Zoological Journal of the Linnean Society, 2023, **198**, 677–690. With 6 figures.

REVIEW

The use of integrative taxonomy in Octocorallia (Cnidaria: Anthozoa): a literature survey

GUSTAV M. KESSEL[1,*], PHILIP ALDERSLADE[2], JARET P. BILEWITCH[3], KAREEN E. SCHNABEL[3] and JONATHAN P. A. GARDNER[1]

[1]*School of Biological Sciences, Te Toki a Rata Building L2, Victoria University of Wellington, Gate 7 Kelburn Parade, Wellington 6012, New Zealand*
[2]*CSIRO Oceans and Atmosphere, Castray Esplanade, Hobart, TAS 7000, Australia*
[3]*National Institute of Water & Atmospheric Research Ltd (NIWA), 301 Evans Bay Parade, Wellington 6021, New Zealand*

Received 12 April 2022; revised 18 September 2022; accepted for publication 21 October 2022

Octocorals are problematic in their systematics, and the extent of their biodiversity is poorly understood. Integrative taxonomy (the use of two or more lines of evidence for the delimitation and description of taxa) is seen as a promising way to produce more robust species hypotheses and achieve taxonomic progress in this group. However, many octocoral descriptions continue to rely on morphological evidence alone, and the prevalence of integrative methods is unclear. Here, a literature survey was conducted to gain an overview of historical description rates and to examine trends in the publication of integrative descriptions between the years 2000 and 2020. We find that recent description rates are among the highest in the history of octocoral taxonomy, and although increasing, integrative taxon descriptions remain in the minority overall. We also find that integrative taxonomy has been applied unevenly across octocoral groups and geographical regions. Description rates show no signs of slowing, and no ceiling of total species richness has yet come into view. Coupled with a continued overreliance on morphological variation, particularly at the species level, this suggests that we might be adding to the workload of taxa requiring future revision faster than such instances can be resolved.

ADDITIONAL KEYWORDS: description rates – *et al*. effect – Linnean shortfall – marine invertebrates – octocorals – publication trends – soft corals – species richness – systematics – taxonomic expertise.

INTRODUCTION

The term ‘integrative taxonomy’ was formalized independently by two seminal papers in 2005 and was proposed primarily to reconcile the rift between morphology- and DNA-centric visions for the future of taxonomy that prevailed at the time (Dayrat, 2005; Will *et al.*, 2005). At its simplest, the integrative approach is predicated on the notion that the delimitation and description of taxa should be based on two or more independent lines of evidence rather than selecting only one (Goulding & Dayrat, 2016). Taxonomic decisions derived from this approach might combine morphological characteristics with, for example, developmental, molecular, ecological or behavioural data. Since its inception, and despite some conceptual disagreements in its application, a formalized integrative approach has broadly been regarded as the most efficient and most objective way to produce robust species hypotheses (de Queiroz, 2007; Padial *et al.*, 2010; Schlick-Steiner *et al.*, 2010). Consequently, the integrative approach is seen as a promising way to overcome the taxonomic impediment (an incomplete knowledge of global biodiversity and a shortage of the expertise required to document it), especially in light

*Corresponding author. E-mail: gustav.kessel@gmail.com

of the modern biodiversity crisis, which threatens the extinction of species even before they can be described (Costello *et al.*, 2013a; Sheth & Thaker, 2017; Vinarski, 2020).

The application of integrative techniques is particularly urgent for taxa that are threatened by anthropogenic change and/or are poorly understood in terms of their diversity. Octocorals form ecologically significant and conspicuous components of benthic communities across most depths and latitudes worldwide (Fabricius & Alderslade, 2001), but now face increasing pressure from disturbances such as destructive fishing practices (Althaus *et al.*, 2009), fossil fuel exploration (De Leo *et al.*, 2015), ocean acidification (Gabay *et al.*, 2013) and thermal stress owing to rising sea surface temperatures (Fabricius, 1999; Bruno *et al.*, 2001; Loya *et al.*, 2001; Gambi *et al.*, 2010; Lõhelaid *et al.*, 2015; Dias & Gondim, 2016). Long seen as problematic, octocoral taxonomy remains in flux, and the effective future management of octocorals will hinge on improved understanding of species boundaries. For the most part, taxonomic difficulties in this group are attributable to a limited range of morphological characters forming the traditional basis for octocoral systematics, further exacerbated by homoplasy, intraspecific plasticity and the enduring legacy of inadequate descriptions published during and before the early 20th century (Pérez *et al.*, 2016). These factors have often led to incongruence between historical classifications and more recent molecular phylogenies (as is the case for many groups of marine invertebrates) and have highlighted the need for revisions throughout Octocorallia at all taxonomic levels (Daly *et al.*, 2007).

Problems persist among genetic techniques when applied to questions of taxonomy, although their application has been instrumental in redressing confusion in octocoral taxonomy. Chiefly, many of the molecular markers chosen for phylogenetic analyses have shown limited variation at the species level (McFadden *et al.*, 2010, 2011). This lack of fine-scale resolution among some taxa is further complicated by hybridization and reticulate evolution, which convolute the recent diversification of some genera (McFadden & Hutchinson, 2004; Quattrini *et al.*, 2019). Additionally, progress in many groups is hampered by a dearth of material suitable for DNA extraction. Notwithstanding these challenges, recent advances, such as the use of ultraconserved elements (Erickson *et al.*, 2020), are encouraging, and the integration of genetic and morphological data is now often cited as key to alleviating the problematic state of octocoral taxonomy (Pérez *et al.*, 2016; Núñez-Flores *et al.*, 2020; Poliseno *et al.*, 2021).

To date, the rate of taxonomic progress for Octocorallia has been reviewed only for certain groups, such as the sea pens (Williams, 2011), or specific areas, such as Asia (Ramvilas *et al.*, 2019), but has not been surveyed for octocorals as a whole at the global scale. Neither has the use of integrative taxonomy been examined formally. This means that there is little by which to judge taxonomic progress in the octocoral literature or by which it might be compared with efforts in other groups. Accordingly, the rate of progress and the impact of integrative techniques in octocoral taxonomy are here assessed through a literature survey focusing on the last 21 years. The aim is to elucidate how current description rates compare with historical rates and how the prevalence of the integrative approach in the literature varies across time, regions and taxa. It is anticipated that this will provide a useful comparative baseline for octocoral taxonomy in the coming decades, and it is hoped that this will encourage more researchers to practise integrative methodologies.

MATERIAL AND METHODS

Records of all currently accepted extant species, genera and families in the subclass Octocorallia (as of June 2021) were downloaded from the World Register of Marine Species database (WoRMS, 2021) using the advanced search function (search terms: status = 'accepted'; rank = 'is species'; belonging to 'Octocorallia'; flags = 'extant') and compiled in a spreadsheet to compare description rates between 1755 (corresponding to the oldest octocoral species description listed in WoRMS) and 2020 (taxa described post-2020 were excluded). Note that synonymizations at any taxonomic level, although a key part in the taxonomy of octocorals, were omitted owing to the sheer number of their implementations in Octocorallia and the logistical difficulty of tracking synonymization histories accurately through WoRMS. The data presented here thus provide an approximation of the rates (per annum) at which species, genera and families of octocorals (going by currently accepted taxa) were described initially. This should be borne in mind for results and discussions relating to 'description rates'.

Trends in the use of integrative taxonomic techniques were examined using original published descriptions, which were retrieved for all species, genera and families described between and including the years 2000–2020 based on taxonomic authorities listed in the WoRMS database. Although the concept of integrative taxonomy was formalized in 2005 (Dayrat, 2005; Will *et al.*, 2005), this timespan was chosen because genetic techniques were available, and studies might have incorporated several lines of

evidence in taxon descriptions before 2005. This also offers a summary of taxonomic research on octocorals throughout the 21st century. Efforts were made to find, as near as possible, all other publications from 2000–2020 (which might not have been listed in WoRMS) featuring any of the following taxonomic actions pertaining to octocorals: new taxon descriptions at the species, genus or family level; resurrections of taxa at any of these levels; elevations (e.g. subfamily to family or subspecies to species); and transfers (e.g. species between genera or genera between families). This was done by searching the names of all octocoral taxa listed in the WoRMS database with the Web of Science research tool using the following fields and logical operators: Topic = 'taxon name' OR Title = 'taxon name' AND Year Published = 2000–2020. The titles and abstracts of all publications in the search results were then viewed, and all judged potentially to include taxonomic actions on the searched-for taxa were retrieved. The relevant sections of all publications in the resulting list were then examined, and each individual occurrence of any of the above taxonomic actions, the types of data used to support them and the taxon to which they applied were tallied in a spreadsheet. This formed the main dataset. Note that for currently accepted taxa that were elevated or resurrected, it is the date of first description, not the date of elevation or resurrection, that was treated as a new taxon description. Geographical distribution can be considered implicitly to support taxonomic decisions, but it was excluded here (*sensu* Pante *et al.*, 2015).

Detailed statistical analyses are not feasible or appropriate because of the relative newness of the formalized integrative taxonomic approach, which meant that these data cover a range of only 21 years and resulted in variable and, on occasion, small annual count values. Instead, data were used directly to examine: general trends in the prevalence of integrative taxonomic techniques across time, regions and taxa; the total number of taxonomic publications per year; the proportion of publications adopting an integrative approach; and trends relating to authorship, including the proportions of publications by one, two and three or more authors and the total author pool per year (recorded as the number of different persons listed as authors for the whole year, with each person counted only once, regardless of how many publications they contributed to in that year).

RESULTS

Description rates from 1755 to 2020

Overall, 3590 currently accepted octocoral species, 399 genera and 56 families were described between 1755 and 2020. For species, yearly description rates are highly variable, but peak markedly in the years 1889, 1906 and 1908–1910 (Fig. 1). When plotted cumulatively, the first decade of the 20th century clearly stands out as a period of exceptionally high description rates, followed by a long period of steady progress and slight acceleration in the late 1990s (Fig. 2A). Accordingly, when broken into 20-year intervals, the mean number of species descriptions per year is highest for the period 1901–1920, and 2001–2020 shows the highest rates of species description since the turn of the 20th century (Fig. 3). For genera, description rates increase dramatically in the 1990s, reaching their highest ever rate (Fig. 2A), whereas family description rates spike post-2005 to levels not seen since the mid-1800s (Fig. 2B).

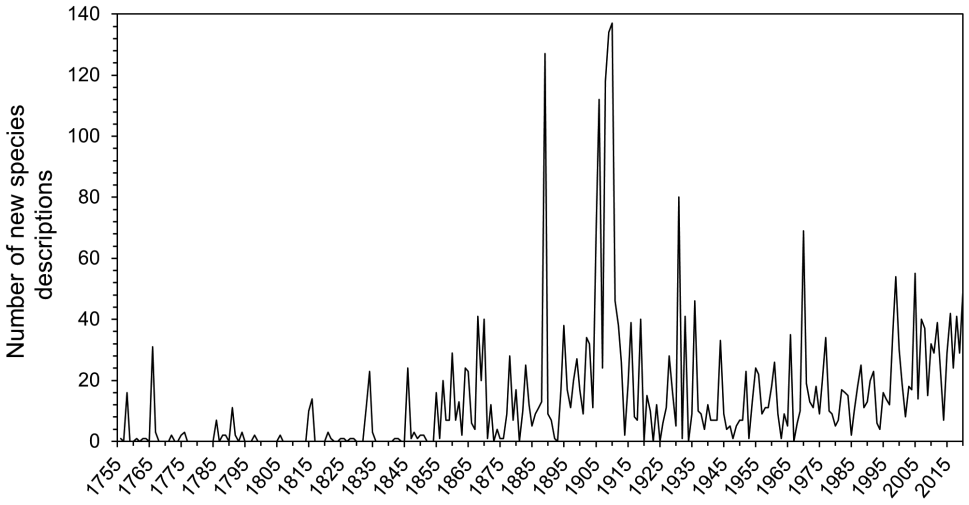

Figure 1. Number of new octocoral species descriptions per year, 1755–2020.

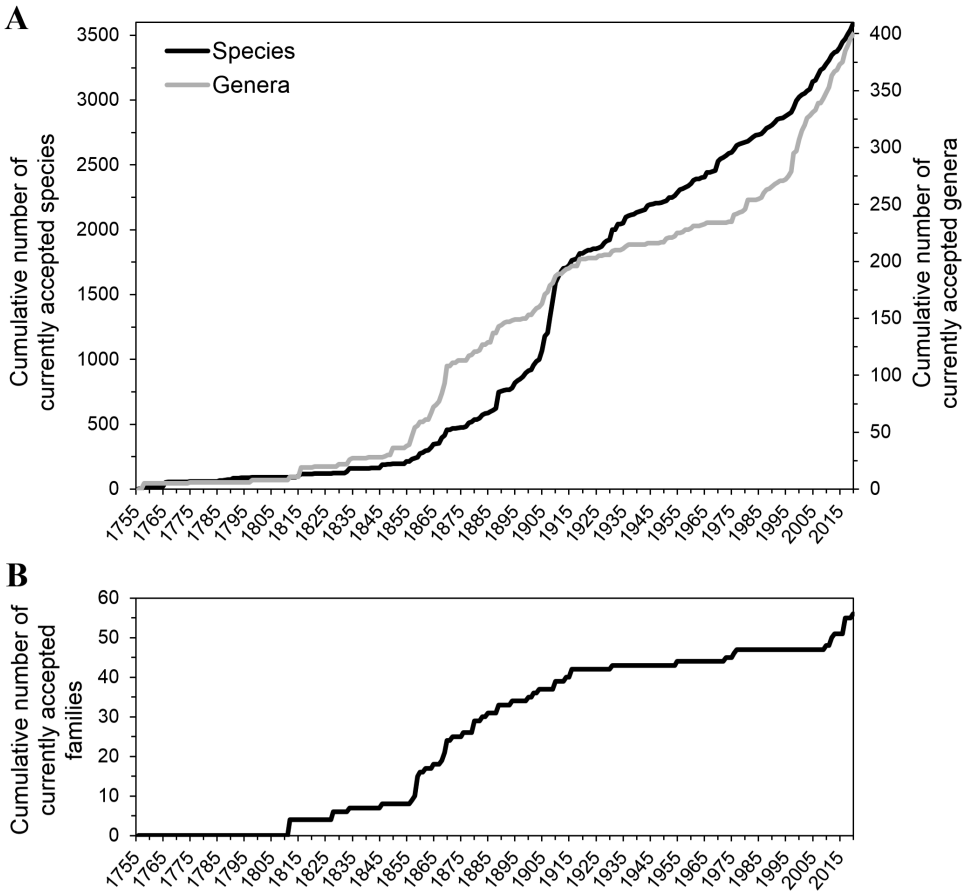

Figure 2. Cumulative number of octocoral species, genus and family descriptions per year (1755–2020): A, species and genera; B, families. Note different axis scales for species (primary *y*-axis in A), genera (secondary *y*-axis in A) and families (B).

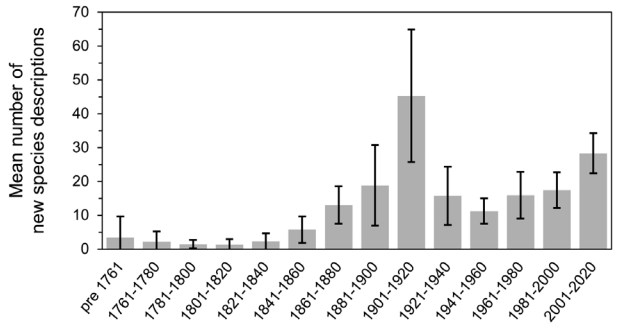

Figure 3. Mean number (±95%) of octocoral descriptions per 20-year interval (1755–2020).

Species descriptions in 2000–2020

Between 2000 and 2020, 596 currently accepted species were described, 135 (23%) of which were described using an integrative taxonomic approach. Almost all integrative descriptions (134 of 135) include genetic evidence in addition to morphological data. Only two species descriptions include other forms of data, in this case reproductive traits (López-González & Gili, 2000; Richards *et al.*, 2018), one of which does include a genetic component.

The proportion of species described using an integrative approach (morphomolecular comparisons in almost all cases) fluctuates from year to year (Fig. 4). Pre-2007, this proportion is uniformly close to zero. Post-2007, integrative descriptions are most often in the minority in comparison to morphology-only descriptions, but they do constitute a majority in 2014 and 2017, noticeably trending up overall (Fig. 4). This is confirmed when viewed in 5-year intervals, as the proportion of integrative species descriptions rises steadily: 2001–2005 = 117 new species, 2% integrative; 2006–2010 = 138 new species, 20% integrative; 2011–2015 = 126 new species, 29% integrative; 2016–2020 = 185 new species, 36% integrative. Between 2000 and 2020, there were also eight elevations to the species level from subspecies (one with an integrative approach) and seven species resurrections (two with an integrative approach).

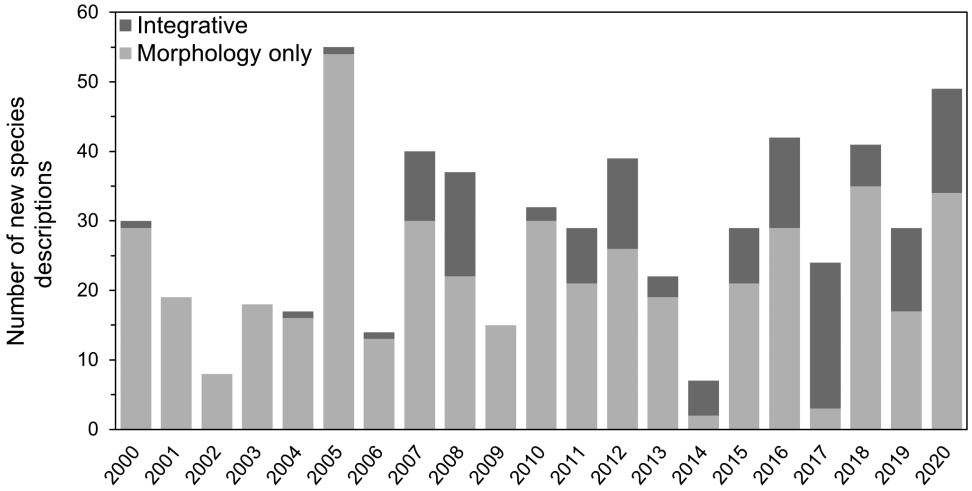

Figure 4. Number of new octocoral species descriptions per year (2000–2020) that used either an integrative approach or morphological data only.

Taxonomic actions at genus and family levels in 2000–2020

At the genus level, there were 105 new descriptions from 2000 to 2020 (Fig. 2A), with 77 of these (73%) using an integrative approach. Two genera described as new in this period were subsequently subsumed into other genera, and both of these were initially described based only on morphological data. There were also seven genus resurrections, five with an integrative approach, and 359 instances of existing species being transferred to a different genus, with 54 of these (15%) using an integrative approach (note that some species were transferred between genera multiple times). Nine new families were described (Fig. 2B), eight (89%) with an integrative approach, and 36 species were transferred to a different family, with 12 of these transfers (33%) based on integrative evidence (note that a family-level change for a given species may or may not have coincided with a genus-level change). In terms of genera, 13 were transferred from one family to another, with 11 of these (85%) based on integrative evidence.

Trends by taxonomic group in 2000–2020

Integrative techniques are not evenly applied in species descriptions across octocoral groups (Table 1). The use of integrative taxonomy is low among sea pens (Pennatulacea) and in the suborder Holaxonia, but high in Stolonifera and Helioporacea (blue corals), although the latter is composed of only two new descriptions between 2000 and 2020 (Table 1). The families Primnoidae, Alcyoniidae and Nephtheidae show the highest numbers of new species descriptions, but Alcyoniidae has by far the most, with 32 integrative descriptions (Table 1). Chrysogorgiidae is notable for having both relatively high description numbers (31) and percentages of integrative descriptions (39%). Most families with higher percentages of integrative descriptions are represented by few descriptions (Table 1).

Trends by geographical region in 2000–2020

Likewise, both the number of species described and the proportionate use of integrative techniques in their descriptions varies widely between geographical regions (Table 2). Palau, South Africa and Western Pacific seamounts are the only regions from which a clear majority of the collected material was described using an integrative approach. In the regions of the Mediterranean, Papua New Guinea and Pacific South America, the proportion is around half, and that for most other regions is 10–30% (Table 2). In contrast, at the scale of whole oceanic regions, the use of integrative taxonomy is relatively even, with ~20–25% of species descriptions adopting this approach for material from the Atlantic, Indian, Pacific and Southern oceans (Table 2). However, oceans vary substantially in their number of species descriptions, with far more descriptions based on Pacific than Atlantic material, for example (Table 2).

Publication and authorship trends in 2000–2020

In total, 255 octocoral publications are recorded as making taxonomic decisions between 2000 and 2020, of which 79 (30%) adopt an integrative approach. The 596 species descriptions published in this timespan appear in 231 of these publications, of which 66 (29%) include

Table 1. Octocoral species descriptions (2000–2020) by taxonomic groups

Order Suborder Family	Number of new species descriptions	Number of genera containing the new species	Number of new species described using integrative approach	Percentage of new species described using integrative approach
Alcyonacea				
Alcyoniina				
Acrophytidae	4	2	1	25.0
Alcyoniidae	98	22	32	32.7
Aquaumbridae	1	1	1	100.0
Leptophytidae	2	2	2	100.0
Nephtheidae	72	5	4	5.6
Nidaliidae	4	2	3	75.0
Paralcyoniidae	6	2	0	0.0
Xeniidae	13	10	1	7.7
TOTAL	200	46	44	22
Calcaxonia				
Chrysogorgiidae	31	8	12	38.7
Ellisellidae	9	2	0	0.0
Huziogorgiidae	1	1	0	0.0
Isididae	16	8	11	68.8
Primnoidae	127	27	14	11.0
TOTAL	184	46	37	20.1
Holaxonia				
Acanthogorgiidae	11	4	0	0.0
Dendrobrachiidae	2	1	0	0.0
Gorgoniidae	43	6	5	11.6
Keroeididae	1	1	0	0.0
Plexauridae	47	23	3	6.4
TOTAL	104	35	8	7.7
Protoalcyonaria				
Haimeidae	1	1	0	0.0
Scleraxonia				
Anthothelidae	3	2	2	66.7
Briareidae	2	2	0	0.0
Coralliidae	12	2	6	50.0
Melithaeidae	14	2	3	21.4
Paragorgiidae	14	2	3	21.4
Spongiodermidae	1	1	1	100.0
Victorgorgiidae	6	1	5	83.3
TOTAL	52	12	20	38.5
Stolonifera				
Arulidae	5	4	5	100.0
Clavulariidae	20	13	15	75.0
Cornulariidae	1	1	0	0.0
Incertae sedis	1	1	0	0.0
TOTAL	27	19	20	74.1
Incertae sedis				
Acanthoaxiidae	1	1	0	0.0
Parasphaerascleridae	3	1	1	33.3
Incertae sedis	1	1	0	0.0
TOTAL	5	3	1	20.0
Helioporacea	2	2	2	100.0
Pennatulacea	21	15	3	14.3
COMBINED TOTAL	596	179	135	22.7

Table 2. Octocoral species descriptions (2000–2020) by geographical origin of collected specimens

Region	Number of new species descriptions	Percentage of total number of species descriptions	Number of new species described using integrative approach	Percentage of new species described using integrative approach
Atlantic Ocean				
Northern Atlantic coasts and seamounts	29	4.9	9	31.0
Caribbean	19	3.2	1	5.3
Coast of South America	13	2.2	2	15.4
Mediterranean	2	0.3	1	50.0
Other western Atlantic	12	2.0	2	16.7
Mid-Atlantic ridge and seamounts	5	0.8	0	0.0
West coast of Africa	9	1.5	1	11.1
TOTAL	89	14.9	16	18.0
South Africa	19	3.2	13	68.4
Indo-West Pacific				
Southeast Asia	33	5.5	10	30.3
South China Sea	5	0.8	1	20.0
Papua New Guinea and New Caledonia	11	1.8	5	45.5
Palau	16	2.7	15	93.8
Broad distribution and other	35	5.9	0	0.0
TOTAL	152	25.5	39	25.7
Indian Ocean				
East coast of Africa	15	2.5	5	33.3
Red Sea	24	4.0	4	16.7
Arabian Sea and Persian Gulf	11	1.8	1	9.1
TOTAL	50	8.4	10	20.0
Pacific Ocean				
Japan, Ryukyu Archipelago and Taiwan	43	7.2	10	23.3
Far northern Pacific	29	4.9	8	27.6
Western Pacific seamounts	10	1.7	10	100.0
Hawaii	16	2.7	2	12.5
Other Pacific Islands	21	3.5	0	0.0
Tasmania	7	1.2	2	28.6
New Zealand	40	6.7	4	10.0
North-eastern Pacific	28	4.7	3	10.7
Coast of Central America	40	6.7	6	15.0
Galapagos	10	1.7	0	0.0
Coast of South America	11	1.8	5	45.5
TOTAL	255	42.8	50	19.6
Southern Ocean and Tierra del Fuego	30	5.0	7	23.3
Undetermined	1	0.2	0	0.0
COMBINED TOTAL	596	100.0	135	22.7

integrative taxonomic techniques. The remaining 24 publications include other decisions, such as genus transfers or species resurrections, and of these, 16 (67%) are integrative. Only two of these publications combined morphological data with non-genetic evidence, including ecological niche differences (Bayer *et al.*, 2014) and polyp pulsation behaviour (Halász *et al.*, 2013). Overall, the total number of taxonomic publications on octocorals, the total author pool and the percentage of taxonomic publications taking an integrative approach are all trending upwards over the last 21 years (Figs 5, 6). In the case of the latter two, this is especially clear since 2011, because post-2011 the lowest yearly author pool and the percentage of integrative publications are similar to, or higher than, the highest of these values pre-2011. For the total number of publications per year, increases are comparatively slight and obscured particularly by a

dip in 2014 (Fig. 6). All data fluctuate from year to year, particularly the percentage of integrative publications (Fig. 5), which is zero in 2001, 2002 and 2009, but spikes in 2014 (but note low total publications), 2017 and 2020. Of the 79 total integrative papers, four are by single authors, 32 by two authors and 43 by three or more. Of the 176 total non-integrative papers, 61 are by one author, 95 by two authors and 20 by three or more.

DISCUSSION

Description rates and the use of integrative taxonomy

The exceptional pace of octocoral species descriptions around the turn of the 20th century is unsurprising, because the same phenomenon has been identified for description rates concerning all life (Costello *et al.*, 2012). For octocorals, this was driven by a number of major scientific expeditions operating around this time and the release of their reports (see Bayer, 2001), which coincide precisely with the peaks in Figure 1. This includes species collected, for example, during the HMS *Challenger* (Wright & Studer, 1889), RIMS *Investigator* (Thomson & Henderson, 1906; Thomson & Simpson, 1909), *Valdivia* (e.g. Kükenthal, 1906) and *Siboga* voyages (e.g. Versluys, 1906; Nutting, 1910). In part, the apparent rapidity of species accumulation during this period might also be attributable to many descriptions from this era still requiring revisions (Pérez *et al.*, 2016), and thus the steepness of the curve in Figure 2A might be somewhat softened in the future. Conversely, had descriptions been plotted for species that were later synonymized or are currently not accepted for other reasons, the steepness of cumulative species descriptions would probably have been more exaggerated in the early 1900s. Although beyond the scope of the present study, the high number of synonymizations in Octocorallia might warrant further investigation regarding temporal, regional and taxonomic patterns of their implementation. By the measure of currently accepted taxa only, the last 21 years have seen higher species description rates than at any other point since the early 1900s. This might not hold true for all groups, but rates in sea pens (Pennatulacea), for example, showed a decline (Williams, 2011).

Crucially, the general acceleration in descriptions pre-dates the formalization of integrative taxonomy in the taxonomic literature (Dayrat, 2005; Will *et al.*, 2005). Taxonomy has integrated multiple lines of evidence for most of its long history (Valdecasas *et al.*, 2008), but the coining of 'integrative taxonomy' marked the most explicit call for the transformation of taxonomy and systematics into a multidisciplinary field and was widely expected to trigger a surge in new taxon descriptions over the following years (see Vinarski, 2020). Yet for octocorals, species description rates began to rise before this, in the late 1990s (see inflection in Fig. 2A). The inception of genetic applications in octocoral taxonomy coincides with this date (e.g. Lasker *et al.*, 1996; McFadden, 1999), but considering that morphomolecular integration was rare before ~2007, this cannot account for the start of elevated description rates alone. Neither can the integration of other forms of data, because integrative taxonomy in octocorals is centred overwhelmingly on the combination of morphological and molecular data, with other forms being numerically negligible.

Integrative taxonomy, more or less exclusively in the form of morphomolecular comparisons, continued to increase in prominence, reaching 36% of publications over the years 2016–2020. The integrative approach might thus have contributed to maintaining historically high species description rates among octocorals during this time, for example by uncovering cryptic species (McFadden & Van Ofwegen, 2013), but it seems not directly to have caused the initial 1990s acceleration

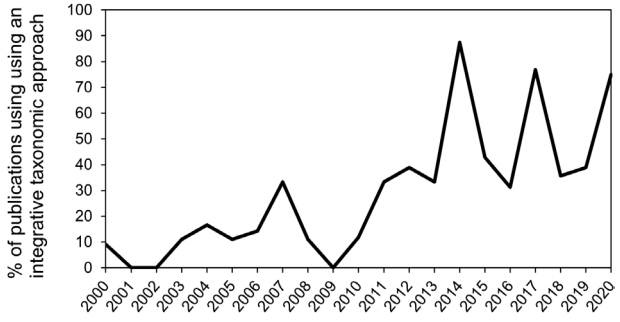

Figure 5. Percentage of all taxonomic publications on octocorals using an integrative approach per year (2000–2020).

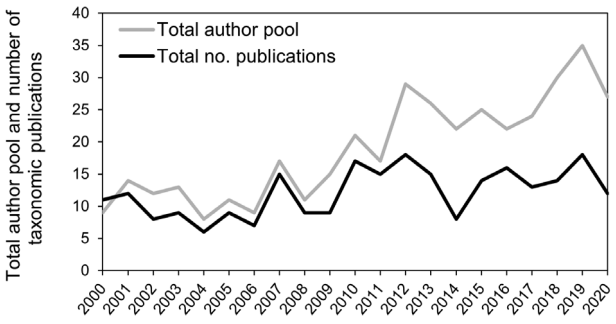

Figure 6. Total author pool and number of taxonomic publications on octocorals per year (2000–2020).

itself. Therefore, since 2005, the impact of integrative taxonomy on octocoral taxonomy at the species level is, for now, better characterized as adjuvant rather than revolutionary. This is not entirely surprising, because it mirrors findings concerning all Animalia by Pante *et al.* (2015) and suggests that for octocorals other factors improved description rates late in the 20th century. This might include increases in revisions, sampling and the number of active researchers, or changes relating to the difficulty of publication. Additionally, by the early 2000s, the publication of the first ever comprehensive soft coral identification guide by Fabricius & Alderslade (2001) introduced a far larger audience to octocoral taxonomic procedure and is likely to have facilitated the discovery of new species.

At the genus level, description rates also began to increase in the late 1990s, unlike at the species level, but a further acceleration is discernible post-2005, and descriptions then continue at their highest ever rates since the mid-1800s. The high proportion of integrative generic descriptions since 2000 (73%), also contrasts with the comparatively low prevalence of this approach at the species level (23%) and indicates that integrative morphomolecular techniques were key in maintaining high genus description rates over the last 21 years. Furthermore, the integrative approach has been applied almost universally at the family level since the year 2000. The impacts of this, in addition to improved genetic techniques, are clearly visible and are manifested as the steepest increase in description rates since the mid-1800s by around the year 2010. In summary, genus- and family-level taxonomic descriptions are made using an integrative approach more frequently than at the species level. This is most probably attributable to the difficulty of finding suitable species-level genetic markers in octocorals, meaning that higher taxa are more readily discernible by comparison (McFadden *et al.*, 2011).

Trends by taxonomic group

The application of integrative species descriptions is uneven across octocoral groups. No single overarching explanation can account for the observed patterns, which are probably caused by factors particular to each taxon. For example, in groups such as the family Clavulariidae, species tend to be small and inconspicuous, with similar morphologies that might necessitate data integration for robust species delimitation (e.g. McFadden & Van Ofwegen, 2012a; Lau & Reimer, 2019). This would lead to a high proportion of integrative descriptions relative to other taxa, which might have more diagnostic morphological features. Equally, patterns might reflect the opportunistic nature by which octocoral sampling is often carried out. In some groups, fresh specimens permitting an integrative approach might be more readily available, particularly for those inhabiting easily accessible depths and environments, whereas others might be limited by the age and the state of preservation of archived material or the relative inaccessibility of their habitat. Likewise, patterns might reflect the personal preferences or expertise of the authors specializing in or focusing on different groups. For example, 70 of the 127 species added to Primnoidae since the year 2000 were described (without the use of genetic data) by Cairns (2006, 2007a, b, 2009, 2010, 2011, 2012a, b, 2015, 2018a, b).

Historically, taxa that are easily discernible as new might simply have been described earlier than more difficult ones. In other words, little 'low-hanging fruit' remains to be picked, leaving mostly cryptic taxa that require genetic data to be recognized and discriminated, particularly at genus and family levels. Accordingly, all groups associated with high proportions of integrative species descriptions (80–100%) are made up of families or composed of genera that were described recently and for which genetic evidence was crucial, including Aquaumbridae (Breedy *et al.*, 2012), Arulidae (McFadden & Van Ofwegen, 2012b), Leptophytidae (McFadden & Van Ofwegen, 2017) and Victorgorgiidae (Moore *et al.*, 2017).

Trends by geographical region

Patterns relating to integrative taxonomy are difficult to discern at the regional or national scale and, again, are likely to stem from idiosyncrasies of each area, such as its size, accessibility, underlying octocoral diversity and resident expertise, in addition to biases in which established institutions and experts choose to (or are able to) focus their efforts. The notably high usage of this approach in South Africa, for example, is likely to result from strong research interest owing to its status as an important centre of endemism for octocorals (McFadden & Van Ofwegen, 2017). In contrast, when whole oceans are considered, the worldwide application of integrative taxonomy to species descriptions is roughly even at ~20% for each ocean, despite the variability in absolute numbers of descriptions between oceans. Indeed, in terms of total species descriptions, the taxonomic literature is as scattered in geographical coverage now as it was when this was recognized by Bayer (1981), and many of the same trends continue; namely, regions with a long history of research, such as the Mediterranean, are considered more or less complete in their species inventories, whereas the octocoral diversity of the vast and species-rich Pacific and Indian oceans is, by comparison, poorly known and continues to provide rich grounds for species discovery (see overview by Pérez *et al.*, 2016).

Authorship and other trends in the literature

Overall, the uptake of integrative taxonomy in octocorals was delayed following its formal introduction in the literature as a modern paradigm and lags behind its usage in numerous other taxa (e.g. see Pante *et al.*, 2015; Vinarski, 2020). Principally, this is likely to be because the years ~2000–2010 acted as a genetic discovery period for octocorals, during which markers were developed, explored and, eventually, adopted as being systematically informative (France & Hoover, 2001; McFadden *et al.*, 2004, 2006, 2011). This is supported by the percentage of integrative taxonomic papers on octocorals increasing only since ~2011. Given that most integrative taxonomic publications featured multiple authors, this, in turn, is likely to have contributed greatly to the roughly concomitant increase in the total author pool. Together, these factors highlight the multidisciplinary nature of the approach and explain why yearly author pools have risen more sharply than the total number of taxonomic publications. The growing number of authors is thus an example of the '*et al*. effect' (an increase in authors per species named; *sensu* Costello *et al.*, 2013b) and illustrates a departure from the lone taxonomist stereotype in favour of modern collaborative approaches between specialists with a range of skill sets.

One step forward, two steps back?

The reasons why many taxonomic researchers tend not to use genetic techniques are unclear, because these are almost never stated. This might represent an enduring generational effect related to the preferences and expertise of long-established researchers (as noted above). Available material might simply not be suitable for DNA extraction in many cases, or access to the technology might be limited by high cost, resource requirements and the existing collaborative networks of individual researchers. Alternatively, reluctance might stem from a reputation that even when attempted, genetic resolution is often insufficient to delimit octocoral species or might be incongruent with other data (e.g. Sánchez *et al.*, 2003; Cairns & Bayer, 2005; Wirshing *et al.*, 2005; Cairns & Baco, 2007; McFadden *et al.*, 2006, 2009).

Where it is applied, the integrative approach revolves almost exclusively around morphomolecular comparisons. In contrast, all other forms of data (e.g. reproductive traits, Richards *et al.*, 2018; López-González & Gili, 2000; polyp pulsation behaviour, Halász *et al.*, 2013; ecological information, Bayer *et al.*, 2014) constitute a small minority in the taxonomic literature (2000–2020) but might, nonetheless, prove highly useful in adjudicating cases of morphological and molecular incongruence in the future. The rarity of other data sources is probably a symptom of the fact that taxonomic research in this group (as in many others) tends to rely heavily on preserved specimens. In addition to possessing potentially degraded DNA, it can be difficult or impossible to glean ecological, reproductive or behavioural data from such material, which can also be accompanied by little or no distributional or habitat context. It could then be said that octocorals are inherently difficult subjects for the integrative taxonomic approach, as indeed are many marine invertebrates (e.g. Wandeler *et al.*, 2007; Zeng *et al.*, 2019). This is problematic because descriptions based solely on morphology are less robust and thus more likely to be erroneous. Therefore, considering the scope of taxonomic problems in Octocorallia, the high rate of contemporary species descriptions and the still gradual uptake of integrative taxonomy (as seen through proportions of integrative species descriptions and publications), we might currently be adding to the workload of instances requiring future revision faster than these are being resolved.

Limitations and future research

Ultimately, 'the integrative future of taxonomy' (Padial *et al.*, 2010) is only beginning to dawn for octocorals, but a new phase of discovery is well underway. Description rates at species, genus and family levels show no signs of slowing and might be indicative of a large number of taxa still to be found. Bayer (1981) estimated a total fauna of ~4000 species globally. This seems certain to be exceeded, especially considering that many genera have never been taxonomically revised, most of the world has never been systematically sampled (Pérez *et al.*, 2016), and a vast amount of material already collected remains to be examined. This, in turn, poses the question, how many species of octocoral are there? As a horizon of total species richness has not yet come into view, this will be difficult to answer. It might be useful to try to estimate this using species discovery curves (e.g. De Clerck *et al.*, 2013; Edie *et al.*, 2017). However, across a broad range of plant and animal taxa, predictions of species richness are associated with high margins of error in groups with highly incomplete inventories (Bebber *et al.*, 2007). This means that until octocoral description rates begin to level off, it might be inappropriate or even impossible to calculate discovery curves and attempt to predict a ceiling for the number of taxa in this group.

Examining how often evidence of unidentified species (or species suspected of being undescribed) is published might contribute to future estimates of diversity. Likewise, ascertaining how the use of integrative techniques in Octocorallia compares with other taxa might inform realistic timeframes

for taxonomic progress, but this will require similar focused literature surveys to be conducted for a range of taxa (beyond those by Pante *et al.*, 2015; Vinarski, 2020 generalizing for all Animalia), and detailed direct comparisons have not yet been made. Answers to these questions will be essential in shaping research priorities in octocoral taxonomy throughout the rest of the 21st century. Fundamentally, this accumulation of biodiversity knowledge will require a substantial increase in the use of integrative taxonomic practices to add to our understanding of octocoral phylogeny and systematics, rather than adding to the burden of lingering taxonomic confusion through the risk of erroneous descriptions based solely on morphological data.

Albeit speculative and in stark opposition to the perceived importance of integrative taxonomy, a future without the need for such an approach might be possible. Although the universal animal *COI* barcode does not distinguish reliably between species of anthozoan cnidarians (McFadden *et al.*, 2011), new methods can do so with increasing, unprecedented efficiency. Modern phylogenomics and RAD-sequencing, in particular, are proving revolutionary for species delimitation purposes (Herrera & Shank, 2016; Erickson *et al.*, 2020). Even species with no evident distinguishing morphological, ecological or distributional characters can now be discriminated using only genetic data (McFadden *et al.*, 2017). To inform this progress, it might be useful to quantify how the success of DNA at species delimitation and the emphasis of morphological or genetic evidence in cases of incongruence has changed over time through further examinations and analyses of the literature. We could then be well placed to ask: what will be the role of integrative taxonomy, let alone morphological methods, in a future where genomic capability is easily available to octocoral researchers? DNA sequences might soon serve as defining diagnostic characters in formal descriptions of octocorals, as they already do in various other plant, animal and fungal taxa (reviewed by Renner, 2016). Perhaps integrative taxonomy is a transitional step between a discipline dominated by morphology in the past and genetics in the future. Without doubt, this carries profound philosophical implications for how we interpret different forms of data and choose from among many competing species concepts in the systematic delineation of species and what data we incorporate into taxonomic descriptions and diagnoses. This will require collective introspection by the taxonomic community that is far beyond the scope of the present study. Regardless, 134 species, 77 genera and eight families were newly described using morphomolecular comparisons over the last two decades, some of which would probably not have been brought to light through morphological study alone. For now, the contribution of integrative taxonomy to our understanding of octocoral diversity and systematics is clear, and the use of this approach is only set to grow.

Conclusion

Currently, octocoral species, genera and families are being described at exceptionally high rates, not seen since the late 19th and early 20th centuries, and the implementation of integrative taxonomy in octocorals has seen a marked increase in recent years. However, since the year 2000, the integrative approach has been applied unevenly across taxonomic levels, taxonomic groups and geographical regions and, crucially, the majority of taxonomic decisions overall continue to be made solely based on morphological data. Descriptions based only on morphological data are problematic, because they are less robust than integrative descriptions and more likely to be erroneous. Many taxonomic problems persist within Octocorallia, and because description rates show no signs of slowing, we might currently be adding to the workload of instances requiring future revision faster than these can be resolved. With no ceiling of total species richness yet apparent, the early 21st century represents an exceptional period of discovery in the history of octocoral taxonomy and, encouragingly, this momentum is being carried forwards by a growing field of authors using rapidly advancing molecular methods.

ACKNOWLEDGEMENTS

This project was funded by Victoria University of Wellington through a VUW Doctoral Scholarship and a Doctoral Submission Scholarship to G.M.K. NIWA supported this study under Coasts and Oceans Research Programme 2 'Marine Biological Resources: discovery and definition of the marine biota of New Zealand' (2018–2021 SCI), and the School of Biological Sciences (Victoria University of Wellington) provided graduate student research support. The authors declare no conflict of interest.

DATA AVAILABILITY

The data underlying this article will be shared on reasonable request to the corresponding author.

REFERENCES

Althaus F, Williams A, Schlacher TA, Kloser RJ, Green MA, Barker BA, Bax NJ, Brodie P, Schlacher-Hoenlinger

MA. 2009. Impacts of bottom trawling on deep- coral ecosystems of seamounts are long-lasting. *Marine Ecology Progress Series* **397**: 279–294.

Bayer FM. 1981. Status of knowledge of octocorals of world seas. In: *Seminários de biologia marinha*. Rio de Janeiro: Academia Brasileira de Ciéncias, 3–11.

Bayer FM. 2001. Octocoral research: past, present and future. *Atoll Research Bulletin* **494**: 79–105.

Bayer FM, Cairns SD, Cordeiro RTS, Pérez CD. 2014. New records of the genus *Callogorgia* (Anthozoa: Octocorallia) in the western Atlantic, including the description of a new species. *Journal of the Marine Biological Association of the United Kingdom* **95**: 905–911.

Bebber DP, Marriott FHC, Gaston KJ, Harris SA, Scotland RW. 2007. Predicting unknown species numbers using discovery curves. *Proceedings of the Royal Society B: Biological Sciences* **274**: 1651–1658.

Breedy O, Van Ofwegen LP, Vargas S. 2012. A new family of soft corals (Anthozoa, Octocorallia, Alcyonacea) from the aphotic tropical eastern Pacific waters revealed by integrative taxonomy. *Systematics and Biodiversity* **10**: 351–359.

Bruno JF, Siddon CE, Witman JD, Colin PL, Toscano MA. 2001. El Nino related coral bleaching in Palau, Western Caroline Islands. *Coral Reefs* **20**: 127–136.

Cairns SD. 2006. Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 6: the genera *Primnoella* Gray, 1858; *Thouarella* Gray, 1870; *Dasystenella* Versluys, 1906. *Proceedings of the Biological Society of Washington* **119**: 161–194.

Cairns SD. 2007a. Calcaxonian Octocorals (Cnidaria; Anthozoa) from Eastern Pacific seamounts. *Proceedings of the California Academy of Sciences* **58**: 511–541.

Cairns SD. 2007b. Studies on western Atlantic Octocorallia (Gorgonacea: Primnoidae). Part 8: new records of Primnoidae from the New England and Corner Rise Seamounts. *Proceedings of the Biological Society of Washington* **120**: 243–263.

Cairns SD. 2009. Review of Octocorallia (Cnidaria: Anthozoa) from Hawai'i and adjacent seamounts. Part 2: genera *Paracalyptrophora*; *Candidella*; and *Calyptrophora*. *Pacific Science* **63**: 413–448.

Cairns SD. 2010. Review of Octocorallia (Cnidaria: Anthozoa) from Hawai'i and adjacent seamounts. Part 3: genera *Thouarella*, *Plumarella*, *Callogorgia*, *Fanellia*, and *Parastenella*. *Pacific Science* **64**: 413–440.

Cairns SD. 2011. A revision of the Primnoidae (Octocoralia: Alcyonacea) from the Aleutian Islands and Bering Sea. *Smithsonian Contributions to Zoology* **634**: 1–51.

Cairns SD. 2012a. New primnoid genus and species (Alcyonacea: Primnoidae) from the southwestern Atlantic. *Proceedings of the Biological Society of Washington* **125**: 180–188.

Cairns SD. 2012b. *The marine fauna of New Zealand: New Zealand Primnoidae (Anthozoa: Alcyonacea). Part 1. Genera Narella, Narelloides, Metanarella, Calyptrophora, and Helicoprimnoa. NIWA Biodiversity Memoir 126*. Wellington: National Institute of Water & Atmospheric Research.

Cairns SD. 2015. New abyssal Primnoidae (Anthozoa: Octocorallia) from the Clarion- Clipperton Fracture Zone, equatorial northeastern Pacific. *Marine Biodiversity* **46**: 141–150.

Cairns SD. 2018a. Deep-water octocorals (Cnidaria, Anthozoa) from the Galapagos and Cocos Islands. Part 1: suborder Calcaxonia. *ZooKeys* **729**: 1–46.

Cairns SD. 2018b. Primnoidae (Cnidaria: Octocorallia: Calcaxonia) of the Okeanos Explorer expeditions (CAPSTONE) to the central Pacific. *Zootaxa* **4532**: 1–43.

Cairns SD, Baco A. 2007. Review and five new Alaskan species of the deep-water octocoral *Narella* (Octocorallia: Primnoidae). *Systematics and Biodiversity* **5**: 391–407.

Cairns SD, Bayer FM. 2005. A review of the genus *Primnoa* (Octocorallia: Gorgonacea: Primnoidae), with the description of two new species. *Bulletin of Marine Science* **77**: 225–256.

Costello MJ, May RM, Stork NE. 2013a. Can we name Earth's species before they go extinct? *Science* **339**: 413–416.

Costello MJ, Wilson S, Houlding B. 2012. Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Systematic Biology* **61**: 871–883.

Costello MJ, Wilson S, Houlding B. 2013b. More taxonomists describing significantly fewer species per unit effort may indicate that most species have been discovered. *Systematic Biology* **62**: 616–624.

Daly M, Brugler MR, Cartwright P, Collins AG, Dawson MN, Fautin DG, France SC, McFadden CS, Opresko DM, Rodriguez E, Romano SL, Stake JL. 2007. The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa* **1668**: 127–182.

Dayrat B. 2005. Towards integrative taxonomy. *Biological Journal of the Linnean Society* **85**: 407–415.

De Clerck O, Guiry MD, Leliaert F, Samyn Y, Verbruggen H. 2013. Algal taxonomy: a road to nowhere? *Journal of Phycology* **49**: 215–225.

De Leo DM, Ruiz-Ramos DV, Baums IB, Cordes EE. 2015. Response of deep-water corals to oil and chemical dispersant exposure. *Deep-Sea Research II* **129**: 137–147.

De Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* **56**: 879–886.

Dias TLP, Gondim AI. 2016. Bleaching in scleractinians, hydrocorals, and octocorals during thermal stress in a northeastern Brazilian reef. *Marine Biodiversity* **46**: 303–307.

Edie SM, Smits PD, Jablonski D. 2017. Probabilistic models of species discovery and biodiversity comparisons. *Proceedings of the National Academy of Sciences* **114**: 3666–3671.

Erickson KL, Pentico A, Quattrini AM, McFadden CS. 2020. New approaches to species delimitation and population structure of anthozoans: two case studies of octocorals using ultraconserved elements and exons. *Molecular Ecology Resources* **21**: 781404–781492.

Fabricius KE. 1999. Tissue loss and mortality in soft corals following mass-bleaching. *Coral Reefs* **18**: 54–54.

Fabricius KE, Alderslade P. 2001. *Soft corals and sea fans: a comprehensive guide to the tropical shallow-water genera of the central West-Pacific, the Indian Ocean and the Red Sea*. Townsville: Australian Institute of Marine Science.

France SC, Hoover LL. 2001. Analysis of variation in mitochondrial DNA sequences (ND3, ND4L, MSH) among

Octocorallia (= Alcyonaria) (Cnidaria: Anthozoa). *Bulletin of the Biological Society of Washington* **10**: 110–118.

Gabay Y, Benayahu Y, Fine M. 2013. Does elevated pCO_2 affect reef octocorals? *Ecology and Evolution* **3**: 465–473.

Gambi MC, Barbieri F, Signorelli S, Saggiomo V. 2010. Mortality events along the Campania coast (Tyrrhenian Sea) in summers 2008 and 2009 and relation to thermal conditions. *Biologia Marina Mediterranea* **17**: 126–127.

Goulding TC, Dayrat B. 2016. Integrative taxonomy: ten years of practice and looking into the future. *Archives of Zoological Museum of Lomonosov Moscow State University* **54**: 116–133.

Halász A, McFadden CS, Aharonovich D, Toonen R, Benayahu Y. 2013. A revision of the octocoral genus *Ovabunda* (Alderslade, 2001) (Anthozoa, Octocorallia, Xeniidae). *ZooKeys* **373**: 1–41.

Herrera S, Shank TM. 2016. RAD sequencing enables unprecedented phylogenetic resolution and objective species delimitation in recalcitrant divergent taxa. *Molecular Phylogenetics and Evolution* **100**: 70–79.

Kükenthal W. 1906. *Alcyonacea. Wissenschaftliche Ergebnisse der Deutschen Tiefsee Expedition auf dem Dampfer 'Valdivia' 1898–1899 Dreizehnter Band*. Jena: Gustav Fischer.

Lasker HR, Kim K, Coffroth MA. 1996. Reproductive and genetic variation among Caribbean gorgonians: the differentiation of *Plexaura kuna*, new species. *Bulletin of Marine Science* **58**: 277–288.

Lau YW, Reimer JD. 2019. A first phylogenetic study on stoloniferous octocorals off the coast of Kota Kinabalu, Sabah, Malaysia, with the description of two new genera and five new species. *ZooKeys* **872**: 127–158.

Lõhelaid H, Teder T, Samel N. 2015. Lipoxygenase-allene oxide synthase pathway in octocoral thermal stress response. *Coral Reefs* **34**: 143–154.

López-González PJ, Gili JM. 2000. A new octocoral genus (Cnidaria: Anthozoa) from Antarctic waters. *Polar Biology* **23**: 452–458.

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, Van Woesik R. 2001. Coral bleaching: the winners and the losers. *Ecology Letters* **4**: 122–131.

McFadden CS. 1999. Genetic and taxonomic relationships among northeastern Atlantic and Mediterranean populations of the soft coral *Alcyonium coralloides*. *Marine Biology* **133**: 171–184.

McFadden CS, Alderslade P, Van Ofwegen LP, Johnsen H, Rusmevichientong A. 2006. Phylogenetic relationships within the tropical soft coral genera *Sarcophyton* and *Lobophytum* (Anthozoa, Octocorallia). *Invertebrate Biology* **125**: 288–305.

McFadden CS, Benayahu Y, Pante E, Thoma JN, Nevarez PA, France SC. 2011. Limitations of mitochondrial gene barcoding in Octocorallia. *Molecular Ecology Resources* **11**: 19–31.

McFadden CS, Haverkort-Yeh R, Reynolds AM, Halász A, Quattrini AM, Zac H, Forsman ZH, Benayahu Y, Toonen RJ. 2017. Species boundaries in the absence of morphological, ecological or geographical differentiation in the Red Sea octocoral genus *Ovabunda* (Alcyonacea: Xeniidae). *Molecular Phylogenetics and Evolution* **112**: 174–184.

McFadden CS, Hutchinson MB. 2004. Molecular evidence for the hybrid origin of species in the soft coral genus *Alcyonium* (Cnidaria: Anthozoa: Octocorallia). *Molecular Ecology* **13**: 1495–505.

McFadden CS, Sánchez JA, France SC. 2010. Molecular phylogenetic insights into the evolution of Octocorallia: a review. *Integrative and Comparative Biology* **50**: 389–410.

McFadden CS, Tullis LD, Hutchinson MB, Winner K, Sohm JA. 2004. Variation in coding (NADH dehydrogenase subunits 2, 3, and 6) and noncoding intergenic spacer regions of the mitochondrial genome in Octocorallia (Cnidaria: Anthozoa). *Marine Biotechnology* **6**: 516–526.

McFadden CS, Van Ofwegen LP. 2012a. A revision of the soft coral genus, *Eunephthya* Verrill, 1869 (Anthozoa: Octocorallia: Nephtheidae), with a description of four new species from South Africa. *Zootaxa* **3485**: 1–25.

McFadden CS, Van Ofwegen LP. 2012b. Stoloniferous octocorals (Anthozoa, Octocorallia) from South Africa, with descriptions of a new family of Alcyonacea, a new genus of Clavulariidae, and a new species of *Cornularia* (Cornulariidae). *Invertebrate Systematics* **26**: 331–356.

McFadden CS, Van Ofwegen LP. 2013. A second, cryptic species of the soft coral genus *Incrustatus* (Anthozoa: Octocorallia: Clavulariidae) from Tierra del Fuego, Argentina, revealed by DNA barcoding. *Helgoland Marine Research* **67**: 137–147.

McFadden CS, Van Ofwegen LP. 2017. Revisionary systematics of the endemic soft coral fauna (Octocorallia: Alcyonacea: Alcyoniina) of the Agulhas Bioregion, South Africa. *Zootaxa* **4363**: 451–488.

McFadden CS, Van Ofwegen LP, Beckman EJ, Benayahu Y, Alderslade P. 2009. Molecular systematics of the speciose Indo-Pacific soft coral genus, *Sinularia* (Anthozoa: Octocorallia). *Invertebrate Biology* **128**: 303–323.

Moore KM, Alderslade P, Miller KJ. 2017. A taxonomic revision of *Anthothela* (Octocorallia: Scleraxonia: Anthothelidae) and related genera, with the addition of new taxa, using morphological and molecular data. *Zootaxa* **4304**: 1–212.

Núñez-Flores M, Gomez-Uchida D, López-González PJ. 2020. Molecular and morphological data reveal three new species of *Thouarella* Gray, 1870 (Anthozoa: Octocorallia: Primnoidae) from the Southern Ocean. *Marine Biodiversity* **50**: 30.

Nutting CC. 1910. *The Gorgonacea of the Siboga Expedition: the Muriceidae. Siboga Expedition Monograph 13*. Leiden: E. J. Brill.

Padial JM, Miralles A, De la Riva I, Vences M. 2010. The integrative future of taxonomy. *Frontiers in Zoology* **7**: 16.

Pante E, Schoelinck C, Puillandre N. 2015. From integrative taxonomy to species description: one step beyond. *Systematic Biology* **64**: 152–160.

Pérez CD, Neves B, Cordeiro RTS, Williams GC, Cairns SD. 2016. Diversity and distribution of Octocorallia. In: Stefano G, Dubinsky Z, eds. *The Cnidaria, past, present and future*. Dordrecht: Springer International, 109–123.

Poliseno A, Altuna A, Puetz LC, Mak SST, Rios P, Petroni E, McFadden CS, Sørensen MV, Gilbert MTP. 2021. An integrated morphological-molecular approach reveals new insights on the systematics of the octocoral *Telestula humilis* (Thomson, 1927) (Octocorallia: Alcyonacea: Clavulariidae). *Invertebrate Systematics* **35**: 261–281.

Quattrini AM, Wu T, Soong K, Jeng MS, Benayahu Y, McFadden CS. 2019. A next generation approach to species delimitation reveals the role of hybridization in a cryptic species complex of corals. *BMC Evolutionary Biology* **19**: 116.

Ramvilas G, Shalu K, Raghavan R, Ranjeet K. 2019. Mapping octocoral (Anthozoa: Octocorallia) research in Asia, with particular reference to the Indian subcontinent: trends, challenges and opportunities. *Journal of Threatened Taxa* **11**: 14691–14721.

Renner SS. 2016. A return to Linnaeus's focus on diagnosis, not description: the use of DNA characters in the formal naming of species. *Systematic Biology* **65**: 1085–1095.

Richards ZT, Yasuda N, Kikuchi T, Foster T, Mitsuyuki C, Stat M, Suyama Y, Wilson NG. 2018. Integrated evidence reveals a new species in the ancient blue coral genus *Heliopora* (Octocorallia). *Scientific Reports* **8**: 15875.

Sánchez JA, McFadden CS, France SC, Lasker HR. 2003. Molecular phylogenetic analyses of shallow-water Caribbean octocorals. *Marine Biology* **142**: 975–987.

Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH. 2010. Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology* **55**: 421–438.

Sheth BP, Thaker VS. 2017. DNA barcoding and traditional taxonomy: an integrated approach for biodiversity conservation. *Genome* **60**: 618–628.

Thomson JA, Henderson WD. 1906. *An account of the alcyonarians collected by the Royal Indian Marine Survey Ship Investigator in the Indian Ocean Part 1: the Alcyonarians of the deep sea*. Calcutta: Printed by order of the Trustees of the Indian Museum.

Thomson JA, Simpson JJ. 1909. *An account of the alcyonarians collected by the Royal Indian Marine Survey Ship Investigator in the Indian Ocean Part 2: the Alcyonarians of the littoral area*. Calcutta: Printed by order of the Trustees of the Indian Museum.

Valdecasas AG, Williams D, Wheeler QD. 2008. 'Integrative taxonomy' then and now: a response to Dayrat (2005). *Biological Journal of the Linnean Society* **93**: 211–216.

Versluys J. 1906. *Die Gorgoniden der Siboga Expedition II: die Primnoidae. Siboga Expedition Monograph 13a*. Leiden: E. J. Brill.

Vinarski MV. 2020. Roots of the taxonomic impediment: is the 'integrativeness' a remedy? *Integrative Zoology* **15**: 2–15.

Wandeler P, Hoeck PAE, Keller LF. 2007. Back to the future: museum specimens in population genetics. *Trends in Ecology & Evolution* **22**: 634–642.

Will KW, Mishler BD, Wheeler QD. 2005. The perils of DNA barcoding and the need for integrative taxonomy. *Systematic Biology* **54**: 844–851.

Williams GC. 2011. The global diversity of sea pens (Cnidaria: Octocorallia: Pennatulacea). *PLoS One* **6**: e22747.

Wirshing HH, Messing CG, Douady CJ, Reed J, Stanhope MJ, Shivji MS. 2005. Molecular evidence for multiple lineages in the gorgonian family Plexauridae (Anthozoa: Octocorallia). *Marine Biology* **47**: 497–508.

WoRMS (World Register of Marine Species). 2021. Available at: https://www.marinespecies.org at VLIZ. Accessed 20 July 2021.

Wright EP, Studer T. 1889. *Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76, zoology 31 (part 64)*. London: Published by Order of Her Majesty's Government.

Zeng C, Clark MR, Rowden AA, Kelly M, Gardner JPA. 2019. The use of spatially explicit genetic variation data from four deep-sea sponges to inform the protection of vulnerable marine ecosystems. *Scientific Reports* **9**: 5482.