate evolutionary systems such as corals where there is significant hybridisation and gene flow across taxa and results must be interpreted with caution.
Cladogram	A diagram (also known as a 'gene tree') showing the cladistic relationship among species that are assumed to have evolved from a common ancestor.
Complex species	A single species which is not well defined (morphologically and/or genetically) and is presumed to be an amalgam of, as yet, poorly distinguished sister or sibling species (see also **species complex**).
Convergence	An evolutionary process where similar morphological traits or genetic changes evolve independently in species or species groups that are not closely related. Convergence can also occur through hybridisation and genetic exchange which may be more frequent where populations of sympatric species are small or are geographically isolated.
Co-occurrence	The occurrence in the same location (habitat, depth) of two or more species (see also **sympatry**, which has a less confined meaning).
Coral bleaching	The whitening of coral resulting from the expulsion of symbiotic algae (zooxanthellae) from their tissues.

Cross-breeding	Genetic exchange between different species.
Cryptic species	Two or more species that are more-or-less indistinguishable morphologically.
Darwinian evolution	Evolution due, primarily, to natural selection. Darwin's theory predated genetics, hence neo-Darwinian evolution which is inclusive of genetics.
Disjunct distribution	One where two or more related populations are geographically separated.
Dispersion	The process of dispersing; in corals, primarily of larvae or via rafting of colonies on floating objects, transported in ocean currents.
Divergence	An evolutionary process whereby a single species or genetic lineage evolves into two or more separate species or genetic lineages.
Eocene	Of Earth's Cenozoic history, 34–55 million years before present.
Epigenetic	A change to gene expression that does not involve alterations to the DNA sequence itself. Such change can be caused by environmental conditions, may come about through chemical modifications (such as DNA methylation or histone modification) and may be heritable.
Extinction	(a) Of a species or biological entity, when that distinctly identifiable taxon can no longer be found anywhere; (b) in a reticulate system, the loss or discontinuation of all phylogenetic lineages of that taxon. In the latter case it is theoretical concept and is not practical to observe. In the former case, it might be possible to observe the extinction of a recognised species or biological entity but it is possible that certain genetic lineages associated with that taxon would be preserved in sibling species elsewhere.
Gene flow	The movement of genetic information within and between species.
Gene leakage	A gradual transfer of genetic information from one species to another.
Genetic diversity	A measure of genetic variation within a population, species or geographic area. The measure may be defined by number and variety of alleles, heterozygosity, nucleotide diversity, chromosome structure or the effects on phenotypic or ecological consequences. Increasingly, numbers of more and less distinct genetic lineages relating to different habitats and environmental conditions may provide a measure of diversity analogous to species diversity, albeit at a sub-species level.
Geographic reticulation	Geographic variation in the morphological and genetic distance among related species resulting from variation in interspecific gene flow.
Gonochoric species	About three-quarters of all zooxanthellate corals are hermaphroditic; the remainder are gonochoric, having separate male and female colonies, albeit with some fascinating exceptions.
Grey zone of speciation	An intermediate phase in the process of species formation where some signs of divergence are present but separation is incomplete such that populations cannot be readily classified into one or more than one species. The phase is characterised by incomplete lineage sorting, ongoing gene flow, variable reproductive barriers and hybridisation, and morphological uncertainties.
Holotype	A single specimen designated by a taxonomist to represent a new species and on which a species name is based.
Hybrid	A natural or artificial taxon or group of individuals derived by combining two different parent species.
Hybridisation	The natural or artificial genetic mixing of separate species via reproduction to form a new organism combining genetic elements of each parent.
ICZN	International Commission of Zoological Nomenclature.
Introgression	The transfer of genetic material between species following hybridisation by repeated backcrossing to the parent species.
Lectotype	A specimen chosen from the original material used to describe a species, if the author of the name has not designated a type or if the type is inadequate or missing (for corals, most commonly applies to older descriptions where designation of a holotype was not mandatory and a lectotype has subsequently been designated from original specimens). See also neotype.
Mass bleaching	The bleaching of corals on a mass scale.
Mesophotic coral ecosystems	Ecosystems where light limitations affect coral diversity, reproduction and growth. Mesophotic habitats are generally defined as those below 30 m down to >200 m depth. The diversity of coral communities in the mesophotic zone depends heavily on water clarity.
Microstructure	The smallest components of coral skeletal architecture.
Molecular taxonomy	Taxonomy based on the study of genetic relationships within and between groups of organisms.

Monophyletic	A monophyletic group of organisms shares a common recent ancestor and includes all descendants of that common ancestor. See also paraphyletic and polyphyletic.
Morphological taxonomy	Taxonomy based on the study of morphological relationships within and between groups of organisms.
Neo-Darwinian evolution	Darwin's concept of evolution in the light of genetics, unknown in Darwin's time.
Neotype	A new specimen chosen by a taxonomic specialist to represent a species when no original type material is available or when original material is inadequate or missing.
Nomenclature	The process of naming species.
Nomenclatural priority	A principle of the ICZN that where various names apply to the same biological entity, the oldest available name should take priority. Note, however, that the ICZN offers alternatives to maintain taxonomic stability where a more recent name has been used consistently for decades or where there is some uncertainty over the identity, description or specimens of the oldest name. In these circumstances a more recent name can be validated.
Nominal species	A taxon at species level that has been formally described and given a scientific name (whether or not it is later found to be valid, a synonym or unrecognisable).
Operational taxonomic unit (OTU)	A practical classification unit used in taxonomy to distinguish it from other similarly determined taxonomic units. Historically OTUs were morphologically recognisable populations or groups of individuals that were distinct from other such groups but which had not necessarily been formally defined as species. In modern usage, OTUs are more commonly defined by clustering algorithms based on similarities in DNA sequences. In either case OTU's may or may not correspond directly to named species and depend on the criteria for clustering and/or recognition.
Palaeozoic	The first of the three geological eras of the Phanerozoic, 252–538 million years ago.
Panmictic	A panmictic population is one in which individuals are highly connected and where there are limited selection pressures or migration barriers, resulting in little genetic differentiation across the distribution range.
Paraphyletic	A paraphyletic group of organisms shares a common recent ancestor but does not include all descendants of that common ancestor. See also monophyletic and polyphyletic.
Paratype	A specimen of the original type series from which a species has been described other than the designated holotype. See also syntype.
Phylogeny	Representation of evolutionary history and relationships among taxa.
Polyphyletic species	A polyphyletic species is one whose members have mixed evolutionary origins. In a non-reticulate system, polyphyly suggests convergent evolution where certain traits are under selection pressure and are developed independently in two unrelated lineages. In a reticulate system such as for corals, however, it can indicate historical separation followed by more recent genetic exchange. It does not necessarily indicate that such a species has been incorrectly delineated or that separating a polyphyletic species into further components is appropriate. Instead, additional study will almost certainly reveal further lineage mixing and highlight the complex influences of reticulation on speciation and evolutionary history.
Repackaging	In a reticulate system, the convergence and/or mixing of lineages which were formerly parts of other lineages.
Reticulate evolution	Evolution dominated by sequential divergence and convergence of lineages through episodic gene flow.
Reticulate pathways	The evolutionary pathway of a species that is interlinked with that of other species by the interweaving of lineages through time.
Sibling species	Two or more species which have parent species in common. Similar species that are assumed to be the product of relatively recent speciation.
Sister species	Similar species which are presumed to have a common parent species.
Species complex	A group of named species whose identities and/or genetic signatures may be distinct in some localities but less distinct or indistinguishable in others due to reticulate intermixing through time and/or space (see also **complex species**).

Species	Named human constructs used to denote an operational taxonomic unit. The use of species names is regulated by the International Commission of Zoological Nomenclature. Species names can apply to museum specimens, described taxonomic units or biological entities. The term 'species' is used in a general way in this article and on the website. The term 'valid species' on the other hand, is a taxon which the authors believe is a valid biological entity, recognisable in the field, and which has a valid name.
Species diversity	The number of species in a given geographic area.
Subsequent designation	The designation of a type subsequent to the original description. This is most commonly done by a later author. This is an occasional source of error.
Symbiosis	The close association between two organisms where there is substantial mutual benefit as in the association between corals and their zooxanthellae.
Sympatric	Entities that occur within the same or overlapping geographic areas (see also **co-occurrence**, which has a more confined meaning).
Syngameon	The term syngameon is defined in different ways by different authors (see discussion in the main text). When used by us, it refers to two or more distinguishable taxa (normally at species level, but may conceptually be at lineage level) which are known or suspected to exchange genetic material through hybridisation. Gene transfer may be frequent, rare or indirect (i.e., via an intermediate taxon) and hybridisation may be present in some geographic areas and not in others. Syngameons are not defined by their reproductive isolation from other syngameons, rather they are 'recognised' by their hybridisation linkages. The species involved do not need to belong to the same genus although this is likely to be more common.
Synonym	A name given to a taxon (e.g., a species) that is not the currently accepted name for that taxon. Normally the accepted name will be designated by priority (the earliest validly published name) and any subsequent names given to taxa which are found to be the same will become synonyms. In a neo-Darwinian world a junior synonym is conceptualised as being the 'same' as the senior synonym. In a reticulate world, a junior synonym may represent a geographic or genomic variant of the senior synonym—'part of the same' but, in some cases, at least somewhat 'distinguishably different'.
Syntype	Any of two or more specimens listed in an original description of a nominal species when a holotype is not designated.
Taxonomy	The scientific discipline of classifying and naming organisms based on shared characteristics and evolutionary relationships.
Type locality	The place where a type specimen was originally found.
Vicariance	A biogeographic process where a physical barrier (such as a change in ocean currents) geographically separates two populations of a formerly continuous species leading to genetic divergence and speciation over time.
WoRMS	World Register of Marine Species. A nomenclatural website.
Zooxanthellae	Photosynthetic single-celled dinoflagellates that live symbiotically within corals and other marine organisms.
Zooxanthellate species	Species which have zooxanthellae.

References

1. Veron, J.E.N. *Corals in Space and Time*; Cornell University Press: New York, NY, USA, 1995; 321p.
2. ICZN. *International Code of Zoological Nomenclature*, 4th ed.; International Trust for Zoological Nomenclature: London, UK, 1999; 306p.
3. Stebbins, G.L. *Variation and Evolution in Plants*; Columbia University Press: New York, NY, USA, 1950; 643p.
4. Grant, V. *Plant Speciation*, 2nd ed.; Columbia University Press: New York, NY, USA, 1981; 563p.
5. Hatta, M.; Fukami, H.; Wang, W.; Omori, M.; Shimoike, K.; Hayashibara, T.; Ina, Y.; Sugiyama, T. Reproductive and genetic evidence for a reticulate evolutionary history of mass-spawning corals. *Mol. Biol. Evol.* **1999**, *16*, 1607–1613. [CrossRef]
6. Veron, J.E.N. *Corals of the World*; Australian Institute of Marine Science: Townsville, QLD, Australia, 2000; Volumes 1–3, 1410p.
7. Riginos, C.; Popovic, I.; Meziere, Z.; Garcia, V.; Byrne, I.; Howitt, S.M.; Ishida, H.; Bairos-Novak, K.; Humanes, A.; Scharfenstein, H. Cryptic species and hybridisation in corals: Challenges and opportunities for conservation and restoration. *Peer Community J.* **2024**, *4*, e106. [CrossRef]

8. Veron, J.E.N.; Pichon, M. *Scleractinia of Eastern Australia. Part I. Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae*; Australian Institute of Marine Science Monograph Series; Australian Institute of Marine Science: Townsville, QLD, Australia, 1976; Volume 1, 86p. Available online: https://www.biodiversitylibrary.org/page/39919739 (accessed on 20 August 2025).
9. Schmidt-Roach, S.; Lundgren, P.; Miller, K.J.; Gerlach, G.; Noreen, A.M.; Andreakis, N. Assessing hidden species diversity in the coral *Pocillopora damicornis* from eastern Australia. *Coral Reefs* **2013**, *32*, 161–172. [CrossRef]
10. Veron, J.E.N.; Stafford-Smith, M.G.; Turak, E.; DeVantier, L.M. CoralsOfTheWorld.org 2016. Available online: https://www.coralsoftheworld.org/page/home/?version=0.01 (accessed on 20 October 2025).
11. Jackson, J.B.C. Modes of dispersal of clonal benthic invertebrates: Consequences for species' distributions and genetic structure of local populations. *Bull. Mar. Sci.* **1986**, *39*, 588–606.
12. Combosch, D.J.; Vollmer, S.V. Mixed asexual and sexual reproduction in the Indo-Pacific reef coral *Pocillopora damicornis*. *Ecol. Evol.* **2013**, *3*, 3379–3387. [CrossRef]
13. Highsmith, R.C. Passive colonization and asexual colony multiplication in the massive coral *Porites lutea* Milne Edwards and Haime. *J. Exp. Mar. Biol. Ecol.* **1980**, *47*, 55–67. [CrossRef]
14. Highsmith, R.C. Reproduction by fragmentation in corals. *Mar. Ecol. Prog. Ser.* **1982**, *7*, 207–226. [CrossRef]
15. Potts, D.C.; Done, T.J.; Isdale, P.J.; Fisk, D.A. Dominance of a coral community by the genus *Porites* (Scleractinia). *Mar. Ecol. Prog. Ser.* **1985**, *23*, 79–84. [CrossRef]
16. DeVantier, L.; Endean, R. Observations of colony fission following ledge formation in massive reef corals of the genus *Porites*. *Mar. Ecol. Prog. Ser.* **1989**, *58*, 191–195. [CrossRef]
17. Sammarco, P.W. Polyp bail-out: An escape response to environmental stress and a new means of reproduction in corals. *Mar. Ecol. Prog. Ser.* **1982**, *10*, 57–65. [CrossRef]
18. Kvitt, H.; Kramarsky-Winter, E.; Maor-Landaw, K.; Zandbank, K.; Kushmaro, A.; Rosenfeld, H.; Fine, M.; Tchernov, D. Breakdown of coral colonial form under reduced pH conditions is initiated in polyps and mediated through apoptosis. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 2082–2086. [CrossRef]
19. Fordyce, A.J.; Camp, E.F.; Ainsworth, T.D. Polyp bailout in *Pocillopora damicornis* following thermal stress. *F1000Research* **2017**, *6*, 687. [CrossRef]
20. Schweinsberg, M.; Gösser, F.; Tollrian, R. The history, biological relevance, and potential applications for polyp bailout in corals. *Ecol. Evol.* **2021**, *11*, 8424–8440. [CrossRef]
21. Chuang, P.-S.; Yamada, Y.; Liu, P.-Y.; Tang, S.-L.; Mitarai, S. Bacterial community shifts during polyp bail-out induction in *Pocillopora* corals. *Microbiol. Spectr.* **2023**, *11*, e00257-23. [CrossRef]
22. Gösser, F.; Raulf, A.; Mosig, A.; Tollrian, R.; Schweinsberg, M. Signaling pathways of heat- and hypersalinity-induced polyp bailout in *Pocillopora acuta*. *Coral Reefs* **2021**, *40*, 1713–1728. [CrossRef]
23. Chuang, P.-S.; Ishikawa, K.; Mitarai, S. Morphological and genetic recovery of coral polyps after bail-out. *Front. Mar. Sci.* **2021**, *8*, 609287. [CrossRef]
24. Chuang, P.-S.; Mitarai, S. Genetic changes involving the coral gastrovascular system support the transition between colonies and bailed-out polyps: Evidence from a *Pocillopora acuta* transcriptome. *BMC Genom.* **2021**, *22*, 694. [CrossRef]
25. Harrison, P.L. Sexual reproduction of scleractinian corals. In *Coral Reefs: An Ecosystem in Transition*; Dubinsky, Z., Stambler, N., Eds.; Springer: Dordrecht, The Netherlands, 2011; pp. 59–85.
26. Guest, J.R.; Baird, A.H.; Goh, B.P.; Chou, L.M. Sexual systems in scleractinian corals: An unusual pattern in the reef-building species *Diploastrea heliopora*. *Coral Reefs* **2012**, *31*, 705–713. [CrossRef]
27. Inoha, K.; Isomura, N.; Morita, M.; Kurihara, H. Combination of hermaphroditic and gonochoric sexual modes in the coral *Porites cylindrica*. *Coral Reefs* **2024**, *43*, 1831–1841. [CrossRef]
28. Jokiel, P.L. Long distance dispersal of reef corals by rafting. *Coral Reefs* **1984**, *3*, 113–116. [CrossRef]
29. Graham, E.M.; Baird, A.H.; Connolly, S.R. Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral Reefs* **2008**, *27*, 529–539. [CrossRef]
30. Randall, C.J.; Giuliano, C.; Stephenson, B.; Whitman, T.N.; Page, C.A.; Treml, E.A.; Logan, M.; Negri, A.P. Larval precompetency and settlement behaviour in 25 Indo-Pacific coral species. *Commun. Biol.* **2024**, *7*, 142. [CrossRef]
31. Rosser, N.L.; Edyvane, K.; Malina, A.C.; Underwood, J.N.; Johnson, M.S. Geography and spawning season drive genetic divergence among populations of the hard coral *Acropora tenuis* from Indonesia and Western Australia. *Coral Reefs* **2020**, *39*, 989–999. [CrossRef]
32. Duvane, J.A.; Dupont, S.; Sola, E.; Ortega-Martinez, O.; Pereyra, R.T. Genetic diversity and structure among *Acropora austera* populations in Mozambique suggest low resilience potential of one of the world's most charismatic coral reefs. *Coral Reefs* **2025**, *44*, 1185–1195. [CrossRef]
33. Denis, H.; Prata, K.E.; Ishida, H.; Popovic, I.; Mocellin, V.J.L.; Boussion, M.; Byrne, I.; Purcell, S.W.; Bay, L.K.; Lecellier, G.; et al. Long-distance gene flow and contrasting population structures of reef-building corals and their algal symbionts inform adaptive potential across the Western Pacific. *bioRxiv* **2025**. [CrossRef]

34. Afiq-Rosli, L.; Wainwright, B.J.; Lee, J.N.; Waheed, Z.; Chou, L.M.; Huang, D. Contrasting patterns of population genomic structure between broadcast-spawning and brooding corals in Southeast Asia. *Divers. Distrib.* **2024**, *30*, e13940. [CrossRef]
35. Duijser, C.M.; Nitschke, M.R.; Rassmussen, S.H.; Camp, E.F. *Pocillopora* host–symbiont interactions along an extreme environmental gradient. *Coral Reefs* **2025**, *44*, 1341–1353. [CrossRef]
36. Burt, A.J.; Vogt-Vincent, N.; Johnson, H.; Sendell-Price, A.; Kelly, S.; Clegg, S.M.; Head, C.; Bunbury, N.; Fleischer-Dogley, F.; Jeremie, M.-M. Integration of population genetics with oceanographic models reveals strong connectivity among coral reefs across Seychelles. *Sci. Rep.* **2024**, *14*, 4936. [CrossRef] [PubMed]
37. Vogt-Vincent, N.S.; Burt, A.J.; van der Ven, R.M.; Johnson, H.L. Coral reef potential connectivity in the southwest Indian Ocean. *Coral Reefs* **2024**, *43*, 1037–1051. [CrossRef]
38. van der Ven, R.M.; Flot, J.-F.; Buitrago-López, C.; Kochzius, M. Population genetics of the brooding coral *Seriatopora hystrix* reveals patterns of strong genetic differentiation in the Western Indian Ocean. *Heredity* **2021**, *126*, 351–365. [CrossRef]
39. Harrison, P.L.; Wallace, C.C. Reproduction, dispersal and recruitment of scleractinian corals. In *Ecosystems of the World: Coral Reefs*; Dubinsky, Z., Ed.; Elsevier: Amsterdam, The Netherlands, 1990; Volume 25, pp. 133–207.
40. Thomas, L.; Underwood, J.N.; Adam, A.A.S.; Richards, Z.T.; Dugal, L.; Miller, K.J.; Gilmour, J.P. Contrasting patterns of genetic connectivity in brooding and spawning corals across a remote atoll system in northwest Australia. *Coral Reefs* **2020**, *39*, 55–60. [CrossRef]
41. Harii, S.; Kayanne, H.; Takigawa, H.; Hayashibara, T.; Yamamoto, M. Larval survivorship, competency periods and settlement of two brooding corals, *Heliopora coerulea* and *Pocillopora damicornis*. *Mar. Biol.* **2002**, *141*, 39–46. [CrossRef]
42. Ramírez-Portilla, C.; Baird, A.H.; Cowman, P.F.; Quattrini, A.M.; Harii, S.; Sinniger, F.; Flot, J.-F. Solving the coral species delimitation conundrum. *Syst. Biol.* **2022**, *71*, 461–475. [CrossRef] [PubMed]
43. Dobzhansky, T. *Genetics and the Origin of Species*; Columbia University Press: New York, NY, USA, 1937; 364p.
44. Mayr, E. *Systematics and the Origin of Species*; Columbia University Press: New York, NY, USA, 1942; 334p.
45. Mayr, E. *Animal Species and Evolution*; Harvard University Press: Cambridge, MA, USA, 1963; 797p.
46. Paterson, H.E. The recognition concept of species. In *Species and Speciation*; Vrba, E., Ed.; Transvaal Museum Monograph No. 4; Transvaal Museum: Pretoria, South Africa, 1985; pp. 21–30.
47. Butlin, R.; Debelle, A.; Kerth, C.; Snook, R.R.; Beukeboom, L.W.; Castillo Cajas, R.F.; Diao, W.; Maan, M.E.; Paolucci, S.; Weissing, F.J.; et al. What do we need to know about speciation? *Trends Ecol. Evol.* **2012**, *27*, 27–39. [CrossRef]
48. Adavoudi, R.; Pilot, M. Consequences of hybridization in mammals: A systematic review. *Genes.* **2022**, *13*, 50. [CrossRef]
49. Stankowski, S.; Shipilina, D.; Westram, A.M. Hybrid zones. *eLS* **2021**, *2*, a0029355. [CrossRef]
50. Brauer, C.J.; Sandoval-Castillo, J.; Gates, K.; Hammer, M.P.; Unmack, P.J.; Bernatchez, L.; Beheregaray, L.B. Natural hybridization reduces vulnerability to climate change. *Nat. Clim. Chang.* **2023**, *13*, 282–289. [CrossRef]
51. Skovrind, M.; Castruita, J.A.S.; Haile, J.; Treadaway, E.C.; Gopalakrishnan, S.; Westbury, M.V.; Heide-Jørgensen, M.P.; Szpak, P.; Lorenzen, E.D. Hybridization between two high Arctic cetaceans confirmed by genomic analysis. *Sci. Rep.* **2019**, *9*, 7729. [CrossRef]
52. Porretta, D.; Canestrelli, D. The ecological importance of hybridization. *Trends Ecol. Evol.* **2023**, *38*, 1097–1108. [CrossRef]
53. Huxel, G.R. Rapid displacement of native species by invasive species: Effects of hybridization. *Biol. Conserv.* **1999**, *89*, 143–152. [CrossRef]
54. Largiadèr, C.R. Hybridization and introgression between native and alien species. In *Biological Invasions*; Nentwig, W., Ed.; Springer: Berlin, Germany, 2008; pp. 275–292.
55. Viard, F.; Riginos, C.; Bierne, N. Anthropogenic hybridization at sea: Three evolutionary questions relevant to invasive species management. *Philos. Trans. R. Soc. B Biol. Sci.* **2020**, *375*, 20190547. [CrossRef]
56. Hellberg, M.E.; Prada, C.; Tan, M.H.; Forsman, Z.H.; Baums, I.B. Getting a grip at the edge: Recolonization and introgression in eastern Pacific *Porites* corals. *J. Biogeogr.* **2016**, *43*, 2147–2159. [CrossRef]
57. Hobbs, J.-P.A.; Richards, Z.T.; Popovic, I.; Lei, C.; Staeudle, T.M.; Montanari, S.R.; DiBattista, J.D. Hybridisation and the evolution of coral reef biodiversity. *Coral Reefs* **2022**, *41*, 535–549. [CrossRef]
58. Lamb, A.M.; Peplow, L.M.; Chan, W.Y.; Crane, Z.J.; Everson, G.A.; Harrison, P.L.; Hite, T.E.; Hoffmann, A.A.; Humphrey, C.A.; Koukoumaftsis, L.P. Fertile hybrids could aid coral adaptation. *Ecol. Evol.* **2024**, *14*, e70570. [CrossRef]
59. Voolstra, C.R.; Hume, B.C.; Armstrong, E.J.; Mitushasi, G.; Porro, B.; Oury, N.; Agostini, S.; Boissin, E.; Poulain, J.; Carradec, Q. Disparate genetic divergence patterns in three corals across a pan-Pacific environmental gradient highlight species-specific adaptation. *npj Biodivers.* **2023**, *2*, 20. [CrossRef] [PubMed]
60. Oury, N.; Noël, C.; Mona, S.; Aurelle, D.; Magalon, H. From genomics to integrative species delimitation? The case study of the Indo-Pacific *Pocillopora* corals. *Mol. Phylogenet. Evol.* **2023**, *184*, 107803. [CrossRef] [PubMed]
61. De Queiroz, K. The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. In *Endless Forms: Species and Speciation*; Howard, D.J., Berlocher, S.H., Eds.; Oxford University Press: New York, NY, USA, 1998; pp. 57–75.

62. van Oppen, M.J.H.; Willis, B.L.; van Vugt, H.W.J.A.; Miller, D.J. Examination of species boundaries in the *Acropora cervicornis* group (Scleractinia, Cnidaria) using nuclear DNA sequence analyses. *Mol. Ecol.* **2000**, *9*, 1363–1373. [CrossRef]
63. Vollmer, S.V.; Palumbi, S.R. Hybridization and the evolution of reef coral diversity. *Science* **2002**, *296*, 2023–2025. [CrossRef]
64. Kitchen, S.A.; Ratan, A.; Bedoya-Reina, O.C.; Burhans, R.; Fogarty, N.D.; Miller, W.; Baums, I.B. Genomic variants among threatened *Acropora* corals. *G3 Genes Genomes Genet.* **2019**, *9*, 1633–1646. [CrossRef]
65. Precht, W.F.; Vollmer, S.V.; Modys, A.B.; Kaufman, L. Fossil *Acropora prolifera* (Lamarck, 1816) reveals coral hybridization is not only a recent phenomenon. *Proc. Biol. Soc. Wash.* **2019**, *132*, 40–55. [CrossRef]
66. Baums, I.B.; Miller, M.W.; Hellberg, M.E. Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Mol. Ecol.* **2005**, *14*, 1377–1390. [CrossRef]
67. Japaud, A.; Bouchon, C.; Magalon, H.; Fauvelot, C. Geographic distances and ocean currents influence Caribbean *Acropora palmata* population connectivity in the Lesser Antilles. *Conserv. Genet.* **2019**, *20*, 447–466. [CrossRef]
68. Kitchen, S.A.; Osborne, C.C.; Fogarty, N.D.; Baums, I.B. Morphotype is not linked to mitochondrial haplogroups of Caribbean acroporid hybrids. *Coral Reefs* **2022**, *41*, 829–836. [CrossRef]
69. Isomura, N.; Iwao, K.; Morita, M.; Fukami, H. Spawning and fertility of F1 hybrids of the coral genus *Acropora* in the Indo-Pacific. *Coral Reefs* **2016**, *35*, 851–855. [CrossRef]
70. Kitanobo, S.; Isomura, N.; Fukami, H.; Iwao, K.; Morita, M. The reef-building coral *Acropora* conditionally hybridize under sperm limitation. *Biol. Lett.* **2016**, *12*, 20160511. [CrossRef]
71. Fukami, H.; Iwao, K.; Kumagai, N.H.; Morita, M.; Isomura, N. Maternal inheritance of F1 hybrid morphology and colony shape in the coral genus *Acropora*. *PeerJ* **2019**, *7*, e6429. [CrossRef]
72. Kitanobo, S.; Iwao, K.; Fukami, H.; Isomura, N.; Morita, M. First evidence for backcrossing of F1 hybrids in *Acropora* corals under sperm competition. *Sci. Rep.* **2022**, *12*, 5356. [CrossRef]
73. Hernández-Agreda, A.; Huckeba, J.; Prata, K.E.; Vermeij, M.J.A.; Bongaerts, P. Hybridization and inbreeding affect the survival of a critically endangered coral. *Curr. Biol.* **2024**, *34*, 5120–5129.e4. [CrossRef] [PubMed]
74. Willis, B.L.; Babcock, R.C.; Harrison, P.L.; Wallace, C.C. Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. *Coral Reefs* **1997**, *16* (Suppl. S1), S53–S65. [CrossRef]
75. Willis, B.L.; van Oppen, M.J.H.; Miller, D.J.; Vollmer, S.V.; Ayre, D.J. The role of hybridization in the evolution of reef corals. *Annu. Rev. Ecol. Evol. Syst.* **2006**, *37*, 489–517. [CrossRef]
76. Márquez, L.; van Oppen, M.; Willis, B.; Reyes, A.; Miller, D. The highly cross-fertile coral species, *Acropora hyacinthus* and *Acropora cytherea*, constitute statistically distinguishable lineages. *Mol. Ecol.* **2002**, *11*, 1339–1349. [CrossRef]
77. Márquez, L.; van Oppen, M.; Willis, B.; Miller, D. Sympatric populations of the highly cross-fertile coral species *Acropora hyacinthus* and *Acropora cytherea* are genetically distinct. *Proc. R. Soc. Lond. B Biol. Sci.* **2002**, *269*, 1289–1294. [CrossRef]
78. Furukawa, M.; Kitanobo, S.; Ohki, S.; Teramoto, M.M.; Hanahara, N.; Morita, M. Integrative taxonomic analyses reveal that rapid genetic divergence drives *Acropora* speciation. *Mol. Phylogenet. Evol.* **2024**, *195*, 108063. [CrossRef] [PubMed]
79. Rose, N.H.; Bay, R.A.; Morikawa, M.K.; Thomas, L.; Sheets, E.A.; Palumbi, S.R. Genomic analysis of distinct bleaching tolerances among cryptic coral species. *Proc. R. Soc. B Biol. Sci.* **2021**, *288*, 20210678. [CrossRef] [PubMed]
80. Ladner, J.T.; Palumbi, S.R. Extensive sympatry, cryptic diversity and introgression throughout the geographic distribution of two coral species complexes. *Mol. Ecol.* **2012**, *21*, 2224–2238. [CrossRef] [PubMed]
81. Rassmussen, S.H.; Cowman, P.F.; Baird, A.H.; Crosbie, A.J.; Quattrini, A.M.; Bonito, V.; Sinniger, F.; Harii, S.; Cabaitan, P.C.; Fadli, N.; et al. The tables have turned: Taxonomy, systematics and biogeography of the *Acropora hyacinthus* (Scleractinia: Acroporidae) complex. *Invertebr. Syst.* **2025**, *39*, IS24049. [CrossRef]
82. Mao, Y.; Economo, E.P.; Satoh, N. The roles of introgression and climate change in the rise to dominance of *Acropora* corals. *Curr. Biol.* **2018**, *28*, 3373–3382.e5. [CrossRef]
83. Richards, Z.T.; van Oppen, M.J.H.; Wallace, C.C.; Willis, B.L.; Miller, D.J. Some rare Indo-Pacific coral species are probable hybrids. *PLoS ONE* **2008**, *3*, e3240. [CrossRef]
84. van Oppen, M.J.H.; Willis, B.L.; van Rheede, T.; Miller, D.J. Spawning times, reproductive compatibilities and genetic structuring in the *Acropora aspera* group: Evidence for natural hybridization and semi-permeable species boundaries in corals. *Mol. Ecol.* **2002**, *11*, 1363–1376. [CrossRef]
85. Forsman, Z.; Knapp, I.; Tisthammer, K.; Eaton, D.; Belcaid, M.; Toonen, R. Coral hybridization or phenotypic variation? Genomic data reveal gene flow between *Porites lobata* and *P. compressa*. *Mol. Phylogenet. Evol.* **2017**, *111*, 132–148. [CrossRef]
86. Miller, K.; Babcock, R. Conflicting morphological and reproductive species boundaries in the coral genus *Platygyra*. *Biol. Bull.* **1997**, *192*, 98–110. [CrossRef]
87. Miller, K.J.; Benzie, J.A.H. No clear genetic distinction between morphological species within the coral genus *Platygyra*. *Bull. Mar. Sci.* **1997**, *61*, 907–917.
88. Miller, K. Morphological variation in the coral genus *Platygyra*: Environmental influences and taxonomic implications. *Mar. Ecol. Prog. Ser.* **1994**, *110*, 19–28. [CrossRef]

89. Miller, K.; Ayre, D. The role of sexual and asexual reproduction in structuring high latitude populations of the reef coral *Pocillopora damicornis*. *Heredity* **2004**, *92*, 557–568. [CrossRef]
90. Pinzón, J.H.; Sampayo, E.; Cox, E.; Chauka, L.J.; Chen, C.A.; Voolstra, C.R.; LaJeunesse, T.C. Blind to morphology: Genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *J. Biogeogr.* **2013**, *40*, 1595–1608. [CrossRef]
91. Oury, N.; Gélin, P.; Magalon, H. Cryptic species and genetic connectivity among populations of the coral *Pocillopora damicornis* (Scleractinia) in the tropical southwestern Pacific. *Mar. Biol.* **2020**, *167*, 46. [CrossRef]
92. Gélin, P.; Postaire, B.; Fauvelot, C.; Magalon, H. Reevaluating species number, distribution and endemism of the coral genus *Pocillopora* Lamarck, 1816 using species delimitation methods and microsatellites. *Mol. Phylogenet. Evol.* **2017**, *109*, 430–446. [CrossRef] [PubMed]
93. Gélin, P.; Fauvelot, C.; Bigot, L.; Baly, J.; Magalon, H. From population connectivity to the art of striping Russian dolls: The lessons from *Pocillopora* corals. *Ecol. Evol.* **2018**, *8*, 1411–1426. [CrossRef]
94. Johnston, E.C.; Burgess, S.C. *Pocillopora tuahiniensis*: A new species of scleractinian coral (Scleractinia, Pocilloporidae) from French Polynesia. *Zootaxa* **2023**, *5369*, 117–124. [CrossRef]
95. Bridge, T.C.; Cowman, P.F.; Quattrini, A.M.; Bonito, V.E.; Sinniger, F.; Harii, S.; Head, C.E.; Hung, J.Y.; Halafihi, T.; Rongo, T. A tenuis relationship: Traditional taxonomy obscures systematics and biogeography of the *Acropora tenuis* (Scleractinia: Acroporidae) species complex. *Zool. J. Linn. Soc.* **2023**, *202*, zlad062. [CrossRef]
96. Ladner, J.T. Hidden Diversity in Corals and Their Endosymbionts. Ph.D. Thesis, Stanford University, Stanford, CA, USA, 2012.
97. Stefani, F.; Benzoni, F.; Yang, S.-Y.; Pichon, M.; Galli, P.; Chen, C. Comparison of morphological and genetic analyses reveals cryptic divergence and morphological plasticity in *Stylophora* (Cnidaria, Scleractinia). *Coral Reefs* **2011**, *30*, 1033–1049. [CrossRef]
98. Flot, J.-F.; Blanchot, J.; Charpy, L.; Cruaud, C.; Licuanan, W.Y.; Nakano, Y.; Payri, C.; Tillier, S. Incongruence between morphotypes and genetically delimited species in the coral genus *Stylophora*: Phenotypic plasticity, morphological convergence, morphological stasis or interspecific hybridization? *BMC Ecol.* **2011**, *11*, 22. [CrossRef] [PubMed]
99. Capel, K.C.C.; Ayalon, I.; Simon-Blecher, N.; Zweifler Zvifler, A.; Benichou, I.J.; Eyal, G.; Avisar, D.; Roth, J.; Bongaerts, P.; Levy, O. Depth-structured lineages in the coral *Stylophora pistillata* of the Northern Red Sea. *npj Biodivers.* **2025**, *4*, 13. [CrossRef]
100. Meziere, Z.; Popovic, I.; Prata, K.; Ryan, I.; Pandolfi, J.; Riginos, C. Exploring coral speciation: Multiple sympatric *Stylophora pistillata* taxa along a divergence continuum on the Great Barrier Reef. *Evol. Appl.* **2024**, *17*, e13644. [CrossRef]
101. Roux, C.; Fraïsse, C.; Romiguier, J.; Anciaux, Y.; Galtier, N.; Bierne, N. Shedding light on the grey zone of speciation along a continuum of genomic divergence. *PLoS Biol.* **2016**, *14*, e2000234. [CrossRef]
102. Nakajima, Y.; Zayasu, Y.; Shinzato, C.; Satoh, N.; Mitarai, S. Genetic differentiation and connectivity of morphological types of the broadcast-spawning coral *Galaxea fascicularis* in the Nansei Islands, Japan. *Ecol. Evol.* **2016**, *6*, 1457–1469. [CrossRef]
103. Wepfer, P.H.; Nakajima, Y.; Sutthacheep, M.; Radice, V.Z.; Richards, Z.; Ang, P.; Terraneo, T.; Sudek, M.; Fujimura, A.; Toonen, R.J. Evolutionary biogeography of the reef-building coral genus *Galaxea* across the Indo-Pacific Ocean. *Mol. Phylogenet. Evol.* **2020**, *151*, 106905. [CrossRef] [PubMed]
104. Weil, E.; Knowlton, N. A multi-character analysis of the Caribbean coral *Montastraea annularis* (Ellis and Solander, 1786) and its two sibling species, *M. faveolata* (Ellis and Solander, 1786) and *M. franksi* (Gregory, 1895). *Bull. Mar. Sci.* **1994**, *55*, 151–175.
105. Szmant, A.; Weil, E.; Miller, M.; Colon, D. Hybridization within the species complex of the scleractinian coral *Montastraea annularis*. *Mar. Biol.* **1997**, *129*, 561–572. [CrossRef]
106. Dziedzic, K.E.; Elder, H.; Tavalire, H.; Meyer, E. Heritable variation in bleaching responses and its functional genomic basis in reef-building corals (*Orbicella faveolata*). *Mol. Ecol.* **2019**, *28*, 2238–2253. [CrossRef]
107. Gómez-Corrales, M.; Prada, C. Cryptic lineages respond differently to coral bleaching. *Mol. Ecol.* **2020**, *29*, 4265–4273. [CrossRef]
108. Prata, K.E.; Riginos, C.; Gutenkunst, R.N.; Latijnhouwers, K.R.W.; Sánchez, J.A.; Englebert, N.; Hay, K.B.; Bongaerts, P. Deep connections: Divergence histories with gene flow in mesophotic *Agaricia* corals. *Mol. Ecol.* **2022**, *31*, 2511–2527. [CrossRef]
109. Diekmann, O.; Bak, R.; Stam, W.; Olsen, J. Molecular genetic evidence for probable reticulate speciation in the coral genus *Madracis* from a Caribbean fringing reef slope. *Mar. Biol.* **2001**, *139*, 221–233. [CrossRef]
110. Alvarado-Cerón, V.; Muñiz-Castillo, A.I.; León-Pech, M.G.; Prada, C.; Arias-González, J.E. A decade of population genetics studies of scleractinian corals: A systematic review. *Mar. Environ. Res.* **2023**, *183*, 105781. [CrossRef]
111. Pinsky, M.L.; Clark, R.D.; Bos, J.T. Coral reef population genomics in an age of global change. *Annu. Rev. Genet.* **2023**, *57*, 87–115. [CrossRef]
112. Baird, A.H.; Guest, J.R.; Willis, B.L. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annu. Rev. Ecol. Evol. Syst.* **2009**, *40*, 551–571. [CrossRef]
113. CoralTraits.org. Coral Traits Database. Available online: https://coraltraits.org (accessed on 20 August 2025).
114. Brazeau, D.A.; Gleason, D.F.; Morgan, M.E. Self-fertilization in brooding hermaphroditic Caribbean corals: Evidence from molecular markers. *J. Exp. Mar. Biol. Ecol.* **1998**, *231*, 225–238. [CrossRef]

115. Okubo, N.; Isomura, N.; Motokawa, T.; Hidaka, M. Possible self-fertilization in the brooding coral *Acropora (Isopora) brueggemanni*. *Zool. Sci.* **2007**, *24*, 277–280. [CrossRef]
116. Sherman, C.D.H. Mating system variation in the hermaphroditic brooding coral, *Seriatopora hystrix*. *Heredity* **2008**, *100*, 296–303. [CrossRef] [PubMed]
117. Warner, P.A.; Willis, B.L.; van Oppen, M.J.H. Sperm dispersal distances estimated by parentage analysis in a brooding scleractinian coral. *Mol. Ecol.* **2016**, *25*, 1398–1415. [CrossRef] [PubMed]
118. Hagedorn, M.; Page, C.A.; O'Neil, K.L.; Flores, D.M.; Tichy, L.; Conn, T.; Chamberland, V.F.; Lager, C.; Zuchowicz, N.; Lohr, K.; et al. Assisted gene flow using cryopreserved sperm in critically endangered coral. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2110559118. [CrossRef]
119. Heyward, A.J.; Babcock, R.C. Self- and cross-fertilization in scleractinian corals. *Mar. Biol.* **1986**, *90*, 191–195. [CrossRef]
120. Woolsey, E.S.; Byrne, M.; Baird, A.H. The effects of temperature on embryonic development and larval survival in two scleractinian corals. *Mar. Ecol. Prog. Ser.* **2013**, *493*, 179–184. [CrossRef]
121. Bassim, K.; Sammarco, P.W.; Snell, T. Effects of temperature on success of (self and non-self) fertilization and embryogenesis in *Diploria strigosa* (Cnidaria, Scleractinia). *Mar. Biol.* **2002**, *140*, 479–488. [CrossRef]
122. Henley, E.M.; Quinn, M.; Bouwmeester, J.; Daly, J.; Lager, C.; Zuchowicz, N.; Bailey, D.W.; Hagedorn, M. Contrasting reproductive strategies of two Hawaiian *Montipora* corals. *Sci. Rep.* **2022**, *12*, 12255. [CrossRef]
123. Yasuda, N.; Kitano, Y.F.; Taninaka, H.; Nagai, S.; Mezaki, T.; Yamashita, H. Genetic structure of the *Goniopora lobata* and *G. djiboutiensis* species complex is better explained by oceanography than by morphological characteristics. *Front. Mar. Sci.* **2021**, *8*, 592608. [CrossRef]
124. Furukawa, M.; Ohki, S.; Kitanobo, S.; Fukami, H.; Morita, M. Differences in spawning time drive cryptic speciation in the coral *Acropora divaricata*. *Mar. Biol.* **2020**, *167*, 72. [CrossRef]
125. Isomura, N.; Iwao, K.; Fukami, H. Possible natural hybridization of two morphologically distinct species of *Acropora* (Cnidaria, Scleractinia) in the Pacific: Fertilization and larval survival rates. *PLoS ONE* **2013**, *8*, e56701. [CrossRef]
126. LaJeunesse, T.C.; Parkinson, J.E.; Gabrielson, P.W.; Jeong, H.J.; Reimer, J.D.; Voolstra, C.R.; Santos, S.R. Systematic revision of *Symbiodiniaceae* highlights the antiquity and diversity of coral endosymbionts. *Curr. Biol.* **2018**, *28*, 2570–2580.e6. [CrossRef]
127. Guinotte, J.M.; Buddemeier, R.W.; Kleypas, J.A. Future coral reef habitat marginality: Temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs* **2003**, *22*, 551–558. [CrossRef]
128. Hoegh-Guldberg, O.; Mumby, P.J.; Hooten, A.J.; Steneck, R.S.; Greenfield, P.; Gomez, E.; Harvell, C.D.; Sale, P.F.; Edwards, A.J.; Caldeira, K.; et al. Coral reefs under rapid climate change and ocean acidification. *Science* **2007**, *318*, 1737–1742. [CrossRef]
129. Taylor, D. Symbiotic marine algae: Taxonomy and biological fitness. In *Symbiosis in the Sea*; Vernberg, C., Ed.; University of South Carolina Press: Columbia, SC, USA, 1974; pp. 245–262.
130. Muscatine, L. The role of symbiotic algae in carbon and energy flux in reef corals. In *Ecosystems of the World: Coral Reefs*; Dubinsky, Z., Ed.; Elsevier: Amsterdam, The Netherlands, 1990; Volume 25, pp. 75–87.
131. Baker, A.C. Zooxanthellae. In *Encyclopedia of Modern Coral Reefs*; Hopley, D., Ed.; Encyclopedia of Earth Sciences Series; Springer: Dordrecht, The Netherlands, 2011; pp. 1189–1192.
132. Galand, P.E.; Ruscheweyh, H.-J.; Salazar, G.; Hochart, C.; Henry, N.; Hume, B.C.C.; Oliveira, P.H.; Perdereau, A.; Labadie, K.; Belser, C.; et al. Diversity of the Pacific Ocean coral reef microbiome. *Nat. Commun.* **2023**, *14*, 3039. [CrossRef]
133. Muscatine, L.; Porter, J.W. Reef corals: Mutualistic symbioses adapted to nutrient-poor environments. *BioScience* **1977**, *27*, 454–460. [CrossRef]
134. Rowan, R. Review—Diversity and ecology of zooxanthellae on coral reefs. *J. Phycol.* **1998**, *34*, 407–417. [CrossRef]
135. Wiedenmann, J.; D'Angelo, C.; Mardones, M.L.; Moore, S.; Benkwitt, C.E.; Graham, N.A.J.; Hambach, B.; Wilson, P.A.; Vanstone, J.; Eyal, G.; et al. Reef-building corals farm and feed on their photosynthetic symbionts. *Nature* **2023**, *620*, 1018–1024. [CrossRef]
136. Titlyanov, F.A.; Titlyanova, T.V.; Leletkin, V.A.; Tsukahara, J.; Van Woesik, R.; Yamazato, K. Degradation of zooxanthellae and regulation of their density in hermatypic corals. *Mar. Ecol. Prog. Ser.* **1996**, *139*, 167–178. [CrossRef]
137. Trench, R.K. Diversity of symbiotic dinoflagellates and the evolution of microalgal–invertebrate symbioses. In Proceedings of the 8th International Coral Reef Symposium, Panama City, Panama, 24–29 June 1996; Volume 2, pp. 1275–1286.
138. Iglesias-Prieto, R.; Beltran, V.; LaJeunesse, T.; Reyes-Bonilla, H.; Thome, P. Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. *Proc. R. Soc. Lond. B Biol. Sci.* **2004**, *271*, 1757–1763. [CrossRef] [PubMed]
139. Cunning, R.; Silverstein, R.N.; Baker, A.C. Investigating the causes and consequences of symbiont shuffling in a multi-partner reef coral symbiosis under environmental change. *Proc. R. Soc. B Biol. Sci.* **2015**, *282*, 20141725. [CrossRef] [PubMed]
140. Ziegler, M.; Roik, A.; Porter, A.; Zubier, K.; Mudarris, M.S.; Ormond, R.; Voolstra, C.R. Coral microbial community dynamics in response to anthropogenic impacts near a major city in the central Red Sea. *Mar. Pollut. Bull.* **2016**, *105*, 629–640. [CrossRef]
141. Sweet, M.; Bythell, J. The role of viruses in coral health and disease. *J. Invertebr. Pathol.* **2017**, *147*, 136–144. [CrossRef]

142. Quigley, K.M.; Willis, B.L.; Kenkel, C.D. Transgenerational inheritance of shuffled symbiont communities in the coral *Montipora digitata*. *Sci. Rep.* **2019**, *9*, 5005. [CrossRef]
143. Johnston, E.C.; Cunning, R.; Burgess, S.C. Cophylogeny and specificity between cryptic coral species (*Pocillopora* spp.) at Mo'orea and their symbionts (*Symbiodiniaceae*). *Mol. Ecol.* **2022**, *31*, 5368–5385. [CrossRef]
144. Bonacolta, A.M.; Weiler, B.A.; Porta-Fitó, T.; Sweet, M.; Keeling, P.; del Campo, J. Beyond the Symbiodiniaceae: Diversity and role of microeukaryotic coral symbionts. *Coral Reefs* **2023**, *42*, 567–577. [CrossRef]
145. Dunphy, C.M.; Gouhier, T.C.; Chu, N.D.; Vollmer, S.V. Structure and stability of the coral microbiome in space and time. *Sci. Rep.* **2019**, *9*, 6785. [CrossRef]
146. Terraneo, T.I.; Fusi, M.; Hume, B.C.C.; Arrigoni, R.; Voolstra, C.R.; Benzoni, F.; Forsman, Z.H.; Berumen, M.L. Environmental latitudinal gradients and host-specificity shape *Symbiodiniaceae* distribution in Red Sea *Porites* corals. *J. Biogeogr.* **2019**, *46*, 2323–2335. [CrossRef]
147. Buerger, P.; Alvarez-Roa, C.; Coppin, C.W.; Pearce, S.L.; Chakravarti, L.J.; Oakeshott, J.G.; Edwards, O.R.; van Oppen, M.J.H. Heat-evolved microalgal symbionts increase coral bleaching tolerance. *Sci. Adv.* **2020**, *6*, eaba2498. [CrossRef] [PubMed]
148. Fox, M.D.; Cohen, A.L.; Rotjan, R.D.; Mangubhai, S.; Sandin, S.A.; Smith, J.E.; Thorrold, S.R.; Dissly, L.; Mollica, N.R.; Obura, D. Increasing coral reef resilience through successive marine heatwaves. *Geophys. Res. Lett.* **2021**, *48*, e2021GL094128. [CrossRef]
149. Butler, C.C.; Turnham, K.E.; Lewis, A.M.; Nitschke, M.R.; Warner, M.E.; Kemp, D.W.; Hoegh-Guldberg, O.; Fitt, W.K.; van Oppen, M.J.H.; LaJeunesse, T.C. Formal recognition of host-generalist species of dinoflagellate (*Cladocopium*, *Symbiodiniaceae*) mutualistic with Indo-Pacific reef corals. *J. Phycol.* **2023**, *59*, 698–711. [CrossRef] [PubMed]
150. Quigley, K.M.; Alvarez-Roa, C.; Raina, J.-B.; Pernice, M.; van Oppen, M.J.H. Heat-evolved microalgal symbionts increase thermal bleaching tolerance of coral juveniles without a trade-off against growth. *Coral Reefs* **2023**, *42*, 1227–1232. [CrossRef]
151. Starko, S.; Fifer, J.E.; Claar, D.C.; Davies, S.W.; Cunning, R.; Baker, A.C.; Baum, J.K. Marine heatwaves threaten cryptic coral diversity and erode associations among coevolving partners. *Sci. Adv.* **2023**, *9*, eadf0954. [CrossRef]
152. Grupstra, C.G.B.; Meyer-Kaiser, K.S.; Bennett, M.-J.; Andres, M.O.; Juszkiewicz, D.J.; Fifer, J.E.; Da-Anoy, J.P.; Gomez-Campo, K.; Martinez-Rugerio, I.; Aichelman, H.E.; et al. Holobiont traits shape climate change responses in cryptic coral lineages. *Glob. Chang. Biol.* **2024**, *30*, e17578. [CrossRef]
153. Buddemeier, R.W.; Fautin, D.G. Coral bleaching as an adaptive mechanism. *BioScience* **1993**, *43*, 320–326. [CrossRef]
154. Buddemeier, R.W.; Smith, S.V. Coral adaptation and acclimatization: A most ingenious paradox. *Am. Zool.* **1999**, *39*, 1–9. [CrossRef]
155. Kemp, D.W.; Hernandez-Pech, X.; Iglesias-Prieto, R.; Fitt, W.K.; Schmidt, G.W. Community dynamics and physiology of *Symbiodinium* spp. before, during, and after a coral bleaching event. *Limnol. Oceanogr.* **2014**, *59*, 788–797. [CrossRef]
156. Silverstein, R.N.; Cunning, R.; Baker, A.C. Change in algal symbiont communities after bleaching, not prior heat exposure, increases heat tolerance of reef corals. *Glob. Chang. Biol.* **2015**, *21*, 236–249. [CrossRef] [PubMed]
157. Thomas, L.; López, E.H.; Morikawa, M.K.; Palumbi, S.R. Transcriptomic resilience, symbiont shuffling, and vulnerability to recurrent bleaching in reef-building corals. *Mol. Ecol.* **2019**, *28*, 3371–3382. [CrossRef] [PubMed]
158. Claar, D.C.; Starko, S.; Tietjen, K.L.; Epstein, H.E.; Cunning, R.; Cobb, K.M.; Baker, A.C.; Gates, R.D.; Baum, J.K. Dynamic symbioses reveal pathways to coral survival through prolonged heatwaves. *Nat. Commun.* **2020**, *11*, 6097. [CrossRef]
159. Sivaguru, M.; Todorov, L.G.; Miller, C.A.H.; Fouke, C.E.; Munro, C.M.O.; Fouke, K.W.; Fouke, K.E.; Baughman, M.E.; Fouke, B.W. Corals regulate the distribution and abundance of *Symbiodiniaceae* and biomolecules in response to changing water depth and sea surface temperature. *Sci. Rep.* **2021**, *11*, 2230. [CrossRef] [PubMed]
160. Palacio-Castro, A.M.; Smith, T.B.; Brandtneris, V.; Snyder, G.A.; van Hooidonk, R.; Maté, J.L.; Manzello, D.; Glynn, P.W.; Fong, P.; Baker, A.C. Increased dominance of heat-tolerant symbionts creates resilient coral reefs in near-term ocean warming. *Proc. Natl. Acad. Sci. USA* **2023**, *120*, e2202388120. [CrossRef]
161. Quigley, K.M.; Ramsby, B.; Laffy, P.; Harris, J.; Mocellin, V.J.L.; Bay, L.K. Symbioses are restructured by repeated mass coral bleaching. *Sci. Adv.* **2022**, *8*, eabq8349. [CrossRef]
162. Dinsdale, E.A.; Pantos, O.; Smriga, S.; Edwards, R.A.; Angly, F.; Wegley, L.; Hatay, M.; Hall, D.; Brown, E.; Haynes, M.; et al. Microbial ecology of four coral atolls in the Northern Line Islands. *PLoS ONE* **2008**, *3*, e1584. [CrossRef] [PubMed]
163. Vega Thurber, R.; Willner-Hall, D.; Rodriguez-Mueller, B.; Desnues, C.; Edwards, R.A.; Angly, F.; Dinsdale, E.; Kelly, L.; Rohwer, F. Metagenomic analysis of stressed coral holobionts. *Environ. Microbiol.* **2009**, *11*, 2148–2163. [CrossRef]
164. Mason, B.; Hayward, D.C.; Moya, A.; Cooke, I.; Sorenson, A.; Brunner, R.; Andrade, N.; Huerlimann, R.; Bourne, D.G.; Schaeffer, P. Microbiome manipulation by corals and other Cnidaria via quorum quenching. *Curr. Biol.* **2024**, *34*, 3226–3232.e3225. [CrossRef]
165. Trench, R.K. The cell biology of plant–animal symbiosis. *Annu. Rev. Plant Biol.* **1979**, *30*, 485–531. [CrossRef]
166. Baker, A.C. Flexibility and specificity in coral–algal symbiosis: Diversity, ecology, and biogeography of *Symbiodinium*. *Annu. Rev. Ecol. Evol. Syst.* **2003**, *34*, 661–689. [CrossRef]
167. Byler, K.A.; Carmi-Veal, M.; Fine, M.; Goulet, T.L. Multiple symbiont acquisition strategies as an adaptive mechanism in the coral *Stylophora pistillata*. *PLoS ONE* **2013**, *8*, e59596. [CrossRef] [PubMed]

168. Quigley, K.M.; Warner, P.A.; Bay, L.K.; Willis, B.L. Unexpected mixed-mode transmission and moderate genetic regulation of *Symbiodinium* communities in a brooding coral. *Heredity* **2018**, *121*, 524–536. [CrossRef]
169. Apprill, A.; Marlow, H.Q.; Martindale, M.Q.; Rappé, M.S. The onset of microbial associations in the coral *Pocillopora meandrina*. *ISME J.* **2009**, *3*, 685–699. [CrossRef]
170. Padilla-Gamiño, J.L.; Pochon, X.; Bird, C.; Concepcion, G.T.; Gates, R.D. From parent to gamete: Vertical transmission of *Symbiodinium* (Dinophyceae) ITS2 sequence assemblages in the reef-building coral *Montipora capitata*. *PLoS ONE* **2012**, *7*, e38440. [CrossRef]
171. Leite, D.C.A.; Leão, P.; Garrido, A.G.; Lins, U.; Santos, H.F.; Pires, D.O.; Castro, C.B.; van Elsas, J.D.; Zilberberg, C.; Rosado, A.S.; et al. Broadcast spawning coral *Mussismilia hispida* can vertically transfer its associated bacterial core. *Front. Microbiol.* **2017**, *8*, 176. [CrossRef]
172. Quigley, K.M.; Willis, B.L.; Bay, L.K. Heritability of the *Symbiodinium* community in vertically- and horizontally-transmitting broadcast spawning corals. *Sci. Rep.* **2017**, *7*, 8219. [CrossRef]
173. Guo, M.; Jiang, L.; Zhou, G.; Lian, J.; Yu, X.; Huang, H. Diversity and dynamics of multiple symbionts contribute to early development of broadcast-spawning reef-building coral *Dipsastraea veroni*. *Appl. Environ. Microbiol.* **2025**, *91*, e02359-24. [CrossRef]
174. DeCarlo, T.M.; Harrison, H.B.; Gajdzik, L.; Alaguarda, D.; Rodolfo-Metalpa, R.; D'Olivo, J.; Liu, G.; Patalwala, D.; McCulloch, M.T. Acclimatization of massive reef-building corals to consecutive heatwaves. *Proc. R. Soc. B Biol. Sci.* **2019**, *286*, 20190235. [CrossRef] [PubMed]
175. Quigley, K.M.; Randall, C.J.; van Oppen, M.J.H.; Bay, L.K. Assessing the role of historical temperature regime and algal symbionts on the heat tolerance of coral juveniles. *Biol. Open* **2020**, *9*, bio047316. [CrossRef] [PubMed]
176. Putnam, H.M. Avenues of reef-building coral acclimatization in response to rapid environmental change. *J. Exp. Biol.* **2021**, *224*, jeb239319. [CrossRef]
177. Rubin, E.T.; Enochs, I.C.; Foord, C.; Mayfield, A.B.; Kolodziej, G.; Basden, I.; Manzello, D.P. Molecular mechanisms of coral persistence within highly urbanized locations in the Port of Miami, Florida. *Front. Mar. Sci.* **2021**, *8*, 695236. [CrossRef]
178. Hackerott, S.; Martell, H.A.; Eirin-Lopez, J.M. Coral environmental memory: Causes, mechanisms, and consequences for future reefs. *Trends Ecol. Evol.* **2021**, *36*, 1011–1023. [CrossRef]
179. Aranda Lastra, M. Epigenetics and acquired tolerance to environmental stress. In *Coral Reef Conservation and Restoration in the Omics Age*; van Oppen, M.J., Aranda Lastra, M., Eds.; Springer: Cham, Switzerland, 2022; pp. 135–150.
180. Liew, Y.J.; Zoccola, D.; Li, Y.; Tambutté, E.; Venn, A.A.; Michell, C.T.; Cui, G.; Deutekom, E.S.; Kaandorp, J.A.; Voolstra, C.R.; et al. Epigenome-associated phenotypic acclimatization to ocean acidification in a reef-building coral. *Sci. Adv.* **2018**, *4*, eaar8028. [CrossRef]
181. Liew, Y.J.; Howells, E.J.; Wang, X.; Michell, C.T.; Burt, J.A.; Idaghdour, Y.; Aranda, M. Intergenerational epigenetic inheritance in reef-building corals. *Nat. Clim. Chang.* **2020**, *10*, 254–259. [CrossRef]
182. Goulet, T.L. Most corals may not change their symbionts. *Mar. Ecol. Prog. Ser.* **2006**, *321*, 1–7. [CrossRef]
183. Voolstra, C.R.; Suggett, D.J.; Peixoto, R.S.; Parkinson, J.E.; Quigley, K.M.; Silveira, C.B.; Sweet, M.; Muller, E.M.; Barshis, D.J.; Bourne, D.G.; et al. Extending the natural adaptive capacity of coral holobionts. *Nat. Rev. Earth Environ.* **2021**, *2*, 747–762. [CrossRef]
184. Rowan, R.; Knowlton, N. Intraspecific diversity and ecological zonation in coral–algal symbiosis. *Proc. Natl. Acad. Sci. USA* **1995**, *92*, 2850–2853. [CrossRef]
185. Chen, B.; Wei, Y.; Yu, K.; Liang, Y.; Yu, X.; Liao, Z.; Qin, Z.; Xu, L.; Bao, Z. The microbiome dynamics and interaction of endosymbiotic *Symbiodiniaceae* and fungi are associated with thermal bleaching susceptibility of coral holobionts. *Appl. Environ. Microbiol.* **2024**, *90*, e01939-23. [CrossRef]
186. Aichelman, H.E.; Benson, B.E.; Gomez-Campo, K.; Martinez-Rugerio, M.I.; Fifer, J.E.; Tsang, L.; Hughes, A.M.; Bove, C.B.; Nieves, O.C.; Pereslete, A.M.; et al. Cryptic coral diversity is associated with symbioses, physiology, and response to thermal challenge. *Sci. Adv.* **2025**, *11*, eadr5237. [CrossRef]
187. Forsman, Z.H.; Ritson-Williams, R.; Tisthammer, K.H.; Knapp, I.S.S.; Toonen, R.J. Host–symbiont coevolution, cryptic structure, and bleaching susceptibility in a coral species complex (Scleractinia; Poritidae). *Sci. Rep.* **2020**, *10*, 16995. [CrossRef]
188. Smith, E.G.; Hazzouri, K.M.; Choi, J.Y.; Delaney, P.; Al-Kharafi, M.; Howells, E.J.; Aranda, M.; Burt, J.A. Signatures of selection underpinning rapid coral adaptation to the world's warmest reefs. *Sci. Adv.* **2022**, *8*, eabl7287. [CrossRef]
189. Kenkel, C.D.; Setta, S.P.; Matz, M.V. Heritable differences in fitness-related traits among populations of the mustard hill coral, *Porites astreoides*. *Heredity* **2015**, *115*, 509–516. [CrossRef]
190. Fisch, J.; Drury, C.; Towle, E.K.; Winter, R.N.; Miller, M.W. Physiological and reproductive repercussions of consecutive summer bleaching events of the threatened Caribbean coral *Orbicella faveolata*. *Coral Reefs* **2019**, *38*, 863–876. [CrossRef]
191. Rosenberg, E.; Koren, O.; Reshef, L.; Efrony, R.; Zilber-Rosenberg, I. The role of microorganisms in coral health, disease and evolution. *Nat. Rev. Microbiol.* **2007**, *5*, 355–362. [CrossRef] [PubMed]

192. Zilber-Rosenberg, I.; Rosenberg, E. Role of microorganisms in the evolution of animals and plants: The hologenome theory of evolution. *FEMS Microbiol. Rev.* **2008**, *32*, 723–735. [CrossRef]
193. Leggat, W.; Ainsworth, T.; Bythell, J.; Dove, S.; Gates, R.; Hoegh-Guldberg, O.; Iglesias-Prieto, R.; Yellowlees, D. The hologenome theory disregards the coral holobiont. *Nat. Rev. Microbiol.* **2007**, *5*, 826. [CrossRef]
194. Rosenberg, E.; Koren, O.; Reshef, L.; Efrony, R.; Zilber-Rosenberg, I. The hologenome theory disregards the coral holobiont: Reply from Rosenberg et al. *Nat. Rev. Microbiol.* **2007**, *5*, 826. [CrossRef]
195. Douglas, A.E.; Werren, J.H. Holes in the hologenome: Why host–microbe symbioses are not holobionts. *mBio* **2016**, *7*, e02099-15. [CrossRef] [PubMed]
196. Roughgarden, J.; Gilbert, S.F.; Rosenberg, E.; Zilber-Rosenberg, I.; Lloyd, E.A. Holobionts as units of selection and a model of their population dynamics and evolution. *Biol. Theory* **2018**, *13*, 44–65. [CrossRef]
197. Shinzato, C.; Mungpakdee, S.; Satoh, N.; Shoguchi, E. A genomic approach to coral–dinoflagellate symbiosis: Studies of *Acropora digitifera* and *Symbiodinium minutum*. *Front. Microbiol.* **2014**, *5*, 336. [CrossRef]
198. Bhattacharya, D.; Agrawal, S.; Aranda, M.; Baumgarten, S.; Belcaid, M.; Drake, J.L.; Erwin, D.; Foret, S.; Gates, R.D.; Gruber, D.F.; et al. Comparative genomics explains the evolutionary success of reef-forming corals. *eLife* **2016**, *5*, e13288. [CrossRef] [PubMed]
199. Gacesa, R.; Hung, J.Y.; Bourne, D.G.; Long, P.F. Horizontal transfer of a natterin-like toxin-encoding gene within the holobiont of the reef-building coral *Acropora digitifera* (Cnidaria: Anthozoa: Scleractinia) and across multiple animal lineages. *J. Venom. Res.* **2020**, *10*, 7–12.
200. Cooke, I.; Ying, H.; Forêt, S.; Bongaerts, P.; Strugnell, J.M.; Simakov, O.; Zhang, J.; Field, M.A.; Rodriguez-Lanetty, M.; Bell, S.C. Genomic signatures in the coral holobiont reveal host adaptations driven by Holocene climate change and reef-specific symbionts. *Sci. Adv.* **2020**, *6*, eabc6318. [CrossRef]
201. Rinkevich, B. Coral chimerism as an evolutionary rescue mechanism to mitigate global climate change impacts. *Glob. Chang. Biol.* **2019**, *25*, 1198–1206. [CrossRef]
202. Oury, N.; Magalon, H. Investigating the potential roles of intra-colonial genetic variability in *Pocillopora* corals using genomics. *Sci. Rep.* **2024**, *14*, 6437. [CrossRef]
203. van Oppen, M.J.H.; Souter, P.; Howells, E.J.; Heyward, A.; Berkelmans, R. Novel genetic diversity through somatic mutations: Fuel for adaptation of reef corals? *Diversity* **2011**, *3*, 405–423. [CrossRef]
204. Rinkevich, B.; Weissman, I.L. Chimeras in colonial invertebrates: A synergistic symbiosis or somatic- and germ-cell parasitism? *Symbiosis* **1987**, *4*, 117–134.
205. Frank, U.; Oren, U.; Loya, Y.; Rinkevich, B. Alloimmune maturation in the coral *Stylophora pistillata* is achieved through three distinctive stages, 4 months post-metamorphosis. *Proc. R. Soc. Lond. B Biol. Sci.* **1997**, *264*, 99–104. [CrossRef]
206. Schweinsberg, M.; Weiss, L.C.; Striewski, S.; Tollrian, R.; Lampert, K.P. More than one genotype: How common is intracolonial genetic variability in scleractinian corals? *Mol. Ecol.* **2015**, *24*, 2673–2685. [CrossRef]
207. Rinkevich, B.; Shaish, L.; Douek, J.; Ben-Shlomo, R. Venturing in coral larval chimerism: A compact functional domain with fostered genotypic diversity. *Sci. Rep.* **2016**, *6*, 19493. [CrossRef]
208. Rinkevich, B.; Shashar, N.; Liberman, T. Nontransitive xenogeneic interactions between four common Red Sea sessile invertebrates. In Proceedings of the 7th International Coral Reef Symposium, Guam, Micronesia, 22–27 June 1992; pp. 833–839.
209. Hidaka, M.; Yurugi, K.; Sunagawa, S.; Kinzie, R.A., III. Contact reactions between young colonies of the coral *Pocillopora damicornis*. *Coral Reefs* **1997**, *16*, 13–20. [CrossRef]
210. Rinkevich, B.; Loya, Y. Intraspecific competitive networks in the Red Sea coral *Stylophora pistillata*. *Coral Reefs* **1983**, *1*, 161–172. [CrossRef]
211. Willis, B.L.; Ayre, D.J. Asexual reproduction and genetic determination of growth form in the coral *Pavona cactus*: Biochemical genetic and immunogenic evidence. *Oecologia* **1985**, *65*, 516–525. [CrossRef]
212. Nozawa, Y.; Hirose, M. When does the window close? The onset of allogeneic fusion 2–3 years post-settlement in the scleractinian coral *Echinophyllia aspera*. *Zool. Stud.* **2011**, *50*, 396–404.
213. Carpenter, K.E.; Abrar, M.; Aeby, G.; Aronson, R.B.; Banks, S.; Bruckner, A.; Chiriboga, A.; Cortés, J.; Delbeek, J.C.; DeVantier, L.; et al. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* **2008**, *321*, 560–563. [CrossRef] [PubMed]
214. Huang, D. Threatened reef corals of the world. *PLoS ONE* **2012**, *7*, e34459. [CrossRef]
215. IUCN. The IUCN Red List of Threatened Species. 2025. Available online: https://www.iucnredlist.org (accessed on 20 October 2025).
216. Cavada-Blanco, F.; Croquer, A.; Vermeij, M.; Goergen, L.; Rodriguez, R. Dendrogyra cylindrus: Extinction risk assessment. In *IUCN Red List of Threatened Species*; Universiteit van Amsterdam: Amsterdam, The Netherlands, 2022. [CrossRef]
217. Sheppard, C.; Sheppard, A.; Fenner, D. Coral mass mortalities in the Chagos Archipelago over 40 years: Regional species and assemblage extinctions and indications of positive feedbacks. *Mar. Pollut. Bull.* **2020**, *154*, 111075. [CrossRef]
218. Logan, C.A.; Dunne, J.P.; Ryan, J.S.; Baskett, M.L.; Donner, S.D. Quantifying global potential for coral evolutionary response to climate change. *Nat. Clim. Chang.* **2021**, *11*, 537–542. [CrossRef]

219. Kenkel, C.D.; Matz, M.V. Gene expression plasticity as a mechanism of coral adaptation to a variable environment. *Nat. Ecol. Evol.* **2016**, *1*, 0014. [CrossRef]
220. Lachs, L.; Donner, S.D.; Mumby, P.J.; Bythell, J.C.; Humanes, A.; East, H.K.; Guest, J.R. Emergent increase in coral thermal tolerance reduces mass bleaching under climate change. *Nat. Commun.* **2023**, *14*, 4939. [CrossRef] [PubMed]
221. Lachs, L.; Bozec, Y.-M.; Bythell, J.C.; Donner, S.D.; East, H.K.; Edwards, A.J.; Golbuu, Y.; Gouezo, M.; Guest, J.R.; Humanes, A. Natural selection could determine whether *Acropora* corals persist under expected climate change. *Science* **2024**, *386*, 1289–1294. [CrossRef] [PubMed]
222. Dixon, A.M.; Forster, P.M.; Heron, S.F.; Stoner, A.M.K.; Beger, M. Future loss of local-scale thermal refugia in coral reef ecosystems. *PLoS Clim.* **2022**, *1*, e0000004. [CrossRef]
223. Lachs, L.; Humanes, A.; Mumby, P.J.; Donner, S.D.; Bythell, J.; Beauchamp, E.; Bukurou, L.; Buzzoni, D.; de la Torre Cerro, R.; East, H.K.; et al. High coral heat tolerance at local-scale thermal refugia. *PLoS Clim.* **2024**, *3*, e0000453. [CrossRef]
224. Serrano, X.; Baums, I.; O'Reilly, K.; Smith, T.; Jones, R.; Shearer, T.; Nunes, F.; Baker, A. Geographic differences in vertical connectivity in the Caribbean coral *Montastraea cavernosa* despite high levels of horizontal connectivity at shallow depths. *Mol. Ecol.* **2014**, *23*, 4226–4240. [CrossRef]
225. Humanes, A.; Lachs, L.; Beauchamp, E.A.; Bythell, J.C.; Edwards, A.J.; Golbuu, Y.; Martinez, H.M.; Palmowski, P.; Treumann, A.; van der Steeg, E.; et al. Within-population variability in coral heat tolerance indicates climate adaptation potential. *Proc. R. Soc. B Biol. Sci.* **2022**, *289*, 20220872. [CrossRef]
226. van Oppen, M.J.H.; Oliver, J.K.; Putnam, H.M.; Gates, R.D. Building coral reef resilience through assisted evolution. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 2307–2313. [CrossRef]
227. Cruz, D.W.d.; Harrison, P.L. Enhanced larval supply and recruitment can replenish reef corals on degraded reefs. *Sci. Rep.* **2017**, *7*, 13985. [CrossRef]
228. Montilla, L.M.; Ascanio, A.; Verde, A.; Croquer, A. Systematic review and meta-analysis of 50 years of coral disease research visualized through the scope of network theory. *PeerJ* **2019**, *7*, e7041. [CrossRef]
229. Burke, S.; Pottier, P.; Macartney, E.L.; Drobniak, S.M.; Lagisz, M.; Ainsworth, T.; Nakagawa, S. Mapping literature reviews on coral health: Protocol for a review map, critical appraisal and bibliometric analysis. *Ecol. Solut. Evid.* **2022**, *3*, e12190. [CrossRef]
230. Muller, E.M.; Sartor, C.; Alcaraz, N.I.; van Woesik, R. Spatial epidemiology of the Stony Coral Tissue Loss Disease in Florida. *Front. Mar. Sci.* **2020**, *7*, 163. [CrossRef]
231. Neely, K.L.; Macaulay, K.A.; Hower, E.K.; Dobler, M.A. Effectiveness of topical antibiotics in treating corals affected by Stony Coral Tissue Loss Disease. *PeerJ* **2020**, *8*, e9289. [CrossRef] [PubMed]
232. MacKnight, N.J.; Dimos, B.A.; Beavers, K.M.; Muller, E.M.; Brandt, M.E.; Mydlarz, L.D. Disease resistance in coral is mediated by distinct adaptive and plastic gene expression profiles. *Sci. Adv.* **2022**, *8*, eabo6153. [CrossRef] [PubMed]
233. Vollmer, S.V.; Kline, D.I. Natural disease resistance in threatened staghorn corals. *PLoS ONE* **2008**, *3*, e3718. [CrossRef] [PubMed]
234. Veron, J.E.N.; Stafford-Smith, M.G.; DeVantier, L.M.; Turak, E. Overview of distribution patterns of zooxanthellate Scleractinia. *Front. Mar. Sci.* **2015**, *1*, 81. [CrossRef]
235. DeVantier, L.; Turak, E. Species richness and relative abundance of reef-building corals in the Indo-West Pacific. *Diversity* **2017**, *9*, 25. [CrossRef]
236. Veron, J.E.N.; Stafford-Smith, M.G.; DeVantier, L.M.; Turak, E. CoralsOfTheWorld.org Version 2026.00 in prep. Available online in 2026.
237. Veron, J.E.N.; Wallace, C. *Scleractinia of Eastern Australia. Part V. Family Acroporidae*; Australian Institute of Marine Science Monograph Series; Australian Institute of Marine Science: Townsville, QLD, Australia, 1984; Volume 6, 485p. Available online: https://www.biodiversitylibrary.org/page/39933506 (accessed on 20 August 2025).
238. Veron, J.E.N. *Corals of Australia and the Indo-Pacific*; University of Hawai'i Press: Honolulu, HI, USA, 1986; 642p.
239. Underwood, J.N. Genetic diversity and divergence among coastal and offshore reefs in a hard coral depend on geographic discontinuity and oceanic currents. *Evol. Appl.* **2009**, *2*, 222–233. [CrossRef]
240. Turak, E.; DeVantier, L. Reef-building corals of the upper mesophotic zone of the Central Indo-West Pacific. In *Mesophotic Coral Ecosystems*; Loya, Y., Puglise, K.A., Bridge, T.C., Eds.; Coral Reefs of the World; Springer International Publishing: Cham, Switzerland, 2019; Volume 12, Chapter 34; pp. 621–651.
241. Loya, Y.; Puglise, K.A.; Bridge, T.C. (Eds.) *Mesophotic Coral Ecosystems*; Coral Reefs of the World; Springer International Publishing: Cham, Switzerland, 2019; Volume 12, 1024p.
242. Malik, A.; Einbinder, S.; Martinez, S.; Tchernov, D.; Haviv, S.; Almuly, R.; Zaslansky, P.; Polishchuk, I.; Pokroy, B.; Stolarski, J.; et al. Molecular and skeletal fingerprints of scleractinian coral biomineralization: From the sea surface to mesophotic depths. *Acta Biomater.* **2021**, *120*, 263–276. [CrossRef] [PubMed]
243. Luck, D.G.; Forsman, Z.H.; Toonen, R.J.; Leicht, S.J.; Kahng, S.E. Polyphyly and hidden species among Hawai'i's dominant mesophotic coral genera, *Leptoseris* and *Pavona* (Scleractinia: Agariciidae). *PeerJ* **2013**, *1*, e132. [CrossRef]

244. Gijsbers, J.C.; Englebert, N.; Prata, K.E.; Pichon, M.; Dinesen, Z.; Brunner, R.; Eyal, G.; González-Zapata, F.L.; Kahng, S.E.; Latijnhouwers, K.R.W.; et al. Global phylogenomic assessment of *Leptoseris* and *Agaricia* reveals substantial undescribed diversity at mesophotic depths. *BMC Biol.* **2023**, *21*. [CrossRef]
245. Gallery, D.N.; Rippe, J.P.; Matz, M.V. Decrypting corals: Does regulatory evolution underlie environmental specialisation of coral cryptic lineages? *Molec. Ecol.* **2025**, *34*, e17546. [CrossRef]
246. Rippe, J.P.; Dixon, G.; Fuller, Z.L.; Liao, Y.; Matz, M. Environmental specialization and cryptic genetic divergence in two massive coral species from the Florida Keys Reef Tract. *Mol. Ecol.* **2021**, *30*, 3468–3484. [CrossRef]
247. Bongaerts, P.; Cooke, I.R.; Ying, H.; Wels, D.; den Haan, S.; Hernandez-Agreda, A.; Brunner, C.A.; Dove, S.; Englebert, N.; Eyal, G. Morphological stasis masks ecologically divergent coral species on tropical reefs. *Curr. Biol.* **2021**, *31*, 2286–2298.e8. [CrossRef]
248. Zapata, F.; Jiménez, I. Species delimitation: Inferring gaps in morphology across geography. *Syst. Biol.* **2012**, *61*, 179. [CrossRef] [PubMed]
249. Więcław, H.; Bosiacka, B.; Hrivnák, R.; Dajdok, Z.; Mesterházy, A.; Koopman, J. Morphological variability of *Carex buekii* (Cyperaceae) as a function of soil conditions: A case study of the Central European populations. *Sci. Rep.* **2022**, *12*, 15894. [CrossRef] [PubMed]
250. Seka, D.; Kouago, B.A.; Bonny, B.S. Assessment of the variability of the morphological traits and differentiation of *Cucurbita moschata* in Côte d'Ivoire. *Sci. Rep.* **2023**, *13*, 30295. [CrossRef]
251. Tsuchiya, K.; Zayasu, Y.; Nakajima, Y.; Arakaki, N.; Suzuki, G.; Satoh, N.; Shinzato, C. Genomic analysis of a reef-building coral, *Acropora digitifera*, reveals complex population structure and a migration network in the Nansei Islands, Japan. *Mol. Ecol.* **2022**, *31*, 5270–5284. [CrossRef]
252. Wang, S.; Yoder, A.D. Synergies between speciation and conservation science yield novel insights for mitigating the biodiversity crisis of the Anthropocene. *Proc. Natl. Acad. Sci. USA* **2025**, *122*, e2500713122. [CrossRef]
253. Yang, H.; Lohmann, G.; Wei, W.; Dima, M.; Ionita, M.; Liu, J. Intensification and poleward shift of subtropical western boundary currents in a warming climate. *J. Geophys. Res. Oceans* **2016**, *121*, 4928–4945. [CrossRef]
254. Fifer, J.E.; Yasuda, N.; Yamakita, T.; Bove, C.B.; Davies, S.W. Genetic divergence and range expansion in a western North Pacific coral. *Sci. Total Environ.* **2022**, *813*, 152423. [CrossRef]
255. Johannes, R.; Wiebe, W.; Crossland, C.; Rimmer, D.; Smith, S. Latitudinal limits of coral reef growth. *Mar. Ecol. Prog. Ser.* **1983**, *11*, 105–111. [CrossRef]
256. Kleypas, J.A.; McManus, J.W.; Menez, L.A.B. Environmental limits to coral reef development: Where do we draw the line? *Am. Zool.* **1999**, *39*, 146–159. [CrossRef]
257. Abrego, D.; Howells, E.J.; Smith, S.D.; Madin, J.S.; Sommer, B.; Schmidt-Roach, S.; Cumbo, V.R.; Thomson, D.P.; Rosser, N.L.; Baird, A.H. Factors limiting the range extension of corals into high-latitude reef regions. *Diversity* **2021**, *13*, 632. [CrossRef]
258. O'Connell, M.J.; Fowler, A.M.; Allan, S.J.; Beretta, G.A.; Booth, D.J. Subtropical coral expansion into SE Australia: A haven for both temperate and expatriating tropical reef fishes. *Coral Reefs* **2023**, *42*, 1257–1262. [CrossRef]
259. Riginos, C.; Hock, K.; Matias, A.M.; Mumby, P.J.; van Oppen, M.J.H.; Lukoschek, V. Asymmetric dispersal is a critical element of concordance between biophysical dispersal models and spatial genetic structure in Great Barrier Reef corals. *Divers. Distrib.* **2019**, *25*, 1684–1696. [CrossRef]
260. Kamata, M.; Kitano, Y.F.; Iguchi, A.; Nozawa, Y.; Nagai, S.; Chen, C.A.; Wada, N.; Tang, S.-L.; Yamakita, T.; Taninaka, H.; et al. Genetic divergence of *Pocillopora damicornis* between temperate and subtropical regions: The need to monitor hidden genetic lineage distribution with regard to migration-load risks under climate change. *Bull. Mar. Sci.* **2025**, *101*, 91–104. [CrossRef]
261. Veron, J.E.N. *Hermatypic Corals of Japan*; Australian Institute of Marine Science: Townsville, QLD, Australia, 1992; Volume 9, 244p.
262. Fujii, T. Catalaphyllia jardinei (Saville-Kent, 1893). In *Online Monograph of Zooxanthellate Corals of Japan*; JST: Tokyo, Japan, 2024.
263. Veron, J.E.N.; How, R.A.; Done, T.J.; Zell, L.D.; Dodkin, M.J.; O'Farrell, A.F. Corals of the Solitary Islands, New South Wales. *Aust. J. Mar. Freshw. Res.* **1974**, *25*, 193–208. [CrossRef]
264. Van Woesik, R. Coral communities at high latitude are not pseudopopulations: Evidence of spawning at 32° N, Japan. *Coral Reefs* **1995**, *14*, 119–120. [CrossRef]
265. Harrison, P.L. Coral spawn slicks at Lord Howe Island, Tasman Sea, Australia; the world's most southerly coral reef. *Coral Reefs* **2008**, *27*, 35. [CrossRef]
266. Yamashiro, H.; Nishihira, M. Radial skeletal dissolution to promote vegetative reproduction in a solitary coral *Diaseris distorta*. *Experientia* **1994**, *50*, 497–498. [CrossRef]
267. Yamashiro, H.; Nishihira, M. Experimental study of growth and asexual reproduction in *Diaseris distorta* (Michelin, 1843), a free-living fungiid coral. *J. Exp. Mar. Biol. Ecol.* **1998**, *225*, 253–267. [CrossRef]
268. Yamashiro, H.; Hidaka, M.; Poung-In, S. Morphological studies on skeletons of *Diaseris fragilis*, a free-living coral which reproduces asexually by natural autotomy. *Galaxea* **1989**, *8*, 283–294.
269. Hoeksema, B.W. Impact of budding on free-living corals at East Kalimantan, Indonesia. *Coral Reefs* **2004**, *23*, 492. [CrossRef]

270. Hoeksema, B.W.; Gittenberger, A. High densities of mushroom coral fragments at West Halmahera, Indonesia. *Coral Reefs* **2010**, *29*, 691. [CrossRef]
271. Grupstra, C.G.; Gómez-Corrales, M.; Fifer, J.E.; Aichelman, H.E.; Meyer-Kaiser, K.S.; Prada, C.; Davies, S.W. Integrating cryptic diversity into coral evolution, symbiosis and conservation. *Nat. Ecol. Evol.* **2024**, *8*, 622–636. [CrossRef] [PubMed]
272. Mallet, J. A species definition for the modern synthesis. *Trends Ecol. Evol.* **1995**, *10*, 294–299. [CrossRef] [PubMed]
273. De Queiroz, K. Species concepts and species delimitation. *Syst. Biol.* **2007**, *56*, 879–886. [CrossRef]
274. Stat, M.; Baker, A.C.; Bourne, D.G.; Correa, A.M.S.; Forsman, Z.; Huggett, M.J.; Pochon, X.; Skillings, D.; Toonen, R.J.; van Oppen, M.J.H.; et al. Molecular delineation of species in the coral holobiont. *Adv. Mar. Biol.* **2012**, *63*, 1–65.
275. Huang, M.; Lawes, M.J.; Zhou, W.; Wei, F. Integrating hotspot dynamics and centers of diversity: A review of Indo-Australian Archipelago biogeographic evolution and conservation. *Mar. Life Sci. Technol.* **2025**, *7*, 420–433. [CrossRef]
276. Lotsy, J.P. Species or linneon. *Genetica* **1925**, *7*, 487–506. [CrossRef]
277. Suarez-Gonzalez, A.; Lexer, C.; Cronk, Q.C. Adaptive introgression: A plant perspective. *Biol. Lett.* **2018**, *14*, 20170688. [CrossRef]
278. Cannon, C.H.; Petit, R.J. The oak syngameon: More than the sum of its parts. *New Phytol.* **2020**, *226*, 978–983. [CrossRef]
279. Buck, R.; Flores-Rentería, L. The syngameon enigma. *Plants* **2022**, *11*, 895. [CrossRef]
280. Boecklen, W.J. Topology of syngameons. *Ecol. Evol.* **2017**, *7*, 10486–10491. [CrossRef] [PubMed]
281. Mallet, J. Hybridization as an invasion of the genome. *Trends Ecol. Evol.* **2005**, *20*, 229–237. [CrossRef] [PubMed]
282. Zlatarski, V.N.; Martínez Estalella, N. *Les Scléractiniaires de Cuba avec des Données sur les Organismes Associés*; Académie Bulgare des Sciences: Sofia, Bulgaria, 1982; 472p.
283. Hoeksema, B.W.; Moka, W. Species assemblages and phenotypes of mushroom corals (Fungiidae) related to coral reef habitats in the Flores Sea. *Neth. J. Sea Res.* **1989**, *23*, 149–160. [CrossRef]
284. Wells, J.W. Recent corals of the Marshall Islands. *Prof. Pap. U.S. Geol. Surv.* **1954**, *260*, 385–486, pls. 94–185.
285. Wallace, C.C. *Staghorn Corals of the World: A Revision of the Genus Acropora*; CSIRO Publishing: Collingwood, VIC, Australia, 1999; 422p.
286. Dana, J.D. *Zoophytes*; Lea and Blanchard: Philadelphia, PA, USA, 1846; Volume 7, 740p.
287. Milne Edwards, H.; Haime, J. Recherches sur les polypiers; Quatrième mémoire. Monographie des astréides (1). Astréens (Astreinae). *Ann. Sci. Nat. Ser. 3* **1849**, *11*, 233–312.
288. Milne Edwards, H. Troisième sous-ordre. Zoanthaires Sclérodermés (Zoantharia Sclerodermata) ou Madréporaires. In *Histoire Naturelle des Coralliaires ou Polypes Proprement Dits*; Milne Edwards, H., Ed.; Librairie Encyclopédique de Roret: Paris, France, 1857; Tome 2, 633p.
289. Brook, G. Descriptions of new species of *Madrepora* in the collection of the British Museum. *Ann. Mag. Nat. Hist.* **1891**, *6*, 458–465. [CrossRef]
290. Brook, G. Preliminary descriptions of new species of *Madrepora* in the collection of the British Museum. *Part II. Ann. Mag. Nat. Hist.* **1892**, *6*, 451–465. [CrossRef]
291. Brook, G. The Genus *Madrepora*. *Cat. Madreporarian Corals Br. Mus. (Nat. Hist.)* **1893**, *1*, 1–212.
292. Bernard, H.M. The Genus *Turbinaria*. The Genus *Astraeopora*. *Cat. Madreporarian Corals Br. Mus. (Nat. Hist.)* **1896**, *2*, 1–106.
293. Bernard, H.M. The Genus *Montipora*. The Genus *Anacropora*. *Cat. Madreporarian Corals Br. Mus. (Nat. Hist.)* **1897**, *3*, 1–192.
294. Bernard, H.M. On the Madreporaria collected by Mr. C.W. Andrews at Christmas Island. *Proc. Zool. Soc. Lond.* **1900**, *70*, 119–127.
295. Veron, J.E.N.; Pichon, M.; Wijsman-Best, M. *Scleractinia of Eastern Australia. Part II. Families Faviidae, Trachyphylliidae*; Australian Institute of Marine Science Monograph Series; Australian Institute of Marine Science: Townsville, QLD, Australia, 1977; Volume 3, 233p. Available online: https://www.biodiversitylibrary.org/page/39926438 (accessed on 20 August 2025).
296. Veron, J.E.N.; Pichon, M. *Scleractinia of Eastern Australia. Part III. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae*; Australian Institute of Marine Science Monograph Series; Australian Institute of Marine Science: Townsville, QLD, Australia, 1980; Volume 4, 422p. Available online: https://www.biodiversitylibrary.org/page/39939812 (accessed on 20 August 2025).
297. Veron, J.E.N.; Pichon, M. *Scleractinia of Eastern Australia. Part IV. Family Poritidae*; Australian Institute of Marine Science Monograph Series; Australian Institute of Marine Science: Townsville, QLD, Australia, 1982; Volume 5, 159p. Available online: https://www.biodiversitylibrary.org/page/39927540 (accessed on 20 August 2025).
298. Bouwmeester, J.; Benzoni, F.; Baird, A.H.; Berumen, M.L. *Cyphastrea kausti* sp. n. (Cnidaria, Anthozoa, Scleractinia), a New Species of Reef Coral from the Red Sea. *ZooKeys* **2015**, *496*, 1–13. [CrossRef]
299. Baird, A.H.; Hoogenboom, M.O.; Huang, D. *Cyphastrea salae*, a new species of hard coral from Lord Howe Island, Australia (Scleractinia, Merulinidae). *ZooKeys* **2017**, *662*, 49–66. [CrossRef]
300. Arrigoni, R.; Berumen, M.L.; Mariappan, K.G.; Beck, P.S.; Hulver, A.M.; Montano, S.; Pichon, M.; Strona, G.; Terraneo, T.I.; Benzoni, F. Towards a rigorous species delimitation framework for scleractinian corals based on RAD sequencing: The case study of *Leptastrea* from the Indo-Pacific. *Coral Reefs* **2020**, *39*, 1001–1025. [CrossRef]

301. Arrigoni, R.; Benzoni, F.; Huang, D.; Fukami, H.; Chen, C.A.; Berumen, M.L.; Hoogenboom, M.; Thomson, D.P.; Hoeksema, B.W.; Budd, A.F.; et al. When forms meet genes: Revision of the scleractinian genera *Micromussa* and *Homophyllia* (Lobophylliidae) with a description of two new species and one new genus. *Contrib. Zool.* **2016**, *85*, 387–422. [CrossRef]
302. Ng, C.S.L.; Jain, S.S.; Nguyen, N.T.H.; Sam, S.Q.; Kikuzawa, Y.P.; Chou, L.M.; Huang, D. New genus and species record of reef coral *Micromussa amakusensis* in the southern South China Sea. *Mar. Biodivers. Rec.* **2019**, *12*, 17. [CrossRef]
303. Arrigoni, R.; Berumen, M.L.; Chen, C.A.; Terraneo, T.I.; Baird, A.H.; Payri, C.; Benzoni, F. Species delimitation in the reef coral genera *Echinophyllia* and *Oxypora* (Scleractinia, Lobophylliidae) with a description of two new species. *Mol. Phylogenet. Evol.* **2016**, *105*, 146–159. [CrossRef]
304. CITES. *Convention on International Trade in Endangered Species of Wild Fauna and Flora*; CITES: Geneva, Switzerland, 2025. Available online: https://cites.org/eng (accessed on 20 October 2025).
305. Veron, J.E.N. The potential of type species to destabilise the taxonomy of zooxanthellate Scleractinia. *Zootaxa* **2015**, *4048*, 433–435. [CrossRef] [PubMed]
306. Wallace, C.C.; Done, B.J.; Muir, P.R. Revision and catalogue of worldwide staghorn corals *Acropora* and *Isopora* (Scleractinia: Acroporidae). *Mem. Qld. Mus.* **2012**, *57*, 1–255.
307. WoRMS. World Register of Marine Species. Available online: https://www.marinespecies.org (accessed on 20 October 2025).
308. Roberty, S.; Vega de Luna, F.; Pierangelini, M.; Bomhals, J.; Plumier, J.-C.; Levy, O.; Cardol, P. Shallow and mesophotic colonies of the coral *Stylophora pistillata* share similar regulatory strategies of photosynthetic electron transport but differ in their sensitivity to light. *Coral Reefs* **2023**, *42*, 645–659. [CrossRef]
309. Ricardo, G.F.; Doropoulos, C.; Babcock, R.C.; Adam, A.A.S.; Buccheri, E.; Robledo, N.; Uribe-Palomino, J.; Mumby, P.J. Spawning asynchrony and mixed reproductive strategies in a common mass spawning coral. *Ecol. Evol.* **2025**, *15*, e71654. [CrossRef]
310. Frade, P.R.; Hoey, J.A.; Goodbody-Gringley, G.; Latijnhouwers, K.R.; Silberhumer, H.E.; Muir, P.; Bongaerts, P. Hybridization as driving force for cryptic species diversity in the Caribbean coral genus *Madracis*. *Sci. Rep.* **2025**, *15*, 33359. [CrossRef]
311. Helmkampf, M.; Coulmance, F.; Heckwolf, M.J.; Acero, P.A.; Balard, A.; Bista, I.; Dominguez, O.D.; Frandsen, P.B.; Torres-Oliva, M.; Santaquiteria, A.; et al. Radiation with reproductive isolation in the near-absence of phylogenetic signal. *Sci. Adv.* **2025**, *11*, eadt0973. [CrossRef]
312. Arrigoni, R.; Benzoni, F.; Terraneo, T.I.; Caragnano, A.; Berumen, M.L. Recent origin and semi-permeable species boundaries in the scleractinian coral genus *Stylophora* from the Red Sea. *Sci. Rep.* **2016**, *6*, 34612. [CrossRef]
313. Keshavmurthy, S.; Yang, S.-Y.; Alamaru, A.; Chuang, Y.-Y.; Pichon, M.; Obura, D.; Fontana, S.; De Palmas, S.; Stefani, F.; Benzoni, F. DNA barcoding reveals the coral "laboratory-rat", *Stylophora pistillata* encompasses multiple identities. *Sci. Rep.* **2013**, *3*, 1520. [CrossRef]
314. Meziere, Z.; Rich, W.A.; Carvalho, S.; Benzoni, F.; Morán, X.A.G.; Berumen, M.L. *Stylophora* under stress: A review of research trends and impacts of stressors on a model coral species. *Sci. Total Environ.* **2022**, *816*, 151639. [CrossRef]
315. Klueter, A.; Andreakis, N. Assessing genetic diversity in the scleractinian coral *Stylophora pistillata* (Esper 1797) from the Central Great Barrier Reef and the Coral Sea. *Syst. Biodivers.* **2013**, *11*, 67–76. [CrossRef]
316. Buitrago-López, C.; Cárdenas, A.; Hume, B.C.; Gosselin, T.; Staubach, F.; Aranda, M.; Barshis, D.J.; Sawall, Y.; Voolstra, C.R. Disparate population and holobiont structure of pocilloporid corals across the Red Sea gradient demonstrate species-specific evolutionary trajectories. *Mol. Ecol.* **2023**, *32*, 2151–2173. [CrossRef] [PubMed]
317. Rachmilovitz, E.N.; Douek, J.; Rinkevich, B. Population genetics assessment of the model coral species *Stylophora pistillata* from Eilat, the Red Sea. *J. Mar. Sci. Eng.* **2024**, *12*, 315. [CrossRef]
318. Takabayashi, M.M.; Carter, D.D.; Lopez, J.J.; Hoegh-Guldberg, O.O. Genetic variation of the scleractinian coral *Stylophora pistillata*, from western Pacific reefs. *Coral Reefs* **2003**, *22*, 17–22. [CrossRef]
319. Monroe, A. Genetic Differentiation Across Multiple Spatial Scales of the Red Sea of the Corals *Stylophora pistillata* and *Pocillopora verrucosa*. Master's Thesis, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia, 2015; 45p.
320. Smith-Keune, C.; van Oppen, M. Genetic structure of a reef-building coral from thermally distinct environments on the Great Barrier Reef. *Coral Reefs* **2006**, *25*, 493–502. [CrossRef]
321. Dixon, G.B.; Davies, S.W.; Aglyamova, G.V.; Meyer, E.; Bay, L.K.; Matz, M.V. Genomic determinants of coral heat tolerance across latitudes. *Science* **2015**, *348*, 1460–1462. [CrossRef] [PubMed]
322. Warner, P.A.; van Oppen, M.J.H.; Willis, B.L. Unexpected cryptic species diversity in the widespread coral *Seriatopora hystrix* masks spatial-genetic patterns of connectivity. *Mol. Ecol.* **2015**, *24*, 2993–3008. [CrossRef]
323. Sturm, A.B.; Eckert, R.J.; Carreiro, A.M.; Simões, N.; Voss, J.D. Depth-dependent genetic structuring of a depth-generalist coral and its *Symbiodiniaceae* algal communities at Campeche Bank, Mexico. *Front. Mar. Sci.* **2022**, *9*, 835789. [CrossRef]
324. Jia, S.; Wu, Z.; Li, Y.; Wang, Y.; Cai, Z.; Shen, J.; Wang, D.; Chen, S. Environmental heterogeneity contributes to population genetic diversity and spatial genetic structure of coral–algal symbiosis of *Platygyra daedalea* in the northern South China Sea. *Ecol. Indic.* **2023**, *154*, 110599. [CrossRef]

325. Black, K.L.; Rippe, J.P.; Matz, M.V. Environmental drivers of genetic divergence in two corals from the Florida Keys. *Evol. Appl.* **2025**, *18*, e70126. [CrossRef]
326. Cabacungan, G.N.; Waduwara Kankanamalage, T.N.; Azam, A.F.; Collins, M.R.; Arratia, A.R.; Gutting, A.N.; Matz, M.V.; Black, K.L. Cryptic coral community composition across environmental gradients. *PLoS ONE* **2025**, *20*, e0318653. [CrossRef]
327. Benzoni, F.; Stefani, F. *Porites fontanesii*, a new species of hard coral (Scleractinia, Poritidae) from the southern Red Sea, the Gulf of Tadjoura, and the Gulf of Aden, and its phylogenetic relationships within the genus. *Zootaxa* **2012**, *3447*, 56–68. [CrossRef]
328. Pichon, M.; Chuang, Y.Y.; Chen, C.A. *Pseudosiderastrea formosa* sp. nov. (Cnidaria: Anthozoa: Scleractinia) a new coral species endemic to Taiwan. *Zool. Stud.* **2012**, *51*, 93–98.
329. Schmidt-Roach, S.; Miller, K.; Andreakis, N. *Pocillopora aliciae*: A new species of scleractinian coral (Scleractinia, Pocilloporidae) from subtropical Eastern Australia. *Zootaxa* **2013**, *3626*, 576–582. [CrossRef]
330. Benzoni, F.; Arrigoni, R.; Waheed, Z.; Stefani, F.; Hoeksema, B.W. Phylogenetic relationships and revision of the genus *Blastomussa* (Cnidaria: Anthozoa: Scleractinia) with description of a new species. *Raffles Bull. Zool.* **2014**, *62*, 358–378.
331. Terraneo, T.I.; Berumen, M.L.; Arrigoni, R.; Waheed, Z.; Bouwmeester, J.; Caragnano, A.; Stefani, F.; Benzoni, F. *Pachyseris inattesa* sp. n. (Cnidaria, Anthozoa, Scleractinia): A new reef coral species from the Red Sea and its phylogenetic relationships. *ZooKeys* **2014**, *433*, 1–30. [CrossRef]
332. Schmidt-Roach, S.; Miller, K.J.; Lundgren, P.; Andreakis, N. With eyes wide open: A revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics *Zool. J. Linn. Soc.* **2014**, *170*, 1–30. [CrossRef]
333. Arrigoni, R.; Berumen, M.L.; Huang, D.; Terraneo, T.I.; Benzoni, F. *Cyphastrea* (Cnidaria: Scleractinia: Merulinidae) in the Red Sea: Phylogeny and a new reef coral species. *Invertebr. Syst.* **2017**, *31*, 141–156. [CrossRef]
334. Arrigoni, R.; Berumen, M.L.; Stolarski, J.; Terraneo, T.I.; Benzoni, F. Uncovering hidden coral diversity: A new cryptic lobophylliid scleractinian from the Indian Ocean. *Cladistics* **2019**, *35*, 301–328. [CrossRef]
335. Terraneo, T.I.; Benzoni, F.; Baird, A.H.; Arrigoni, R.; Berumen, M.L. Morphology and molecules reveal two new species of *Porites* (Scleractinia, Poritidae) from the Red Sea and the Gulf of Aden. *Syst. Biodivers.* **2019**, *17*, 491–508. [CrossRef]
336. Kishi, D.; Nomura, K.; Nozawa, Y.; Arakaki, S.; Fukami, H. *Paragoniastrea variabilis* Kishi, Nomura & Fukami, sp. nov. (Cnidaria, Anthozoa, Scleractinia), a new coral species previously considered as a variant of *Paragoniastrea deformis*, from Japan and northern Taiwan. *ZooKeys* **2024**, *1205*, 205–222. [CrossRef]
337. Mao, Y. Genomic insights into hybridization of reef corals. *Coral Reefs* **2020**, *39*, 61–67. [CrossRef]
338. Verrill, A.E. Synopsis of the polyps and corals of the North Pacific Exploring Expedition, 1853–1856, with descriptions of some additional species from the West Coast of North America. *III. Madreporaria. Commun. Essex Inst.* **1866**, *5*, 17–32.
339. Bernard, H.M. The Family Poritidae. I. The Genus *Goniopora*. *Cat. Madreporarian Corals Br. Mus. (Nat. Hist.)* **1903**, *4*, 1–206.
340. Bernard, H.M. The Family Poritidae. II. The Genus *Porites*. *Cat. Madreporarian Corals Br. Mus. (Nat. Hist.)* **1905**, *5*, 1–303.
341. Bernard, H.M. The Family Poritidae. II. The Genus *Porites* Part II. *Porites* of the Atlantic and West Indies, with the European fossil forms. The Genus *Goniopora*, a supplement to Volume IV. *Cat. Madreporarian Corals Br. Mus. (Nat. Hist.)* **1906**, *6*, 1–173.
342. Bernard, H.M. On the structure of *Porites*, with preliminary notes on the soft parts. *J. Linn. Soc. Lond. Zool.* **1900**, *27*, 487–503. [CrossRef]
343. Bernard, H.M. The prototheca of the Madreporaria, with special reference to the genera *Calostylis* Linds. and *Moseleya* Quelch. *J. Nat. Hist.* **1904**, *13*, 1–33. [CrossRef]
344. Huang, D.; Benzoni, F.; Fukami, H.; Knowlton, N.; Smith, N.D.; Budd, A.F. Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia). *Zool. J. Linn. Soc.* **2014**, *171*, 277–355. [CrossRef]
345. Huang, D.; Arrigoni, R.; Benzoni, F.; Fukami, H.; Knowlton, N.; Smith, N.D.; Stolarski, J.; Chou, L.M.; Budd, A.F. Taxonomic classification of the reef coral family Lobophylliidae (Cnidaria: Anthozoa: Scleractinia). *Zool. J. Linn. Soc.* **2016**, *178*, 436–481. [CrossRef]
346. Fautin, D.G. Hexacorallians of the World. 2013. Available online: http://ipt.iobis.org/caribbeanobis/resource?r=hexacoralliansoftheworld (accessed on 20 October 2025).
347. Atlas of Living Australia. Available online: http://www.ala.org.au (accessed on 20 August 2025).
348. CORDIO. *Coastal Oceans Research and Development—Indian Ocean*; CORDIO: Mombasa, Kenya, 1999. Available online: https://cordioea.net (accessed on 20 August 2025).
349. Reeflex. *Interactive Online Encyclopedia for Marine Life and Its Husbandry*; Reeflex: Rome, Italy, 2000. Available online: https://www.reeflex.net (accessed on 20 August 2025).
350. Veron, J.E.N.; Turak, E.; DeVantier, L.M.; Stafford-Smith, M.G. New and revised genera and species of reef-building corals from the Indo-Pacific. in prep.
351. GenBank. *National Center for Biotechnology Information*; GenBank: Bethesda, MD, USA, 2022. Available online: https://www.ncbi.nlm.nih.gov/genbank (accessed on 20 August 2025).

352. Han, T.; Liao, X.; Guo, Z.; Chen, J.-Y.; He, C.; Lu, Z. Comparative transcriptome analysis reveals deep molecular landscapes in stony coral *Montipora* clade. *Front. Genet.* **2023**, *14*, 1297483. [CrossRef]
353. Hennig, W. *Grundzüge Einer Theorie der Phylogenetischen Systematik*; Deutscher Zentralverlag: Berlin, Germany, 1950; 370p.
354. Hennig, W. *Phylogenetic Systematics*; University of Illinois Press: Urbana, IL, USA, 1966; 265p.
355. Mayr, E. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*; Harvard University Press: Cambridge, MA, USA, 1982; 974p.
356. Rieppel, O. Willi Hennig's dichotomization of nature. *Cladistics* **2011**, *27*, 103–112. [CrossRef] [PubMed]
357. McDade, L.A. Hybrids and phylogenetic systematics II. The impact of hybrids on cladistic analysis. *Evolution* **1992**, *46*, 1329–1346. [CrossRef]
358. Hull, D.L. The limits of cladism. *Syst. Biol.* **1979**, *28*, 416–440. [CrossRef]
359. Reeves, P.A.; Richards, C.M. Distinguishing terminal monophyletic groups from reticulate taxa: Performance of phenetic, tree-based and network procedures. *Syst. Biol.* **2007**, *56*, 302–320. [CrossRef]
360. Degnan, J.H.; Rosenberg, N.A. Gene tree discordance, phylogenetic inference and the multispecies coalescent. *Trends Ecol. Evol.* **2009**, *24*, 332–340. [CrossRef]
361. Mallet, J.; Besansky, N.; Hahn, M.W. How reticulated are species? *BioEssays* **2016**, *38*, 140–149. [CrossRef]
362. Ronquist, F.; Huelsenbeck, J.P. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **2003**, *19*, 1572–1574. [CrossRef]
363. Gittenberger, A.; Reijnen, B.T.; Hoeksema, B.W. A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. *Contrib. Zool.* **2011**, *80*, 107–132. [CrossRef]
364. Arrigoni, R.; Richards, Z.T.; Chen, C.A.; Baird, A.H. Taxonomy and phylogenetic relationships of the coral genera *Australomussa* and *Parascolymia* (Scleractinia, Lobophylliidae). *Contrib. Zool.* **2014**, *83*, 195–210. [CrossRef]
365. Oku, Y.; Naruse, T.; Fukami, H. Morpho-molecular evidence for polymorphism in the mushroom coral *Cycloseris hexagonalis* (Scleractinia: Fungiidae), with a new phylogenetic position and the establishment of a new genus for the species. *Zool. Sci.* **2017**, *34*, 242–251. [CrossRef]
366. Wells, J.W. Scleractinia. In *Treatise on Invertebrate Paleontology, Part F: Coelenterata*; Moore, R.C., Ed.; Geological Society of America and University of Kansas Press: Lawrence, KS, USA, 1956; pp. 328–444.
367. Chevalier, J.-P. *Les scléractiniaires de la Mélanésie Française. I Expédition Française sur les récifs coralliens de la Nouvelle-Calédonie*; Singer-Polignac: Paris, France, 1971; Volume 5, 307p.
368. Chevalier, J.-P. *Les scléractiniaires de la Mélanésie Française. II Expédition Française sur les récifs coralliens de la Nouvelle-Calédonie*; Singer-Polignac: Paris, France, 1975; Volume 7, 407p.
369. Stolarski, J.; Kitahara, M.V.; Miller, D.J.; Cairns, S.D.; Mazur, M.; Meibom, A. The ancient evolutionary origins of Scleractinia revealed by azooxanthellate corals. *BMC Evol. Biol.* **2011**, *11*, 316. [CrossRef]
370. Stolarski, J.; Bosellini, F.R.; Wallace, C.C.; Gothmann, A.M.; Mazur, M.; Domart-Coulon, I.; Gutner-Hoch, E.; Neuser, R.D.; Levy, O.; Shemesh, A. A unique coral biomineralization pattern has resisted 40 million years of major ocean chemistry change. *Sci. Rep.* **2016**, *6*, 27579. [CrossRef]
371. Nicolle, D.; Ritter, M.K.; Jones, R.C.; Phillips, G.P.; French, M.E.; Cumming, R.; Bell, S.A.J. The genus problem—*Eucalyptus* as a model system for minimising taxonomic disruption. *Taxon* **2024**, *74*, 495–506. [CrossRef]
372. Benzoni, F.; Arrigoni, R.; Stefani, F.; Reijnen, B.T.; Montano, S. Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsi* (Scleractinia: Fungiidae): Lost mushroom corals find their way home. *Contrib. Zool.* **2012**, *81*, 125–146. [CrossRef]
373. Huang, D.; Licuanan, W.; Baird, A.; Fukami, H. Cleaning up the "Bigmessidae": Molecular phylogeny of scleractinian corals from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae. *BMC Evol. Biol.* **2011**, *11*, 37. [CrossRef]
374. Budd, A.F.; Fukami, H.; Smith, N.D.; Knowlton, N. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zool. J. Linn. Soc.* **2012**, *166*, 465–529. [CrossRef]
375. Huang, D.; Benzoni, F.; Arrigoni, R.; Baird, A.H.; Berumen, M.L.; Bouwmeester, J.; Chou, L.M.; Fukami, H.; Licuanan, W.Y.; Lovell, E.R.; et al. Towards a phylogenetic classification of reef corals: The Indo-Pacific genera *Merulina*, *Goniastrea* and *Scapophyllia* (Scleractinia, Merulinidae). *Zool. Scr.* **2014**, *43*, 531–548. [CrossRef]
376. Arrigoni, R.; Stefani, F.; Pichon, M.; Galli, P.; Benzoni, F. Molecular phylogeny of the Robust clade (Faviidae, Mussidae, Merulinidae, and Pectiniidae): An Indian Ocean perspective. *Mol. Phylogenet. Evol.* **2012**, *65*, 183–193. [CrossRef] [PubMed]
377. Fukami, H.; Chen, C.A.; Budd, A.F.; Collins, A.; Wallace, C.; Chuang, Y.-Y.; Chen, C.; Dai, C.-F.; Iwao, K.; Sheppard, C.; et al. Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). *PLoS ONE* **2008**, *3*, e3222. [CrossRef] [PubMed]
378. Vaughan, T.W. Recent Madreporaria of the Hawaiian Islands and Laysan. *Bull. U.S. Natl. Mus.* **1907**, *59*, 1–427. [CrossRef]
379. Vaughan, T.W.; Wells, J.W. Revision of the suborders, families, and genera of the Scleractinia. *Geol. Soc. Am. Spec. Pap.* **1943**, *44*, 1–363. [CrossRef]

380. Verrill, A.E. Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Captain John Rodgers, U.S.N., from 1853 to 1856. Collected by Dr. Wm. Stimpson, naturalist to the expedition. With descriptions of some additional species from the west coast of North America. Part 4. Actiniaria, continued. *Commun. Essex Inst.* **1869**, *6*, 51–104.
381. Quelch, J.J. Report on the reef-corals collected by H.M.S. Challenger during the years 1873–1876. *Rep. Sci. Results Voy. H.M.S. Challenger Zool.* **1886**, *46*, 1–203.
382. Chevalier, J.-P.; Beauvais, L. Ordre des Scléractiniaires. XI Systématique. In *Traité de Zoologie: Anatomie, Systématique, Biologie. Cnidaires, Anthozoaires*; Grassé, P.-P., Ed.; Masson: Paris, France, 1987; Volume 3, pp. 679–764.
383. Wijsman-Best, M. Biological results of the Snellius expedition: XXVII. Faviidae collected by the Snellius expedition. II. The genera *Favites*, *Goniastrea*, *Platygyra*, *Oulophyllia*, *Leptoria*, *Hydnophora* and *Caulastrea*. *Zool. Meded.* **1976**, *48*, 45–63.
384. Mitsuki, Y.; Isomura, N.; Nozawa, Y.; Tachikawa, H.; Huang, D.; Fukami, H. Distinct species hidden in the widely distributed coral *Coelastrea aspera* (Cnidaria, Anthozoa, Scleractinia). *Invertebr. Syst.* **2021**, *35*, 876–891. [CrossRef]
385. Arrigoni, R.; Huang, D.; Berumen, M.L.; Budd, A.F.; Montano, S.; Richards, Z.T.; Terraneo, T.I.; Benzoni, F. Integrative systematics of the scleractinian coral genera *Caulastraea*, *Erythrastrea* and *Oulophyllia*. *Zool. Scr.* **2021**, *50*, 509–527. [CrossRef]
386. Scheer, G.; Pillai, C.S.G. *Report on the Stony Corals from the Red Sea*; Zoologica: Hong Kong, China, 1983; Heft 133; pp. 1–198.
387. Ma, T.Y.H. *Effect of Water Temperature on Growth Rate of Corals*; The World Book Co.: Taipei, Taiwan, 1959; Volume 1, 116p.
388. Arrigoni, R.; Kitano, Y.F.; Stolarski, J.; Hoeksema, B.W.; Fukami, H.; Stefani, F.; Galli, P.; Montano, S.; Castoldi, E.; Benzoni, F. A phylogeny reconstruction of the Dendrophylliidae (Cnidaria, Scleractinia) based on molecular and micromorphological criteria, and its ecological implications. *Zool. Scr.* **2014**, *43*, 661–688. [CrossRef]
389. Mehrotra, R.; Chavanich, S.; Monchanin, C.; Jualaong, S.; Hoeksema, B.W. Biodiversity, ecology, and taxonomy of sediment-dwelling Dendrophylliidae (Anthozoa, Scleractinia) in the Gulf of Thailand. *Contrib. Zool.* **2023**, *92*, 468–509. [CrossRef]
390. Kitano, Y.F.; Benzoni, F.; Arrigoni, R.; Shirayama, Y.; Wallace, C.C.; Fukami, H. A phylogeny of the family Poritidae (Cnidaria, Scleractinia) based on molecular and morphological analyses. *PLoS ONE* **2014**, *9*, e98406. [CrossRef]
391. Claereboudt, M.R.; Al-Amri, I.S. *Calathiscus tantillus*, a new genus and new species of scleractinian coral (Scleractinia, Poritidae) from the Gulf of Oman. *Zootaxa* **2004**, *532*, 1–8. [CrossRef]
392. Arrigoni, R.; Terraneo, T.I.; Galli, P.; Benzoni, F. Lobophylliidae (Cnidaria, Scleractinia) reshuffled: Pervasive non-monophyly at genus level. *Mol. Phylogenet. Evol.* **2014**, *73*, 60–64. [CrossRef]
393. Arrigoni, R.; Berumen, M.L.; Terraneo, T.I.; Caragnano, A.; Bouwmeester, J.; Benzoni, F. Forgotten in the taxonomic literature: Resurrection of the scleractinian coral genus *Sclerophyllia* (Scleractinia, Lobophylliidae) from the Arabian Peninsula and its phylogenetic relationships. *Syst. Biodivers.* **2015**, *13*, 140–163. [CrossRef]
394. Terraneo, T.I.; Benzoni, F.; Arrigoni, R.; Berumen, M.L.; Mariappan, K.G.; Antony, C.P.; Harrison, H.B.; Payri, C.; Huang, D.; Baird, A.H. A genomic approach to *Porites* (Anthozoa: Scleractinia) megadiversity from the Indo-Pacific. *Mol. Phylogenet. Evol.* **2025**, *203*, 108238. [CrossRef]
395. Studer, T. Zweite Abtheilung der Anthozoa polyactinia, welche während der Reise S.M.S. Corvette *Gazelle* um die Erde gesammelt wurden. *Monatsber. Königl. Preuss. Akad. Wiss. Berl.* **1878**, *25*, 524–550.
396. Shirai, S. (Ed.) *Ecological Encyclopedia of the Ryukyu Islands (Revised Edition)*; Okinawa Kyoiku Shuppan: Okinawa, Japan, 1980; 636p.
397. Cowman, P.F.; Quattrini, A.M.; Bridge, T.C.L.; Watkins-Colwell, G.J.; Fadli, N.; Grinblat, M.; Roberts, T.E.; McFadden, C.S.; Miller, D.J.; Baird, A.H. An enhanced target-enrichment bait set for Hexacorallia provides phylogenomic resolution of the staghorn corals (Acroporidae) and close relatives. *Mol. Phylogenet. Evol.* **2020**, *153*, 106944. [CrossRef] [PubMed]
398. Quek, Z.R.; Jain, S.S.; Richards, Z.T.; Arrigoni, R.; Benzoni, F.; Hoeksema, B.W.; Carvajal, J.I.; Wilson, N.G.; Baird, A.H.; Kitahara, M.V. A hybrid-capture approach to reconstruct the phylogeny of Scleractinia (Cnidaria: Hexacorallia). *Mol. Phylogenet. Evol.* **2023**, *186*, 107867. [CrossRef]
399. ICZN. Coral taxon names published in Corals of the World by J.E.N. Veron (2000): Potential availability confirmed under Article 86.1.2. *Bull. Zool. Nomencl.* **2011**, *68*, 162–166.
400. Torrado, H.; Rios, D.; Primov, K.; Burdick, D.R.; Bentlage, B.; Lemer, S.; Combosch, D. Evolutionary genomics of two co-occurring congeneric fore reef coral species on Guam (Mariana Islands). *Genome Biol. Evol.* **2025**, *17*, evae278. [CrossRef]
401. Randall, R.H.; Myers, R.F. *The Corals: Guide to the Coastal Resources of Guam*; University of Guam Press: Mangilao, Guam, 1983; 128p.
402. Nunes, F.; Fukami, H.; Vollmer, S.V.; Norris, R.D.; Knowlton, N. Re-evaluation of the systematics of the endemic corals of Brazil by molecular data. *Coral Reefs* **2008**, *27*, 423–432. [CrossRef]
403. Hodgson, G. A new species of *Montastrea* (Cnidaria, Scleractinia) from the Philippines. *Pac. Sci.* **1985**, *39*, 283–290.
404. Benzoni, F.; Stefani, F.; Pichon, M.; Galli, P. The name game: Morpho-molecular species boundaries in the genus *Psammocora* (Cnidaria, Scleractinia). *Zool. J. Linn. Soc.* **2010**, *160*, 421–456. [CrossRef]
405. Oury, N.; Berumen, M.L.; Paulay, G.; Benzoni, F. One species to rule them all: Genomics sheds light on the *Pocillopora* species diversity and distinctiveness around the Arabian Peninsula. *Coral Reefs* **2025**, *44*, 983–998. [CrossRef]

406. Ahrens, D.; Fujisawa, T.; Krammer, H.-J.; Eberle, J.; Fabrizi, S.; Vogler, A.P. Rarity and incomplete sampling in DNA-based species delimitation. *Syst. Biol.* **2016**, *65*, 478–494. [CrossRef]
407. Johnston, E.C.; Wyatt, A.S.; Leichter, J.J.; Burgess, S.C. Niche differences in co-occurring cryptic coral species (*Pocillopora* spp.). *Coral Reefs* **2022**, *41*, 767–778. [CrossRef]
408. Rosser, N.L.; Veron, J.E.N. Australian corals thriving out of water in an extreme environment. *Coral Reefs* **2011**, *30*, 21. [CrossRef]

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