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Commentary

Modern Coral Taxonomy Requires Reproducible Data Alongside Field Observations—Comments on Veron et al. (2025)

Peter F. Cowman [1,2,*], Tom C. L. Bridge [1,2], Tracy D. Ainsworth [3], Francesca Benzoni [4], Victor Bonito [5], Ann Budd [6], Patrick Cabaitan [7], Emma F. Camp [8], Chaolun Allen Chen [9], Sean R. Connolly [10], Augustine J. Crosbie [1,2], Joana Figueiredo [11], Douglas Fenner [12], Zac Forsman [13], Hironobu Fukami [14], Catherine E. I. Head [15,16], Bert W. Hoeksema [17,18], Danwei Huang [19], Marcelo V. Kitahara [20], Nancy Knowlton [21], Chao-Yang Kuo [22], Mei-Fang Lin [23], Joshua S. Madin [13], Hanaka Mera [2], Keiichi Nomura [24], Nicolas Oury [4], Andrea M. Quattrini [21], Kate M. Quigley [2,25,26], Sage H. Rassmussen [27], Kaveh Samimi-Namin [17,28,29], Frederic Sinniger [30], David J. Suggett [8,27,31] and Andrew H. Baird [2]

[1] Biodiversity and Geosciences Program, Queensland Museum Tropics, Townsville, QLD 4810, Australia
[2] College of Science and Engineering, James Cook University, Townsville, QLD 4814, Australia
[3] Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, NSW 2033, Australia
[4] Marine Science Program, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal 23955, Saudi Arabia
[5] Reef Explorer Fiji, Votua Village, Baravi, Nadroga, Fiji
[6] Department of Earth and Environmental Sciences, The University of Iowa, Iowa City, IA 52242, USA
[7] Marine Science Institute, College of Science, University of the Philippines Diliman, Quezon City 1101, Philippines
[8] Climate Change Cluster, Faculty of Science, University of Technology Sydney, Sydney, NSW 2007, Australia
[9] Biodiversity Research Center, Academia Sinica, Taipei 115029, Taiwan
[10] Naos Marine Laboratories, Smithsonian Tropical Research Institute, Ancón, Apartado, Panama City 0843-03092, Panama
[11] National Coral Reef Institute, Nova Southeastern University, Fort Lauderdale, FL 33004, USA
[12] Coral Reef Consulting, Pago Pago 96799, American Samoa
[13] Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kaneohe, HI 96744, USA
[14] Unit of Marine Life Science, Faculty of Agriculture, University of Miyazaki, Miyazaki 889-2155, Japan
[15] Institute of Zoology, Zoological Society of London, London NW1 4RY, UK
[16] Division of Biosciences, University College London, London WC1E 6BT, UK
[17] Marine Evolution and Ecology Group, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands
[18] Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands
[19] Lee Kong Chian Natural History Museum, National University of Singapore, Singapore 117377, Singapore
[20] Center for Marine Biology, University of São Paulo, Sao Paulo 11612-109, Brazil
[21] Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA
[22] Planning and Research Department, National Museum of Marine Biology and Aquarium, Pintung 944401, Taiwan
[23] Department of Marine Biotechnology and Resources, National Sun Yat-Sen University, Kaohsiung 804201, Taiwan
[24] Sabiura Marine Park Research Station, Kushimoto Marine Park Center Arita, Kushimoto, Wakayama 649-3514, Japan
[25] Oceans Institute, University of Western Australia, Perth, WA 6009, Australia
[26] The Minderoo Foundation, Perth, WA 6009, Australia
[27] KAUST Coral Restoration Initiative, King Abdullah University of Science and Technology, Thuwal 23955, Saudi Arabia
[28] Department of Biology, University of Oxford, Oxfordshire, Oxford OX1 3SZ, UK
[29] Natural History Museum, Cromwell Road, London SW7 5BD, UK
[30] Sesoko Marine Research Station, Tropical Biosphere Research Centre, University of the Ryukyus, 3422 Sesoko, Motobu 905-0227, Japan
[31] Biological and Environmental Science and Engineering Division (BESE), King Abdullah University of Science and Technology, Thuwal 23955, Saudi Arabia
* Correspondence: peter.cowman@qm.qld.gov.au

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Abstract

The recent review by Veron et al. (2025) posits that quantitative genomic evidence used to understand coral evolution should be secondary to species hypotheses derived from expert opinion based on field experience. The authors argue that morphological "*biological entities*" should take precedence over molecular evidence when conflicts arise. This perspective required the rejection of extensive, independent molecular datasets that have progressively converged on a robust evolutionary framework for reef corals. Here, we reaffirm how prioritising subjective visual assessments over quantitative genetic and genomic data is methodologically unsound and scientifically regressive. We reject the framing of this perspective as "morphology versus molecules". Rather, it is a fundamental divergence between two opposing philosophies: a static system anchored in non-reproducible expert judgement, and an integrative framework where genetic data provide the necessary independent test of morphological hypotheses. We show how a reliance on "*field entities*" obscures true morphological patterns by failing to distinguish between phenotypic plasticity, convergence, and evolutionary divergence. Effective taxonomy requires species hypotheses to be testable, and to stand or fall on the strength of reproducible evidence. Such a framework does not replace morphology; it validates it by providing an explicit, testable basis for evaluating morphological hypotheses. The integration of testable, reproducible molecular analysis with other lines of evidence including morphology is the benchmark of modern taxonomy across all Kingdoms of Life. We address the logical inconsistencies in the general arguments put forward by Veron et al. (2025) and refute their specific rejection of recent *Acropora* species-level revision with reproducible data.

Keywords: integrative taxonomy; phylogenomics; Scleractinia; *Acropora*; reticulate evolution; species delimitation; nomenclature; topotype; reproducibility

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1. Introduction

The review by Veron et al. [1] (Veron et al. hereafter) argues that coral taxonomy must be reframed through the lens of reticulate evolution, suggesting that coral species are evolutionary continua with blurred genetic, morphological and geographic boundaries. We agree with some of the points raised by Veron et al., such as the benefits to taxonomists of spending extensive time observing corals in the field and in multiple geographic locations. Such experience provides a more complete picture of the undoubted variation exhibited by corals across multiple spatial scales. We acknowledge that the authors, in particular Dr. Veron, have made substantial contributions to coral taxonomy founded in decades of field work on reefs across the world. The contributions of the authors to the field are exemplified by the fact that Veron and colleagues have described over 180 coral species. The 'Scleractinia of Eastern Australia' monographs by Veron and colleagues [2–6] provided the first comprehensive revision of reef corals based on extensive observations and collections using SCUBA, representing a significant methodological advance on the previous 250 years of taxonomic research. However, this work, along with other taxonomic revisions of the late 20th century [7,8] was conducted immediately before the broadscale application of molecular phylogenetics to taxonomic and systematic research. More broadly, we recognise that long-term field taxonomists have built an extraordinary body of knowledge through decades of careful observation and documentation. Our argument is that this expertise is most powerful when coupled to, rather than substituted for, reproducible, quantitative methods. Molecular data are now essential and fundamental tools for resolving taxonomy and reconstructing the systematic relationships because they provide an independent line

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of evidence to evaluate whether morphological similarity is due to close evolutionary relationships or convergence. We acknowledge that molecular data are not without their limitations; they face inherent biological challenges such as incomplete lineage sorting (ILS) in rapid radiations and potential discordance between mitochondrial and nuclear markers. These limitations, however, necessitate an integrative approach where genomic evidence is cross-validated with morphological synapomorphies, ecological data, and other independent lines of evidence to resolve complex evolutionary histories [9], not the wholesale dismissal of molecular evidence where it appears to conflict with classifications based on preferred morphological characters. Moreover, while they do present challenges for species delimitation analyses, they also provide vital information about the evolutionary history of the lineage to assist decisions regarding species boundaries [10].

Veron's work commendably provided testable hypotheses for both the morphological characters that delineate species, genera and families [11] and the processes influencing the evolution of corals [12]. However, like other scientific hypotheses, these ideas can and should continue to be tested as new evidence comes to light. The reality is that a huge volume of research [13–48], primarily but not entirely based on molecular phylogenetic data and conducted by many authors around the world, is fundamentally incongruent with most of the taxonomy proposed by Veron [11]. Many of these studies, particularly earlier studies, focus on higher taxonomic levels, leading to widespread changes to families and genera. However, contrary to the assertion by Veron et al. that *"there have been few fundamental challenges to the overarching biological units designated as species"*, the increasing application of genomic-scale data are revealing that these issues are just as prevalent at the species level. Put simply, now that suitable analytical tools for tackling species-level relationships are available, it is clear that the species-level taxonomy presented in Veron [11] is just as problematic as the higher-level framework.

While Veron et al. cite many of the studies referred to above, their results are either dismissed or misinterpreted. For example, the synonymy of *Symphyllia* with *Lobophyllia* [29], which was foreshadowed by earlier molecular work [31] and is now supported by both gene trees [36,39] and genome-wide phylogenies [48,49], demonstrates that traditional skeletal characters such as wall fusion are often poor predictors of evolutionary relationships. Veron et al. dismiss this revision by claiming that Huang et al.'s [29] *"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"*. This statement by Veron et al. is demonstrably false. Figure 2 in Huang et al. [29] explicitly demonstrates that *Symphyllia* and *Lobophyllia* are not distinct in either molecular (Figure 2a; Huang et al. [29]) or morphological phylogenies (Figure 2b Huang et al. [29]). Furthermore, Huang et al. [29] provide diagnostic characters that confirm this paraphyly, underscoring the unreliable nature of wall fusion for genus-level diagnostics in this family. In addition to the specific cases of the *Acropora* species, discussed in detail below (see Section 7), the *Symphillia/Lobophyllia* example is one of several cases where Veron et al. selectively ignore published evidence demonstrating that the characters used to delineate genera and clades are convergent and/or not phylogenetically informative.

Advances in molecular phylogenetic methods have enabled systematic relationships among corals to be examined in increasing detail, both in terms of the relationships themselves and of the processes generating them. Those advances have revealed that the macro-morphological characters used by Veron to delineate taxa at multiple levels are plagued by convergence [13,50]. The incongruence between Veron's taxonomy and the evolutionary history of reef corals inferred from molecular phylogenetics was first illuminated by Romano and Palumbi [15], which focused on the family level. By the middle of the last decade, it was clear that this incongruence extended to the genus level, to the extent that only one of the 18 families and few of the 110 genera presented in Veron [11] are currently considered monophyletic (summarised in Kitahara et al. [51]). In the last few years, genomic-scale data are revealing the same pattern at the species level [16–18,52,53]. Moreover, studies of morphological characters ignored in traditional taxonomy has often supported molecular results [19,21].

We emphasise that this is not a ‘morphology versus molecules’ debate. We share the goal of taxonomic utility and stability in application; our concern is the evidentiary standard used to resolve conflict. Morphological study and extensive field observation are essential to coral taxonomy. Our disagreement is narrower: when conflicts arise, species hypotheses should be evaluated using explicit, reproducible tests based on multiple lines of evidence, rather than being resolved primarily by qualitative and subjective opinion.

Below, we outline how the review by Veron et al. relies on non-reproducible expert judgement as primary evidence over data-driven, hypothesis-testing approaches. Contrary to their assertions, the arguments presented by Veron et al., are incongruent with the large body of evidence produced over the last three decades on the evolution, systematics and taxonomy of reef corals. To demonstrate this incongruence, we critically examine the hypotheses proposed by Veron et al. to reject studies that conflict with their assertions; specifically, (1) that coral species do not exist as bounded entities because of rampant hybridization and (2) that morphological similarity should take precedence over all other lines of evidence. We then show that these hypotheses are not supported by the majority of available evidence. Instead, we argue that coral taxonomy, like any science, must be underpinned by data-driven testing of hypotheses, and that species boundaries and systematic relationships must be adjusted according to the weight of evidence.

2. The Species Concept: Lineages Not ‘Entities’

In response to Veron et al. we first clarify our unit of classification–species. While we point out that many of the issues raised here also apply to other taxonomic levels, we focus specifically on the species level because this is the level at which the claims of Veron et al. regarding reticulate evolution are most applicable. To paraphrase the statistician George Box, while all species concepts are essentially models (conceptual models, in any case)—and therefore “wrong”—some are significantly more useful than others. While the boundaries we draw to delineate species are human constructs, they are intended to represent the fundamental units of biological organisation that underpin both theoretical and applied research [54]. Consequently, differences in taxonomy can fundamentally alter conclusions regarding a taxon’s conservation status, ecology, or physiological tolerance [55,56].

Despite the widely acknowledged difficulties in coral identification due to factors such as morphological plasticity, convergent evolution and lack of reliable characters [13,57], the apparent disagreement in coral taxonomy rarely stems from a genuine conflict over data. Instead, it results primarily from a failure to distinguish between three fundamental levels of taxonomic reasoning: the species concept (what a species is), the evidentiary criteria used to infer species boundaries (e.g., morphology, monophyly, reproductive isolation), and the formal diagnosis (the characters that distinguish one species from others). Veron et al. imply that the conflict arises from disagreement over what constitutes a species, yet their arguments reveal a conflation of evidentiary criteria with both a species definition and its diagnoses. Veron et al. rely on the concept of the “*Biological Entity*”, a qualitative unit defined principally by visual recognition of specimens in the field. They critique the use of the Unified Species Concept [58] in recent coral taxonomic revision papers [17,18], incorrectly asserting that it “*permits delineation without requiring species to be distinguishable morphologically*. . . [and lacks] *reliance on morphological and/or reproductive* *supporting evidence*" [1]. This assertion is a fundamental misrepresentation of both the concept itself and of the studies cited.

Under the Unified Species Concept (USC hereafter), a species is defined as an independently evolving metapopulation lineage [58]. Importantly, this definition distinguishes the concept of a species (the lineage) from the operational criteria used to define it. Morphological characters therefore function as evidence to be tested, not as the definition of species boundaries given that morphological similarity does not necessarily indicate a close evolutionary relationship. In contrast, the traditional view taken by Veron et al. treats morphological recognisability simultaneously as species evidentiary criteria and species diagnosis. If the morphology of two 'species' overlaps (due to plasticity or convergence), or if the identity of the name-bearing type specimen is ambiguous and lacking in diagnostic morphological characters, then the species is rejected as a "*variant*" rather than being evaluated as a potentially distinct evolutionary lineage.

In contrast, the integrated view that we define here treats morphology as one line of evidence among several independent others. This integrated approach is implemented by Bridge et al. [17] and Rassmussen et al. [18] as well as many other major taxonomic revisions of reef corals over the last 20 years at all taxonomic levels that explicitly employ molecular phylogenetic and morphological analysis (e.g., [22–26,28–33,35–39,41–47,51]). Strikingly, every one of these studies cited is incongruent to varying extents with the taxonomic scheme advocated by Veron et al. The USC does not "*lack reliance*" on morphology, rather it requires that morphological hypotheses be tested against other independent lines of evidence to delineate between homologous and analogous morphological characters. Contrary to the assertions of Veron et al., most of the studies cited above explicitly incorporate morphological evidence in their analyses and identify synapomorphies that delineate families, genera and species morphologically where they exist.

For example, the revision of the genera *Caulastraea*, *Oulophyllia* and *Astreaosmilia* by Arrigoni et al. [40], discussed by Veron et al., quantifies 44 macromorphological, micromorphological and microstructural elements of the coral skeleton shown to be phylogenetically informative by Budd and Stolarski [19,20] in both type specimens and newly collected material. These characters are used in many of the taxonomic revisions cited here and enable the authors to highlight apomorphies that delineate genera. Critically, microstructural characters are less influenced by environmental factors than macromorphology, and are therefore more reliable indicators of phylogeny [19]. The molecular data showing that *Caulastraea* and *Astreaosmilia*, which were synonymized by Veron [11], are distinct is supported by three morphological characters: *Astreaosmilia* has non-confluent costosepta, partial septotheca and weak costa centre clusters, despite the two genera sharing many other morphological characters [40]. This same approach is used to find taxonomically informative morphological characters that are congruent with molecular evidence in many other genera.

Importantly, the taxonomic changes made in these publications were conservative measures enacted only if multiple lines of evidence (multiple studies, multiple genes, and skeletal microstructure) supported a taxonomic change. Such a conservative, data-centric approach has, contrary to the assertions of Veron et al., maintained "*taxonomic and nomenclatural stability*" when "*evidence for change* [was] *clear and without contradictions*". In some cases, the authors of these integrative studies highlight that additional changes are required, but decline to make changes until further evidence is obtained. For example, the phylogenomic-scale phylogeny of Quek et al. [48] supports previous findings that several coral genera are not monophyletic and require additional taxonomic and systematic study (e.g., *Pavona*, *Goniastrea*, *Favites*, *Pectinia* and *Dipsastraea*). However, contrary to the assertions of Veron, these findings do not cast doubt on the molecular results; instead, they highlight additional problems with the taxonomy of Veron [11] that require additional sampling and analysis to formally resolve.

Furthermore, the taxonomic changes from these studies rejected by Veron et al. (e.g., the synonymy of *Symphyllia* with *Lobophyllia* and the establishment of *Paragoniastrea*, including the recovery of *P. russelli* outside of *Favites*) have been supported by more recent studies using higher resolution phylogenomic methods [48,49]. Veron et al. explicitly reject these multiple, congruent lines of evidence in favour of non-independent visual assessments based on *"field experience"* that are not subjected to external or quantitative testing. When genomic data reveals that a single "*Biological Entity*" comprises multiple deeply divergent, non-reticulating lineages (e.g., *Acropora tenuis* vs. *A. kenti*), the USC deems they be recognised as distinct species, even if morphological diagnostic characters are subtle or overlapping. Under the USC, reticulation (i.e., gene flow) is not ignored where it exists; however, it does require empirical data to distinguish between actual reticulation (gene flow) and the retention of ancestral polymorphisms or convergences. Only then do we robustly delineate the species in question. Simply relying on "*field entities*" fails this test because it cannot delineate convergent look-alikes from close relatives.

Overall, the review functions as a defence of the taxonomic framework developed by Veron and colleagues [2–6,11,59,60] in the face of overwhelming evidence demonstrating that it is incongruent with the systematic relationships and evolutionary history of the Scleractinia. Their taxonomy is based on the evolutionary hypothesis established in the book Corals in Space and Time [12], which was not peer reviewed and presents no primary data. Veron et al. reject three decades of evidence that tests this framework using multiple lines of evidence [13–15,21,51]. While the hypothesis of pervasive reticulate evolution served as a foundational conceptual framework thirty years ago, it has calcified into a putative axiom used by the authors to dismiss, rather than interpret, the large volume of genomic evidence that is incongruent with their pre-conceived ideas. Veron et al. construct a fictitious dichotomy between the "*biological entity*" and the molecular lineage, treating the former as the ground truth. When genomic data conflict with these biological entities, the authors attribute the discordance to reticulation, ignoring the eminently plausible alternatives of human error, plasticity, phenotypic variation, incomplete linage sorting (recent speciation), or convergent evolution (homoplasy). Adhering to the amorphous concept of the "*biological entity*" when it is contradicted by robust independent genomic evidence is, in our view, scientifically unsound.

3. Reticulation as an Untestable Axiom

Reticulate evolution is a testable evolutionary hypothesis, not a default explanation for phylogenetic incongruence. Demonstrating reticulation requires explicit evidence of introgression or ongoing gene flow, such as asymmetric allele sharing or consistent discordance patterns across independent loci (e.g., [61–63]). Veron et al. acknowledge that there are presently too few data to define syngameons rigorously, yet the review repeatedly invokes syngameons and reticulate evolution as an explanatory framework when genomic results conflict with their proposed morphological *"biological entities"*. They deploy "*reticulate evolution*" as a kind of null hypothesis, asserting that any molecular lineage conflicting with their morphological concepts must be the result of a *"syngameon"*.

While hybridisation is a demonstratable biological phenomenon in corals [64], the authors present no supporting evidence for this claim in the lineages they reject or their associated figures of supposed 'hybrids'. Analyses that explicitly test for reticulation, such as ABBA-BABA tests for introgression [65,66], coalescent-based networks (e.g., PhyoNet [67]; Species Network [68]) or demographic modelling (e.g., fastsimcoal2 [69]), are necessary to evaluate whether gene flow has occurred among taxa. Instead, Veron et al. rely on visual anecdote (e.g., Figure 16 and Figure 17, displaying *"putative hybrids")* and a selective reading of the literature [70] while ignoring recent research [71–73] suggesting that hybridisation is not the dominant driver of *Acropora* diversity. Thus, as a scientific hypothesis, reticulate evolution should be (and can be) tested. By invoking reticulate evolution as an untestable null hypothesis, the authors create a theoretical shield that prevents their "*biological entities*" from being interrogated. When such interrogation is applied via genome-wide tests, providing sampling is adequate, the absence of gene-flow signals would provide evidence against the existence of pervasive syngameons at the species level. A species concept that cannot, even in principle, be tested objectively against data is not a productive basis for scientific inquiry.

4. The Double Standard of Sampling Criteria

Veron et al. repeatedly dismiss phylogenomic lineages based on sample sizes of N = 1 or 2, arguing that such small numbers are insufficient to capture species-level variation. While larger sample sizes per lineage (e.g., 5–10 individuals) can increase confidence in species delimitation, phylogenomic analyses that include thousands of independent loci can reliably resolve evolutionary divergence even with only one or two individuals [74,75]. Dismissing lineages solely based on small N reflects a misunderstanding of molecular systematics, conflating population genetics—which requires large samples to estimate allele frequencies and recent gene-flow [76]—with phylogenomics, where thousands of independent loci provide the statistical power to resolve deep evolutionary splits and topology even at N = 1–2 per lineage.

More critically, this argument exposes a stark methodological double standard. While Veron et al. demand population-level sampling to accept genomic results, they simultaneously propose synonymies based on visual inspection of single, often degraded type specimens (N = 1; e.g., *Acropora nana* in Figure 52 [1]). In essence, the authors reject relationships supported by thousands of independent molecular markers in favour of expert opinions based on subjective assessments of morphological characters. By applying rigorous statistical criteria to genomic data while exempting their own morphological assessments from quantitative testing, Veron et al. attempt to insulate their "*biological entities*" from being challenged by empirical evidence.

5. Selective Application of the ICZN

The review by Veron et al. exhibits both a misinterpretation of, and a selective adherence to the International Code of Zoological Nomenclature (ICZN; here after referred to as 'the Code'). The Code provides the universal set of rules that govern the scientific naming of animals, ensuring that names are unique and objectively anchored to physical specimens through the principal of typification. The authors invoke the Code to preserve familiar names while rejecting the fundamental tenet of typification when the type material does not suit their "*biological entities*". This creates a contradiction: they appeal to the Code to save a familiar name but reject the Code's fundamental axiom of typification when it is inconsistent with their proposed classification. Their appeal for an artificially stable taxonomy represents both a misinterpretation of the meaning of the term 'stability' in the Code and carries risks for applied research [54].

The term 'stability' in the Code refers to the stability and applicability of valid names, not of the science itself. The Preamble of the Code is explicit in this regard: while its objects are to promote stability and universality, it clearly states that none of its provisions *"restricts the freedom of taxonomic thought or actions"*. The Code is specifically intended to accommodate changes deemed necessary to any taxonomy undergoing rigorous and regular revision. Therefore, the Code aims to preserve stability in the face of change by providing clear guidelines on how to incorporate changes in a consistent manner, not artificial 'stability' to prevent necessary change as interpreted by Veron et al. There are obvious practical consequences for maintaining an artificially stable taxonomy as proposed by Veron et al.

We also recognise that "stability" has practical consequences for end-users regarding how names are presented in widely used aggregators (e.g., WoRMS [77]), and that changes such as treating a name as *nomen dubium* can affect whether a name appears as "accepted" to non-specialist users. However, nomenclatural decisions cannot be determined by database convenience or display status. Such resources should track and reflect the best-supported taxonomic and nomenclatural judgement grounded in typification and evidence. Where a name cannot be reliably linked to a type, recognising this uncertainty is not destabilising taxonomy, but clarifying it. The following quote by Gutiérrez and Helgen [56] refers to a parallel argument in mammalogy in the early 2000s but is equally applicable to corals, and eloquently highlights the problems with prioritising convenience over precision and the concomitant risk of obscuring biodiversity and accelerating extinction:

> *"Mammalogy is beleaguered by a dogmatic regard for mid-twentieth-century propositions, which were seldom based on critical study and lacked phylogenetic information. Species were lumped together and incorporated into influential classification checklists to simplify regional faunas and make them more manageable for non-taxonomists. Modern integrative approaches have shown that this tactic has hidden an incommensurable number of distinctive species from conservation efforts thereby increasing the risk of extinctions. Scepticism should be accorded to any taxonomy that is not based on comprehensive revisionary work, phylogenetic studies or, ideally, both"*

The issues highlighted by Gutiérrez and Helgen [56] regarding the potential for incorrect taxonomy to increase extinction risk are illustrated by the newly described *Acropora harriottae* Baird & Rassmussen 2025. Previously hidden within the widespread *A. hyacinthus* complex, this independently evolving lineage is restricted to subtropical eastern Australia [18], a region warming at three to four times the global average [78]. Under the "stable" taxonomy advocated by Veron at al., this species would remain invisible to management and therefore face a high risk of 'silent extinction' [79]. Similarly, incorrectly lumping distinct lineages can dramatically affect conclusions regarding critical ecological processes such as growth rates [80], thermal tolerance [81] and connectivity [82] that are vital for conservation and management of coral populations. Technically precise taxonomy that reflects evolutionary history as accurately as possible is a conservation necessity rather than an academic luxury. It is foundational to the efficacy of expanding coral restoration initiatives that depend on high-fidelity data regarding species-specific habitat preferences, geographic ranges, and thermal tolerance [83]. Without this resolution the application of widespread names to locally or regionally endemic species can fundamentally distort IUCN Red List assessments and lead to maladapted restoration or conservation efforts. Ultimately, we cannot protect what we cannot accurately define; thus, taxonomic precision is the prerequisite for the strategic management and long-term survival of reef ecosystems.

6. The Topotype Approach vs. The Abandonment of Nomenclature

We acknowledge that historical type specimens are at times challenging to locate and identify, an issue not unique to corals. However, the type specimen remains the sole objective anchor of nomenclature. To discard typification because it is inconvenient—as Veron et al. advocate here and elsewhere [59,84]—results in abandoning the rules of the ICZN, discarding the stability in nomenclatural procedures defined by the Code; and risks drifting toward the kinds of non-typified name usage criticised as 'taxonomic vandalism' (e.g., Taxonomy Australia [85]). Veron et al. argue that because the physical type specimen is ambiguous, the evolutionary lineage it represents must be invalid. This is a non sequitur. The ambiguity of a skeleton is a failure of human curation, not evidence of a biological continuum.

For many taxa, the increasing ability to sequence old, degraded and even formalin-preserved type specimens provides a potential solution to this problem [86–88]. Unfortunately, many coral types are bleached skeletons that lack tissue; nonetheless, this challenge is specifically addressed by the topotype approach [89], which seeks to sequence fresh material from the type locality and thereby link historical names to modern genomic lineages. A fundamental strength of this integrative framework is the high degree of compliance typically observed between morphological and molecular datasets when both are rigorously evaluated, particularly when using micromorphological and microstructural characters that are more phylogenetically conserved and less prone to environmental plasticity than macromorphology [17–19,21,33]. Rather than producing conflict, the synergy of these independent lines of evidence often reveals stable, diagnostic morphological characters that validate genomic lineages, providing a robust and reproducible basis for species recognition. Where this linkage is possible, it anchors field identification with quantitative data; where it is not, formal designation as *nomen dubium* remains a valid nomenclature solution. To make this approach operational for future revisions, we propose a four-step taxonomic decision tree:

1. prioritise the collection and sequencing of topotype specimens to link legacy names to genomic lineages;
2. where genomic data from topotype and samples from other geographic collections are congruent with the original type description and locality, anchor the name and update the morphological and/or geographic diagnosis;
3. where historical types are morphologically unresolvable, lost, or demonstrably incongruent with all extant lineages at the type locality, designate the name as *nomen dubium* to clear the nomenclatural landscape; and
4. reject the use of subjective synonymy as a ‘safe’ default for visual ambiguity, treating synonymy instead as a testable hypothesis requiring empirical support.

In contrast to this approach, Veron et al. bypass this due diligence entirely by installing broad, untestable synonymies based on *“internal assessment”* of field observations. This effectively decouples the name of the physical specimen, allowing the “*biological entity*” to drift based on the observer’s shifting opinion.

7. Case Studies in Unsubstantiated Synonymy: Specific Rebuttals of the *Acropora* Revisions

In their Section 7 [1], Veron et al. discuss numerous studies at multiple taxonomic levels where molecular data have illuminated incongruence between the taxonomic scheme proposed by the authors and coral systematics revealed through molecular phylogenies that have necessitated taxonomic changes. It is beyond the scope of this article to systematically address each comment raised by Veron et al. other than noting that the authors do not present any new data or re-analysis of published data to refute any of the taxonomic changes discussed. However, to illustrate some of the failures of logic and fact presented by Veron et al. in this section, we specifically comment on Section 7.3, which targets taxonomic decisions at the species level for the genus *Acropora* by Bridge et al. [17] and Rassmussen et al. [18]. The arguments presented by Veron et al. rely exclusively on assertions of morphological overlap or geographic ubiquity that are directly contradicted by the genomic and other evidence presented in the papers. In addition, while Veron et al. state that their publication is a review rather than a formal taxonomic revision, their explicit advocacy for these synonymies promotes confusion regarding valid species concepts and requires clarification of the primary evidence.

7.1. *Acropora rongoi*

Veron et al. suggest that *A. rongoi* Bridge and Cowman, 2023 (South Pacific) is a synonym of *A. striata* (Japan) based on visual resemblance, despite acknowledging the *"molecular differences"* between *A. rongoi* and the Japanese sequences. This assessment relies on a superficial visual resemblance while ignoring overwhelming molecular and biogeographic evidence that they represent distinct but convergent species; indeed, this case highlights why it is critical to examine multiple independent lines of evidence to delineate morphological similarity from convergence. We agree that the types of the two species share morphological similarities, but also exhibit differences:

- Branching Complexity: *Acropora rongoi* exhibits three distinct cycles of branching (images presented in Bridge et al. [17]), whereas *A. striata* is limited to only two (type images shown in Supplementary Material of Bridge et al. [17]). Veron et al. assert that the type of *A. striata* has three orders of branching, but the image presented supports the description of Bridge et al. [17] that only two orders of branching are visible, potentially with a few incipient axial corallites.
- Branch Dimensions: The primary branches of *A. rongoi* are significantly more robust (20–30 mm thick vs. 15 mm) and longer (300 mm vs. 150 mm) than those of *A. striata*. Conversely, the final branchlets of *A. rongoi* are shorter (2–4 mm vs. 4–5 mm).
- Corallite Dimensions: The axial corallites of *A. rongoi* are nearly double the size of those in *A. striata* (1.8–2.2 mm wide vs. 1.0–1.2 mm).
- Diagnostic Morphology: The dominant radial corallite shape differs fundamentally; they are tubular with oblique openings in *A. rongoi*, compared to the more appressed and cochleariform radials of *A. striata*.

Bridge et al. [17] note that the morphology of *A. rongoi* varies depending on habitat, leading to specimens in the QMT collections being identified as three different species from the morphological 'species groups': *A. striata* (selago group), *A. florida* (florida group), and *A. elseyi* (echinata group). Therefore, it is not surprising that it overlaps in morphology with other species, and molecular data provide a powerful tool to understand the extent of morphological variability within the species. Subsequent sequencing of additional specimens (Mera et al., in prep) provides further evidence that the species is restricted to the South Pacific (Cook Islands and French Polynesia), almost 10,000 kilometres from the type locality in Japan. Therefore, the synonymy proposed by Veron et al. is phylogenetically incoherent, and the most parsimonious explanation is that *A. rongoi* and *A. striata* are distinct, morphologically convergent lineages. By treating these as a single entity, Veron et al. not only obscure the unique evolutionary history of the South Pacific fauna, but also systematically underestimate true scleractinian diversity in favour of a non-reproducible visual assessment.

7.2. *Acropora tenuissima*

Veron et al. assert that *Acropora tenuissima* Bonito, Bridge, Fenner & Baird, 2023 is a synonym of *A. nana* (Studer, 1878). Veron et al.'s assessment overlooks fundamental structural differences between the species visible in the types and in the field (Figure S1; Supplementary Materials; and images presented in Bridge et al. [17]). A direct comparison of the holotypes, neither of which are provided by Veron et al., demonstrates that they share little in common beyond thin branch diameters (3–6 mm). The differences are multi-scale and distinct:

- Colony Growth: *A. nana* is digitate, whereas *A. tenuissima* is corymbose.
- Branch Structure: *A. tenuissima* possesses significantly longer branches (up to 10 cm vs. 2 cm in the type of *A. nana*, although potentially longer in adult colonies) and taller axial corallites (3 mm vs. 1 mm).

- Corallite Morphology: the dominant radial shape differs fundamentally (*A. nana* is tubular vs. *A. tenuissima* is appressed tubular or cochleariform). Septal development is distinct, with prominent septa in *A. nana* (2/3R) compared to the reduced septa of *A. tenuissima* (1/4R).
- Coenosteum Structure: the *A. nana* holotype displays a coenosteum composed of simple spinules, whereas *A. tenuissima* features a costate coenosteum lacking spinules.

While the *A. nana* holotype likely represents a juvenile colony, diagnostic features such as radial corallite shape are stable ontogenetic traits unlikely to change with age. Veron et al. present a drawing of the type material of *A. nana*, rather than actual images of the type, and a single image of an "*A. nana*" specimen (see Figure 52 [1]), both of which lack sufficient resolution to see these features. Furthermore, the gross morphology of their "*A. nana*" is also consistent with *A. tenuissima*, which would make the proposed comparison, and any resulting synonymy, to be circular. The field images in Figure S2 (Supplemental Materials) show *A. tenuissima* and *A. nana* sensu Veron side by side, providing further evidence of their morphological distinctiveness in the field as well as in Museum collections. Furthermore, as outlined in Bridge et al. [17], Veron et al. [60] include an image of *A. tenuissima* (Figure S3; Supplemental Materials) but identify the colony not as *A. nana* but a different species, *A. subulata*. The identification of the same species as both *A. subulata* and *A. nana* by Veron et al. [60] raises concerns about their consistency of identifications for this species, and therefore any decision regarding its validity.

Our topotype-based approach supports morphological separation. The phylogenomic analyses of Bridge et al. [17] definitively place *A. tenuissima* in Clade I. In contrast, phylogenomic analysis of the *A. nana* topotype places it in Clade V (Crosbie et al. in prep). These two clades diverged over 50 million years ago [90]. To claim these species are synonyms requires ignoring both 50 million years of genomic divergence and distinct, measurable morphological traits. This case study exemplifies the power of integrative taxonomy: genomic data did not obscure the morphology; it forced a re-examination that confirmed *A. tenuissima* and *A. nana* are both genetically and morphologically distinct.

7.3. *Acropora tenuis* Complex

Veron et al. reject *A. kenti*, *A. bifaria*, and *A. africana*, as "*geographic variants*" of a widespread *A. tenuis*. They assert that *A. tenuis* varies in a "*gradual and predictable way*" across the Indo-Pacific and argue that "*reliance on geographic distance. . .is not appropriate*" for species delimitation. This argument reveals a fundamental misunderstanding of the phylogenomic results presented in Bridge et al. [17]. The resurrection of *A. kenti* is not merely a matter of geographic distance, it is a matter of polyphyly. The genomic data demonstrate that the lineages described as *A. tenuis* (Fiji) and *A. kenti* (Australia) are not sister taxa. In the evolutionary tree, *A. echinata*, a species with vastly different skeletal morphology, is positioned phylogenetically between these two lineages. Therefore, Veron et al.'s proposal to synonymize *A. kenti* with *A. tenuis* leads to a taxonomically problematic consequence: to lump them, one would also have to subsume *A. echinata* into *A. tenuis*. By ignoring the topology of the tree, Veron et al. advocate for the maintenance of a polyphyletic taxon.

Veron et al. assert that variation in *A. tenuis* is "*gradual and predictable*," yet they do not present any data to support this hypothesis. In contrast, Bridge et al. [17] provided quantitative evidence of discrete genomic clustering with no sign of recent admixture with *A. kenti*. The assertion that these distinct lineages are "*geographic variants*" is a hypothesis that has been falsified by the genomic data. Maintaining *A. tenuis* as a catch-all for these disparate lineages masks deep evolutionary divergence and requires ignoring the presence of morphologically distinct species (*A. echinata*) nested within their constructed "*continuum*".

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7.4. *Acropora microclados*

Veron et al. reject the designation of *A. microclados* (Ehrenberg, 1834) as a *nomen dubium*, stating: "*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*". The premise that this field entity is "*well established*" is demonstrably incorrect. Wallace [8] explicitly noted that *A. microclados* "*is difficult to identify in the field, often being confused with A. cerealis or slender branching forms of A. nasuta*". If the two leading authorities of the 20th century could not agree on the field limits of the species, the stability Veron et al. seek to protect is an illusion.

Furthermore, this statement serves as a critical admission: the authors explicitly value "*long-held names*" (tradition) over "*technical precision*". They acknowledge the type specimen is problematic but argue that the "*field entity*", a subjective concept defined by their own experience, should take precedence over the physical type. This stance is inconsistent with the Code, where a scientific name is anchored to a type specimen not to a "*field entity*" or a consensus opinion. If a type is ambiguous and cannot be distinguished from other taxa, the name can be declared a *nomen dubium*.

Veron et al.'s defence of *A. microclados* exposes a persistent logical inconsistency: they opportunistically call upon the Code to defend names they prefer (citing priority) yet dismiss the Code's fundamental requirement of typification when it threatens the status quo. The Code exists to ensure names are unambiguous; maintaining a name that cannot be linked to a physical reality does not create stability, it creates a "unanchored taxon concept" that persists as an untestable entity.

7.5. *Acropora hyacinthus*

Veron et al. reject the restriction of *A. hyacinthus* to the Western Pacific, asserting that the species is "*very widespread across the central and Western Indian Ocean, as reported by numerous authors*". They suggest that the analysis of Rassmussen et al. [18] is a "*dismissal of all prior work*".

This line of reasoning is a textbook example of *Argumentum ad Populum*—an appeal to the frequency of reporting or traditional usage over quantitative and independent evidence. Veron et al. argue that because *A. hyacinthus* has been historically recorded in the Indian Ocean by many researchers (using visual identification), it must be present there. However, this argument overlooks a critical methodological point: many of those records are explicitly derived from, or informed by, the taxonomic framework proposed by Veron himself. If *A. hyacinthus* was stated to occur in the Indian Ocean under that framework, it is entirely expected that subsequent authors working within said taxonomic framework would report observing it there. Repetition of an identification based on a popular taxonomic hypothesis does not constitute independent corroboration; it is just circular confirmation of the original assumption.

Scientific nomenclature is not determined by consensus usage or citation frequency; it is determined by the identity of the name-bearing type. The holotype of *A. hyacinthus* (Dana, 1846) is from Fiji. The data and analyses presented in Rassmussen et al. [18] demonstrate that the Fiji lineage (typical *A. hyacinthus*) is genetically distinct from any tabular *Acropora* species from the Indian Ocean. The "Indian Ocean *A. hyacinthus*" mentioned in prior reports is a case of mistaken identity, a distinct evolutionary lineage that has converged on a similar tabular morphology (homoplasy) or a morphologically distinct species that has been synonymised because observed differences were attributed to intraspecific rather interspecific variation. Without genetic evidence linking Indian Ocean populations to the Fiji type, these reports most likely represent historical errors, not biological reality. To prioritise "*numerous authors*" over genomic data from topotypic material is not an evaluation of evidence, but a reinforcement of tradition.

7.6. *Acropora nyinggulu*

Veron et al. suggest that *Acropora nyinggulu* Bridge & Rassmussen, 2025 is a synonym of *A. spicifera* (Dana, 1846), arguing that despite genetic differences, the morphology overlaps. In this section, the authors' argument collapses under its own inconsistency. In their critique of *Acropora nyinggulu*, Veron et al. explicitly acknowledge the phylogenetic reality, stating: "*In their analysis, it* [*A. nyinggulu*, N = 17] *appears genetically distinct from the four samples identified as A. spicifera*" [1]. Yet, in the same paragraph, they suggest these distinct lineages be lumped under a single name based on superficial resemblance and a "*paucity of samples*" and "*lack of co-occurrence*". This dismissal ignores the genomic sampling of *A. spicifera* from Western Australia present in Rassmussen et al. [18], which demonstrates robust phylogenomic separation across hundreds of kilometres of sympatry. By ignoring the reported geographic sampling of this study, Veron et al. construct a strawman argument to reject a species hypothesis that meets both their morphological and molecular criteria.

This statement highlights a central tension in the premises of their review. Veron et al. concede that *A. nyinggulu* and *A. spicifera* are genetically distinct, yet they advocate for synonymy because they look similar. This exemplifies the failure of the authors to accept convergent evolution—that two species can overlap morphologically due to convergence rather than recent common ancestry. By suggesting that distinct lineages be synonymized, Veron et al. conflate morphological similarity with lineage identity. This approach does not simplify nature; it misrepresents it. To classify two organisms as the same species while acknowledging they belong to different evolutionary subclades is an abandonment of the fundamental principles of systematics; indeed, it is a rejection of the scientific imperative to follow the data where it leads.

8. Final Remarks

The arguments presented in Veron et al. regarding reticulation, type specimens, and the primacy of field observation are substantively identical to those presented by Veron [60]. In the intervening twelve years, the field of integrated taxonomy has progressed rapidly in resolution and rigour. That the authors' criticisms have remained static while the science has transformed suggests a lack of engagement with the weight of recent evidence rather than a critique of it.

Ultimately, as emphasised by philosophers of science for decades, reproducibility is a fundamental tenet of the scientific method [91]. Recent taxonomic revisions that are grounded in an integrated approach combining quantitative morphology, genomics and ecology are transparent, testable and reproducible. Strikingly, not one of the many taxonomic revisions of reef corals cited above that combines quantitative morphological and molecular evidence is consistent with the taxonomic hypothesis presented by Veron [12], leading to extensive revisions at all taxonomic levels. Where Veron et al. invoke reticulation, we agree this is a valid evolutionary possibility, but it must be evaluated with explicit, reproducible tests of introgression and gene flow (e.g., ABBA–BABA statistics, demographic modelling, and network-based approaches). We welcome such analyses and expect that, where supported, evidence of gene flow should be incorporated into integrative species hypotheses alongside morphology and field observations. Where such tests do not support reticulation, discordance should not be resolved by defaulting to "*biological entities*".

The species hypotheses advocated by Veron et al. place primary weight on the non-reproducible foundation of "*20,000 h of diving*" and an idiosyncratic "*internal assessment*". This creates an exclusionary barrier to entry that undermines the training of future taxonomists at a time when the field is already in crisis [92]. The reliance on a non-verifiable "*internal assessment*" establishes an impasse: a new student of taxonomy cannot replicate the internal assessment of a senior researcher; they can only accept their authority as faith. When a method cannot be taught, tested or transferred to the next generation, it falls short of the basic requirements of a transparent, testable scientific method. It becomes dogma.

Our disagreement is not about whether these issues matter, but about how to evaluate competing hypotheses and when to enact taxonomic changes. While we recognise the value of expert opinion in cases where quantitative data are unavailable, in the present case extensive quantitative data exist to adjudicate between the views of experts. Veron et al. instead contend that the opinions of researchers with more field experience trumps opinions supported by multiple lines of quantitative, reproducible evidence.

To advance the field of coral reef science, we must ensure that the taxonomic and systematic research that underpins all other aspects of the field is supported by a quantitative, data-driven framework. The future of reef conservation depends on a new generation of taxonomists trained in the rigorous application of integrated methods, where morphological hypotheses are not treated as immutable truths but as models to be tested against independent genomic and ecological evidence. This is not an abandonment of the value of "*field experience*" highlighted in Veron et al., which is shared by the authors of this paper; rather, it is a call to ground that experience in the reproducible rigour that modern science demands. We must embrace a healthy scepticism toward any classification that resists external validation. Only by following the data where it leads, even when it contradicts stability or long-held concepts, can we build a taxonomy sufficiently robust to address the urgent task of coral reef conservation, restoration and management in a changing climate.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d18020060/s1, Figure S1: Differences between Acropora nana (Studer, 1878) and A. tenuissima Bonito, Bridge, Fenner & Baird, 2024. Holotype of A. nana ZMB Cni1941 (A,C,E) and A. tenuissima MTQ G78343 (B,D,F) showing differences in skeletal morphology; Figure S2: Field image of A. tenuissima (left) and A. nana sensu Veron (right) co-occurring in Fiji (A); detail of A showing the morphological differences between A. tenuissima (B) and A. nana (C).; Figure S3: Image of *A. tenuissima* colony in Fiji identified as *A. subulata* (Dana, 1846) in Veron et al. [60].

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