



Benchmarking global biodiversity of decapod crustaceans (Crustacea: Decapoda)

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ABSTRACT

A new assessment of the global biodiversity of decapod Crustacea (to 31 December 2022) records 17,229 species in 2,550 genera and 203 families. These figures are derived from a well-curated dataset maintained on the online platform DecaNet, a subsidiary of the World Register of Marine Species (WoRMS). Distinct phases are recognised in the discovery process (as measured by species descriptions) corresponding to major historical and geopolitical time periods, with the current rate of species descriptions being more than three times higher than in the Victorian age of global exploration. Future trends are briefly explored, and it is recognised that a large number of species remain to be discovered and described.

KEY WORDS: biodiversity, species richness, inventories, taxonomy

INTRODUCTION

Biologists are endlessly fascinated with estimating the number of species living on the planet, with these largely based on one of

three methods: extrapolation from past rates of species descriptions, proportions of undescribed species in samples, and expert opinion polls. While such calculations are intriguing and may be intellectually worth exploring, the vital, underlying foundation

of such mathematical constructs is known biodiversity, usually expressed as the number of described species, an authoritative appraisal of which is still lacking for many invertebrate taxa. More confidence in such metrics can be expressed for terrestrial vertebrates, and to a more limited extent, aquatic vertebrates. Exhaustive global catalogues for the majority of invertebrate groups are lacking, especially so for insects, which make up the bulk of present-day species richness. In fact, even authoritative yet simple estimates of total currently known biodiversity, a basic metric of biodiversity, are lacking for many taxa in the literature, including Decapoda. Such metrics feature in numerous invertebrate textbooks, for example Brusca *et al.* (2022) gave a number of 'over 15,000 named species' for decapods, but it is usually unclear how these approximations were derived and of their accuracy.

Even for Decapoda, a relatively well-documented group compared to other invertebrates, global estimates are few and far between. Chace (1951) arrived at a total of 8,321 species in 1,001 genera described up to 1945, based on the exhaustive card index maintained in the Invertebrate Zoology Department of the United States National Museum (USNM). The next attempt was by Martin & Davis (2006), with an estimate of 7,905 species, admittedly based on an underlying database said to contain only half of all crustacean species, which explains the lower number than that of Chace (1951). De Grave *et al.* (2009) approximated there to be 14,335 species, based on published and unpublished species lists. Appeltans *et al.* (2012) used an early version of the World Register of Marine Species (WoRMS) database (cut-off date not specified) and determined there to be 12,029 marine-only species of Decapoda. Ah Yong *et al.* (2011) brought the earlier estimate of De Grave *et al.* (2009) up to date and derived a total of 15,033 described marine, freshwater, and terrestrial species, based on species lists held by global experts. Most recently, Poore & Ah Yong (2023) interrogated WoRMS and obtained a total of 13,501 species of marine-only Decapoda. It is not straight forward to reconcile global assessments that ignore freshwater and terrestrial species diversity because, depending on definitions, there are as many as 3,581 known decapod species inhabiting these biotopes (Cumberlidge *et al.*, 2009; De Grave *et al.*, 2015; Cumberlidge, 2016; Crandall & De Grave, 2017; Santos *et al.*, 2017, and updates in those groups on WoRMS until December 2022, see below). Although these are the only authoritative decapod-wide estimates in the literature, numbers do exist at a more inclusive level in the various checklists produced over the last few decades, all of which are now outdated (Baba *et al.*, 2008; Ng *et al.* 2008; Osawa & McLaughlin, 2010; Boyko & McLaughlin, 2010; Chan, 2010, 2019; McLaughlin *et al.*, 2010a, b; De Grave & Fransen, 2011; Crandall & De Grave, 2017) and the summary by Dworschak (2000) for Axiidea and Gebiidea.

Invertebrate checklists are nowadays *de facto* electronically maintained, many on the WoRMS platform, and the Decapoda are no exception. The authors of this contribution are all involved in maintaining or supplying information to maintain the recently established sub-register on Decapoda on the WoRMS platform known as DecaNet (<https://www.decanet.info>), which has matured into an authoritative and continuously curated checklist for the group. We are also broadening its scope to also include a rapidly increasing amount of associated

information, such as validated photographs, and distributional and ecological data. By interrogating DecaNet, it is now possible to obtain an accurate value of decapod diversity in total or for any of its subgroups (e.g., Anomura, Brachyura), families and even genera directly from the website, but such numbers are in continual flux, often on a daily basis, due to taxonomic changes, new species descriptions, and newly established synonymies. Perhaps somewhat unfortunately, the age of printed catalogues is coming to an end with the increased digitisation of our world.

Due to the ephemeral nature of information contained in online biodiversity databases, even those such as WoRMS/DecaNet that are stable in themselves, it remains useful to benchmark the global biodiversity of Decapoda in a more enduring format, to serve as a valuable reference point for future studies.

MATERIAL AND METHODS

Data at the species and subspecies level were downloaded from WoRMS on 31 December 2022 (<https://www.marinespecies.org>; accessed 2022-12-31), together with their higher classification, which essentially follows De Grave *et al.* (2009). The dataset included all taxonomically valid species (termed 'accepted' in WoRMS) irrespective of database environment flags, with 'marine,' 'brackish,' 'freshwater,' and 'terrestrial' species included. Only 'Recent' and 'Recent+fossil' (i.e., not exclusively fossil) taxa were downloaded (see Horton *et al.*, 2017 for definitions). The data underwent an iterative curation process, checking both status and year of publication with cross-verification and corrections by several of the authors as needed. In the final dataset, subspecies were deleted and all counts given refer to species alone, and to numbers at the end of 2022, except where stated. The final dataset is continually curated on the DecaNet portal (<https://www.decanet.info>) and can be consulted there.

RESULTS AND DISCUSSION

History of discovery

Although decapods have been known and eaten by humans since antiquity, the starting point of nomenclature across all taxa is the 10th edition of *Systema Naturae* by Linnaeus (1758). In this monumental compilation, 46 currently valid species of Decapoda were named, primarily in the genus *Cancer* Linnaeus, 1758. Using currently recognised infraorders, these belong to Achelata (two species), Anomura (five species), Astacidea (three species), Brachyura (34 species) and Caridea (two species).

'*Wunderkammer era*' (1759–1836). In the approximately 75-year period after Linnaeus, a slow accretion of knowledge took place, with on average seven species described per year with numerous zero-year intervals (Fig. 1), but with significant peaks in the years 1775 (27 species) and 1798 (35 species) due to the works of Forskål (1775) and Fabricius (1775, 1798). Other notable taxonomists during this era were J.F.W. Herbst (1743–1807), W.E. Leach (1791–1839), A. Risso (1777–1845), T. Pennant (1726–1798), G.A. Olivier (1756–1824), and P.A. Latreille (1762–1833). This period culminated in the publication of *Histoire Naturelles des Crustacés* by Henri Milne Edwards,

the first two volumes of which were published in 1834 and 1837 (H. Milne Edwards, 1834–1840), and contained descriptions of a further 55 and 80 species, respectively, while providing a near complete review of all prior taxonomic information.

'Victorian era' (1838–1913). Taxonomic productivity stepped up an order of magnitude over the next ca. 75 years with, on average, 65 new species being described per year (Fig. 1), with a notable peak of 234 species in 1902. Much of the material during this period was obtained by the great oceanographic voyages, such as the United States Exploring Expedition reported upon by Dana (1852), the *Challenger* Expedition (Miers, 1886; Henderson, 1888; Spence Bate, 1888), the French voyages of the *Talisman* and *Travailleur* reported upon by A. Milne-Edwards & Bouvier (1900), and the *Investigator* surveys of the Indian Ocean, reported upon by Alcock (1901), amongst numerous other significant contributions by A. Alcock (1859–1933) and J. Wood-Mason (1846–1893). The 'Victorian era' also saw significant growth in museum collections, which greatly benefitted resident taxonomists such as H. Balss (1886–1957), J.G. De Man (1850–1930), F. Doflein (1873–1924), W. Faxon (1848–1920), G. Nobile (1877–1908), M.J. Rathbun (1860–1943), S.I. Smith (1843–1926), and T.R.R. Stebbing (1835–1926), who described numerous species from these global and smaller expeditions as well as many donations to their collections from explorers, collectors and naturalists.

'World in turmoil era' (1914–1955). Unsurprisingly, this period saw a marked drop in taxonomic output due to the social and economic turmoil of the First World War (1914–1918), the Great Depression (1929–1939), and the Second World War (1939–1945) and its aftermath. Species description fell to an average of 51 per year (Fig. 1), but this average was buoyed up by relatively higher productivity during the inter-war period that was even higher than the pre-1914 levels. For example, 129 species were described in 1933 by notable taxonomists such as T. Sakai (1903–1986), Y. Yokoya (1891–1969), A.J. Van Dam, and M. Ward (1903–1966), amongst others. Noticeable also is the

low point of 1945, in which a mere nine species were described in only five papers.

'Sputnik era' (1958–2000). There has been a steady increase in the number of species described since the mid-1950s, averaging 120 per annum for 1958–2000, effectively double the productivity seen in the 'Victorian era' of major expeditions and museum expansion. The productivity of this period was a direct result of the considerable Western investment in geoexploration and science in general following the launch of the Soviet Sputnik spacecraft in 1957, especially so in the United States and Europe. Notably, both the then United States National Museum, Washington D.C. (now National Museum of Natural History) and Muséum national d'Histoire naturelle, Paris (MNHN) recruited a cohort of taxonomists, firmly establishing themselves as global powerhouses for decapod biodiversity research for decades to come. The 'Sputnik era' crashes to a rather abrupt end around 1999–2002 (Fig. 1), with the senescence of this generation and the loss of many in their number (e.g., F.A. Chace Jr. (1908–2004), A.-Y. Dai (1930–2005), M. de Saint Laurent (1926–2003), L.B. Holthuis (1921–2008), B.F. Kensley (1944–2004), R.B. Manning (1934–2000), S. Miyake (1908–1998), N.M. Tirmizi (1933–2005), A.B. Williams (1919–1999)) through death or retirement, the 'Valhalla chasm.'

'New Taxonomy era' (2002–present). Per annum descriptions increased to an average of 201 species in the last two decades. Although the drivers of this are not yet fully understood, it is evident that global electronic communication, online editing systems, and the increased speed of the publication process as a whole (the vanguard of which was the megajournal *Zootaxa*) have played a more prominent role than the adoption of genetic techniques (also see Bouchet et al., 2023). Genetic studies have nevertheless led to significant discovery of previously unrealised diversity. For example, Crivellaro et al. (2018) recovered a minimum of 14 potentially novel species within *Aegla longirostri* Bond-Buckup & Buckup, 1994, all from a single, large

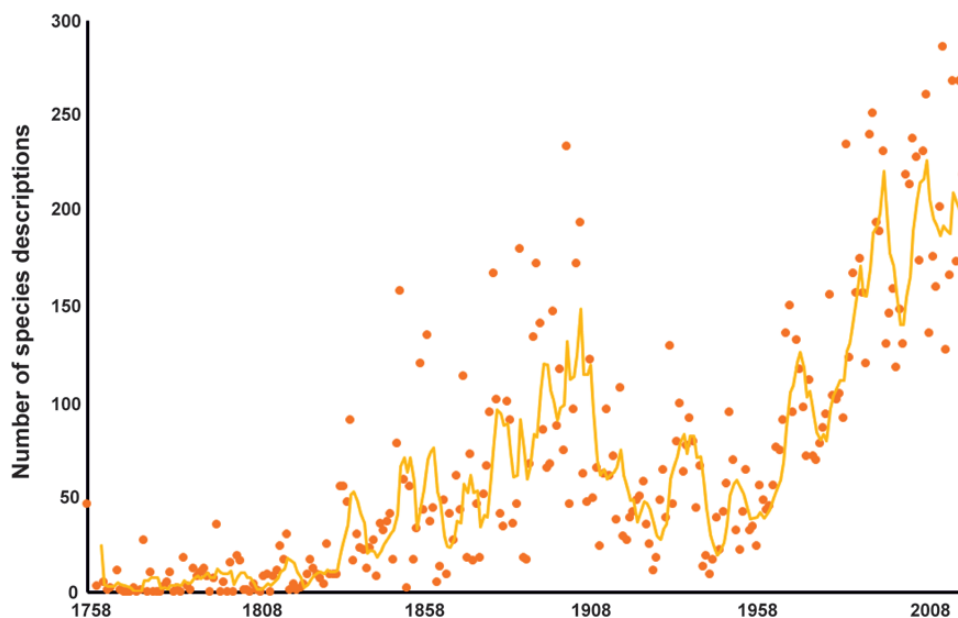


Figure 1. Number of species of Decapoda described per year (1758–2022); line is the five-year moving average.

river drainage in southern Brazil. Similarly, Xu *et al.* (2022) discovered up to 15 potentially novel species within the coral-dwelling crab genus *Opecarcinus* Kropp & Manning, 1987, currently containing only nine species. Despite the extensive use of genetic information in some species descriptions, so called integrative taxonomy (Fransen *et al.*, 2022 to cite but one example), truly cryptic 'named' species remain rare in Decapoda. A notable exception is the commercially important and Lessepsian invasive prawn *Penaeus pulchricaudatus* Stebbing, 1914 (see Tsoi *et al.*, 2014).

At the infraordinal level, Brachyura (Fig. 2) largely follow the trend outlined above for Decapoda as a whole, perhaps unsurprisingly as they account for 44.6% of the global biodiversity of decapod crustaceans (Table 1). It is, however, notable in comparison with the other species-rich infraorders (Fig. 2) that they dominate description patterns in the 'Wunderkammer era.' This was already noted by De Grave (2003) for the North East Atlantic fauna and potentially attributed to their relative ease of collection, study, and preservation rather than any intrinsic traits, such as body size or bathymetric distribution. Caridea and Anomura show similar description trends (Fig. 2) and account for 22.3% and 19.0% of global biodiversity, respectively. One notable trend, however, is that the proportion of anomurans being described annually in the 'New Taxonomy era' is almost twice as that of the 'Victorian era', on average being 25% in 1990–2022 versus 15% in 1838–1913. deep waters across the Indo-West Pacific region by the French MUSORSTOM program and its successors run by MNHN (see Richer de Forges

et al., 2013). Conversely, the average proportion of Brachyura has dropped from 53% of all descriptions in the 'Victorian era' to 38% in the 'New Taxonomy era', perhaps linked to taxonomic fashion. Astacidea, the fourth most speciose infraorder at 4.7% does not display the same pattern of description (Fig. 2), with the post-WWII slump being absent, and with the continual increase in descriptions since the late 1950s observed in the other groups being equally absent. This infraorder is numerically dominated by the families of freshwater crayfishes (enumerated by Crandall & De Grave, 2017), with only a minor component of marine lobsters (listed in Chan, 2010, 2019). It is not, however, assumed that the overall ecology of the group plays an important role in this pattern, as both Brachyura and Caridea hold a significant freshwater component (Cumberlidge *et al.*, 2009; De Grave *et al.*, 2015), most of which have been described post-1950. We attribute this pattern to the prodigious publication output of H.H. Hobbs Jr. (1914–1994), who dominated the taxonomy of North American crayfishes for five decades.

Present-day species richness

The number of accepted, described species of Decapoda reached 17,229 at the end of 2022, distributed across 2,550 genera in 203 families (Table 1), with 70 species subdivided into a total of 172 (including nominotypical) subspecies. Of course, these numbers are in constant flux, as new taxonomic discoveries are made, older names resurrected, and synonyms identified. Although the majority of these adjustments

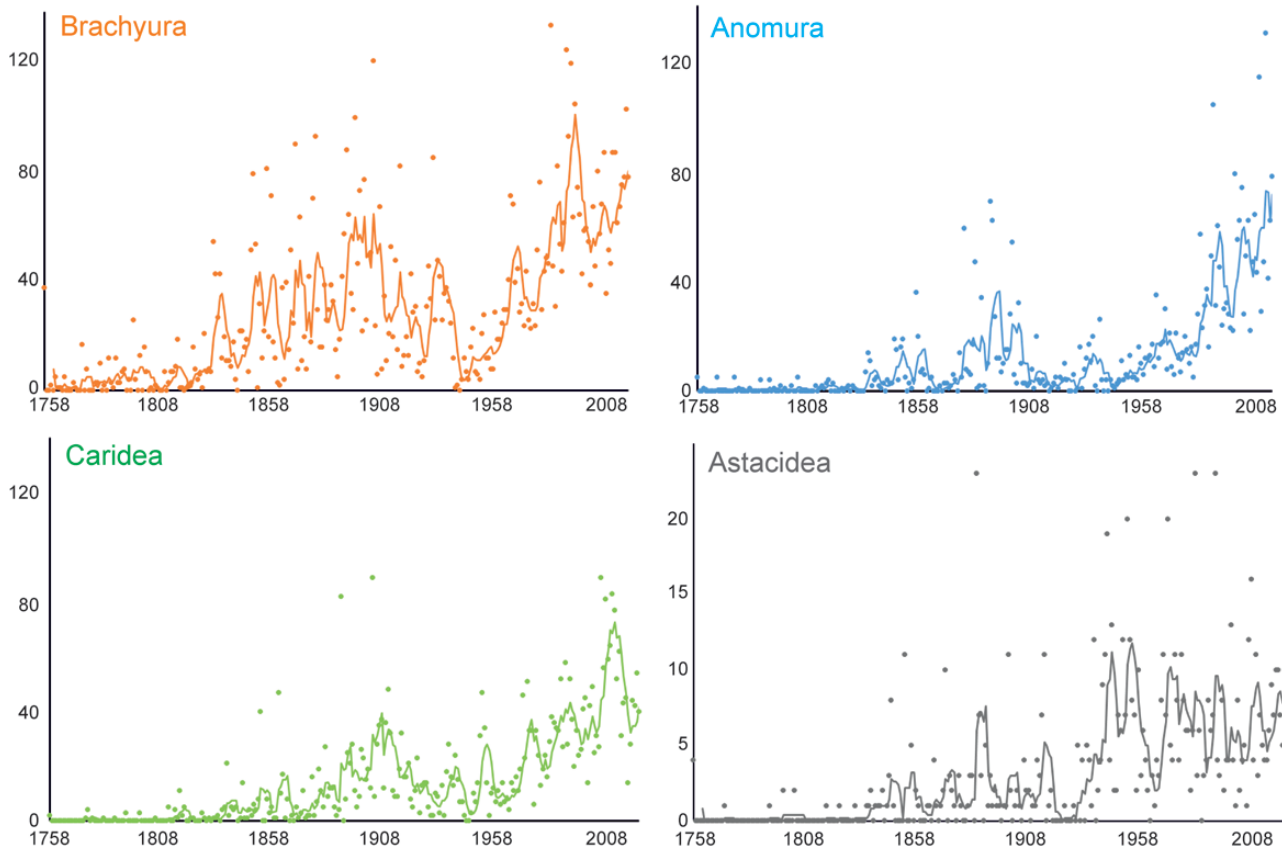


Figure 2. Numbers of species described per year (1758–2022) for the four most species-rich infraorders (Brachyura, Anomura, Caridea, Astacidea); lines are the five-year moving averages.

are relatively trivial (if cumulative) and only add slowly to the total species count, exceptions are large monographs, such as the 100 new species of *Uroptychus* Henderson, 1888 described in Baba (2018). Not affecting the total number of species is the transfer of species from one genus to another, a typical taxonomic pastime, or splitting genera, such as *Munida* Leach, 1820 into 12 genera, 11 of which were newly established (Machordom *et al.*, 2022) or adjusting the higher classification, e.g., by reviving a previously synonymised family in Brachyura and establishing a new one (e.g., Tsang & Naruse, 2023).

Three of the pleocyematan infraorders together make up the bulk (85%) of living biodiversity, with Brachyura alone accounting for almost half of the total richness (44.5%), followed by Caridea (22.3%) and Anomura (19.1%). The species-richness of brachyuran crabs is in no small measure due to the group having conquered not only the marine realm, from the deep sea to the intertidal, but also with being successful in a multitude of freshwater and terrestrial environments (Cumberlidge *et al.*, 2009). Caridean shrimps have not invaded the terrestrial realm on a permanent basis, although species of *Merguia* Kemp, 1914 are semi-arboreal in tropical mangroves and several larger shrimps in the genera *Atya* Leach 1816, *Palaemon* Weber, 1795,

and *Macrobrachium* Spence Bate, 1868 are known to migrate across meadows and areas adjacent to waterfalls (e.g., Hongjamrassilp *et al.*, 2021). Carideans are, however, abundant and species-rich in freshwater ecosystems (De Grave *et al.*, 2015), as well as in the marine pelagic environment, both undoubtedly contributing to their overall species richness. Anomura, by contrast, are rare in freshwater (outside of the South American *Aegla* Leach, 1820 with 92 species), and only modestly successful in the terrestrial realm, with some diogenid and coenobitid hermit crabs (*Coenobita* Latreille, 1829 with 17 species and the monotypic *Birgus* Leach, 1816) occupying that environment. Two superfamilies, Chirostyloidea and Galatheoidea, however, are abundant and species-rich in deep marine waters (Schnabel *et al.*, 2011).

Three infraorders are species-poor: the deep-sea Polychelida with 38 species, the anchialine Procarididea with six species, and Glypheidea with only two Recent species. The latter group has a much more substantial fossil record (Schweitzer *et al.*, 2010; Charbonnier *et al.*, 2013), with extant species being regarded as 'living fossils.' All other infraorders have moderate species richness (Table 1).

Ten families of Decapoda account for over one-third of total richness at 36.2% (Table 2). By contrast, the largest size class (as

Table 1. Number of families, genera and species for each (sub/intra) ordinal taxon, the first year of description (YOD) of an included species and the quartile years of the species inventory.

	Families	Genera	Species	First YOD	25%	50%	75%
Order Decapoda	203	2550	17,229	1758	1898	1968	1999
Suborder Dendrobranchiata	7	80	533	1765	1893	1934	1976
Suborder Pleocyemata							
Infraorder Achelata	2	32	153	1758	1869	1946	1976
Infraorder Anomura	23	245	3,311	1758	1902	1989	2007
Infraorder Astacidea	6	49	767	1758	1929	1962	1990
Infraorder Axiidea	11	127	566	1792	1928	1992	2007
Infraorder Brachyura	107	1567	7,683	1758	1886	1937	1994
Infraorder Caridea	37	405	3,825	1758	1908	1974	2004
Infraorder Gebiidea	4	20	248	1792	1956	1989	2006
Infraorder Glypheidea	1	2	2	1975	-	-	-
Infraorder Polychelida	1	6	38	1862	-	-	-
Infraorder Procarididea	1	2	6	1972	-	-	-
Infraorder Stenopodidea	3	14	97	1811	1973	1990	2012

Table 2. Ten most species-rich families of Decapoda, their generic and species richness, and the quartiles of the species inventory.

	Genera	Species	25%	50%	75%
Palaemonidae	156	1107	1922	1976	2004
Alpheidae	50	777	1908	1968	2004
Potamidae	131	669	1971	1993	2004
Xanthidae	135	628	1865	1906	1974
Paguridae	87	611	1893	1986	2003
Atyidae	46	544	1927	1992	2008
Leucosiidae	75	498	1878	1918	1992
Cambaridae	14	463	1940	1964	1985
Munididae	21	480	1988	1996	2009
Epiplatidae	97	467	1869	1907	1985

herein defined) is of families comprising 2–10 species (Fig. 3). The most speciose family is Palaemonidae with 1,107 species/subspecies, accounting for 6.5% of total decapod richness, a significant component of that being in the freshwater/low-salinity *Macrobrachium* with 267 species. Other species-rich freshwater families are Atyidae, Cambaridae, and Potamidae. As perhaps expected, families with high abundance and richness in tropical, shallow waters, such as Alpheidae and Xanthidae, also feature in the top-ten, as does the deep-water anomuran Munididae. On the opposite end of the scale, 13 families are monospecific, including the deep-water Poupiniidae from French Polynesia and the southern Australian crab-like Lomisidae, both ‘evolutionary novelties’.

In terms of genera, 35% are monospecific, with a further 50% harbouring 2–10 species (Fig. 3). By contrast, two genera of caridean shrimps, *Caridina* H. Milne Edwards, 1837 [H. Milne Edwards, 1834–1840] (345) and *Alpheus* Fabricius, 1798 (331) jointly account for 3.9% of global decapod species richness. Up until October 2022, the anomuran genus *Munida* was also in this category, with 304 species, but it has since been split into twelve genera (Machordom et al., 2022). Other mega-diverse genera include *Uroptychus* (285), *Munidopsis* Whiteaves, 1874

(272), *Pagurus* Fabricius, 1775 (180), *Galathea* Fabricius, 1793 (176), *Synalpheus* Spence Bate, 1888 (176), and *Procambarus* Ortmann, 1905 (169). Each of these is morphologically diverse and it seems likely that most will be split into several genera in due course, as has already been hinted at for *Alpheus* by Hurt et al. (2021).

How many decapod species could there be?

The species accumulation curves of Decapoda as a whole (Fig. 4A) and of the six sub/infraorders with more than 500 species (Fig. 4B) show no sign of reaching an asymptote, with the possible exception of Dendrobranchiata, in which species descriptions have slowed down in the last few decades. Appeltans et al. (2012) used an earlier version of the decapod information on WoRMS and estimated that described marine biodiversity of Decapoda (12,029 species) was 50–57% of total biodiversity, and provided two estimates of the number of species remaining to be described to complete the global inventory. Based on their mathematical model, they estimated a further 4,500–5,100 unknown marine species. An independent estimate based on ‘expert opinions’ (Appeltans et al., 2012) was that around 9,034–12,141 species remained to be described. It is evident that the

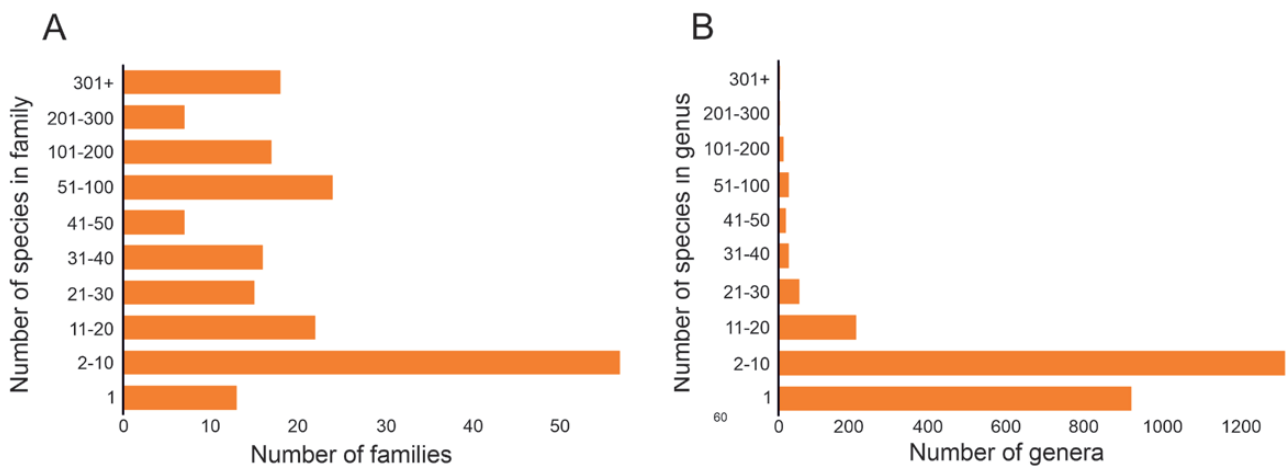


Figure 3. Bar charts of family (A) and generic (B) richness across Decapoda. Note that categories were arbitrarily delineated to aid discussion of richness patterns.

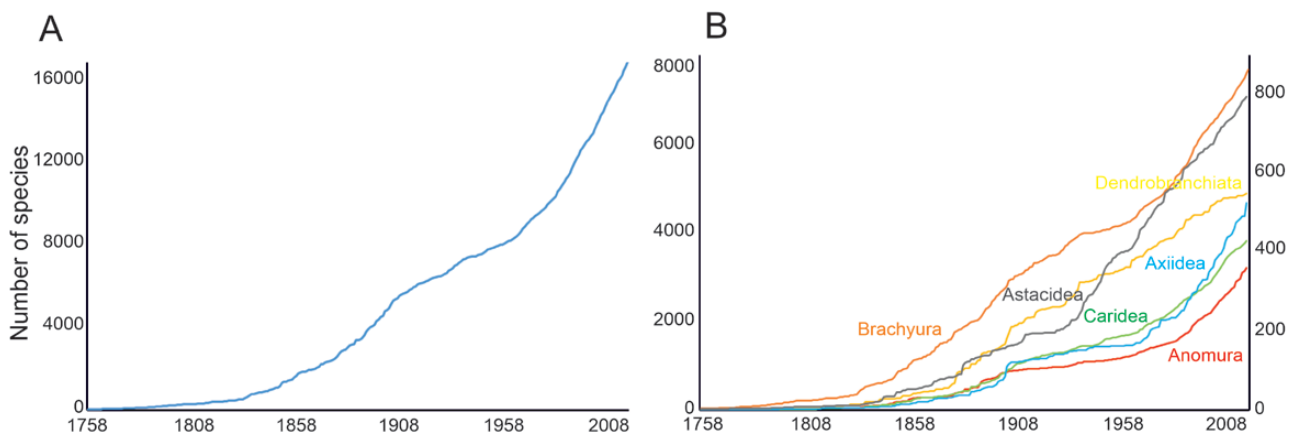


Figure 4. Accumulation curves (1758–2022) for Decapoda (A) and the six most species-rich infra/suborders (Anomura, Astacidea, Axiidea, Brachyura, Caridea, Dendrobranchiata) (B). Note that in (B) Astacidea, Axiidea, and Dendrobranchiata are plotted on the secondary y-axis.

model estimate was an underestimate as the current (December 2022) known number of species stands at 17,229 and the rate of description remains high (Fig. 4). The ‘expert opinion’ seems to be more realistic, but, for the same reason, is still likely still to be a substantial underestimate.

Despite the uncertainty in estimating a number for a complete global inventory of Decapoda, the quartiles in the discovery trajectory (Table 1) suggest that numerous new species await description not only in the already species-rich infraorders Anomura, Brachyura, and Caridea, but also in the moderately rich Axiidea and Gebiidea and even in the relatively species-poor Stenopodidea. Conversely, the discovery process (as measured by species descriptions) in Dendrobranchiata, Achelata, and Astacidea appears to have slowed down, which, at least in the latter groups, is not related to being species-poor as such.

Based on the 75% quartile, the dataset may indicate that the discovery process for Brachyura is potentially also slowing down, although this needs further atomising at the superfamily and family level to identify a clearer trend, as certainly the description rate for Asian and Afrotropical freshwater crabs remains high to this day (e.g., Potamidae; see Table 2). While it seems logical to expect that a large proportion of this undiscovered diversity is in the already species-rich families of Brachyura (Table 2), this may not hold true for all of them. For example, the brachyuran families Xanthidae, Leucosiidae, and Epialtidae reached this quartile between 1974 and 1992, although new species continue to be described to this day (e.g., Lee *et al.*, 2023; Mendoza, 2023). The species description process is of course not constant through time, and often consists of protracted periods of high activity by a single taxonomist on a small group of species, followed by longer periods of inactivity on that group. It is therefore difficult, if not impossible, to truly know whether a lack of descriptions of novel taxa in recent years or even decades is caused by the group being well known (as is the case for birds and mammals) or simply a lack of taxonomic scrutiny. Any trends in the description of new species may also have been influenced by the publication of monographs on certain groups. Among several examples, the publication by Baba (1988) on the squat lobsters of the *Albatross* expedition in the western Pacific paved the way for an increased number of studies in subsequent years (Fig. 2). For freshwater ecosystems, the major revisions by Bott (1970) and Rodriguez (1982) on Old World and Neotropical freshwater crabs, respectively, catalysed a flurry of work on these crabs that continues to this day. Other influential monographs, such as Sakai (1976) on the crabs of Japan, the seminal work by Bond-Buckup & Buckup (1994) on *Aegla*, and the revision of crayfishes of Georgia by Hobbs (1981) had similar effects. Equally major, regional monographs, such as books on the Chinese freshwater crabs and Atyidae by Dai (1999) and Liang (2004), respectively, have determined the direction of taxonomy on these groups in subsequent years. Other methods of calculating unknown biodiversity have relied on the ratio of already named to unnamed species in comprehensive localised surveys, often considered a more reliable estimate. Such methods, however, are as fraught with difficulty as any other method when extrapolating to a global arena, as, for example, no such comprehensive survey has been undertaken in freshwater biotopes, where a considerable fraction of global decapod biodiversity resides. Similarly, the discovery potential of unusual or difficult-to-sample habitats such as

deep coral rubble beds, vertical mesophotic tropical-reef interstices, and even shallow-water tropical infauna that can be only be sampled by yabby pumps or underwater aspiration remain to be seriously addressed.

Irrespective of the method of estimation or the scale of the derived estimate, it is abundantly clear that a considerable number of decapod species remain to be described, a formidable task given the dwindling number of taxonomists and the scarcity of resources for this type of fundamental work, particularly during the current environmental crises.

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