Zootaxa 5114 (1): 290–317
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5114.1.2
http://zoobank.org/urn:lsid:zoobank.org:pub:F9A66AF1-4087-4955-9C4C-65DE32D33059

Phylum Nematoda: trends in species descriptions, the documentation of diversity, systematics, and the species concept

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Abstract

This paper summarizes the trends in nematode species description and systematics emerging from a comparison of the latest comprehensive classification and census of Phylum Nematoda (Hodda 2022a, b) with earlier classifications (listed in Hodda 2007). It also offers some general observations on trends in nematode systematics emerging from the review of the voluminous literature used to produce the classification. The trends in nematodes can be compared with developments in the systematics of other organisms to shed light on many of the general issues confronting systematists now and into the future.

Introduction

The phylum Nematoda was only formally recognized relatively recently (Cobb 1932). Despite nematodes being known from ancient times, their classification has changed many times (summarized by Hodda 2007). Changes in classification have occurred at all taxonomic levels, from sub-specific to classes (and even included whether nematodes themselves should be considered a class within a larger phylum or a phylum themselves).

The frequent changes in classification have perhaps arisen because nematodes pose many systematic challenges. They are very diverse, with nearly 30,000 species described so that keeping track of the classification of the entire phylum is a substantial task: Nematoda is the phylum with 5th most described species, less than Arthropoda, Mollusca, Craniata and just less than Platyhelminthes, but more than Echinodermata, Annelida and Cnidaria (Hodda 2022a, Zhang 2011, 2013). Not only are there many species described, but there are probably a much larger number undescribed: even the lowest estimates of total nematode species numbers start at half a million species, and the highest estimates are more than 10 million species (Hodda 2022a). They are also mostly small, cryptic and morphologically simple, meaning that diagnosis by traditional morphological characters is often hard. But, for small, simple organisms, the genetic relationships among nematodes can be highly complex, meaning that molecular diagnoses also pose many challenges.

The original construction and more recent update of a comprehensive classification and census of all valid species and genera of nematodes (Hodda 2007, 2011, 2022a, b) has afforded the opportunity to examine trends in nematode systematics, and the nature of the challenges they reveal. Common trends and issues in nematode systematics emerging from the review of several thousand taxonomic publications are examined. Some of the issues raised in using these publications to construct a classification of all nematodes and a census of species have emerged recently and others are more long-standing. These trends are compared with some previous assessments of nematode species numbers and rates of species descriptions (Allen & Sher 1967, Hammond 1992, Hodda 2011, Hugot *et al*. 2001, Hyman 1951, Mayr *et al.* 1953, Stork 1993). The trends in nematode systemtics are compared and contrasted with trends and developments in the systematics of other organisms to perhaps illuminate many of the general issues confronting systematists now and those likely to emerge in the future. In this comparison, the emphasis is on the consequences of documented biological features of nematodes and other organisms for practical aspects of systematics. An extensive discussion of theoretical issues in the taxonomic system has been presented recently by Dubois *et al*. (2021).

 Accepted by Z.-Q. Zhang: 29 Jan. 2022; published: 10 Mar. 2022

Rate of species descriptions

The new classification and census adds about 3800 new species in over 300 new genera, including fossil species as well (Hodda 2011, Hodda 2022a).

This rate of new nematode species descriptions can be compared with the rate of descriptions of other invertebrates detailed by Zhang (2021) when those data are adjusted for a similar time interval. When this is done, the absolute number of new nematode species descriptions from 2011 to 2019 is higher than that for many less speciose groups, but less than that in groups where more species have been described (Table 1). As a percentage of the number of described species, new descriptions of nematodes are near the high end of the range of values for other taxonomic groups (Table 1). This means that for many groups between about one sixth and one ninth of the currently recognized species have been described in the last decade: of the over 28 500 valid species and 3000 valid genera of nematodes currently recognized, about one eighth were described in the 9 years between the censuses—from end 2010 (Hodda 2011) to end 2019 (Hodda 2022a)—so nematodes were in the middle of this range. While this may appear encouraging, it is important to note that as a percentage of the estimated total number of species, the rate of new species descriptions for nematodes is the lowest of any in the table. The implications of this are discussed further below.

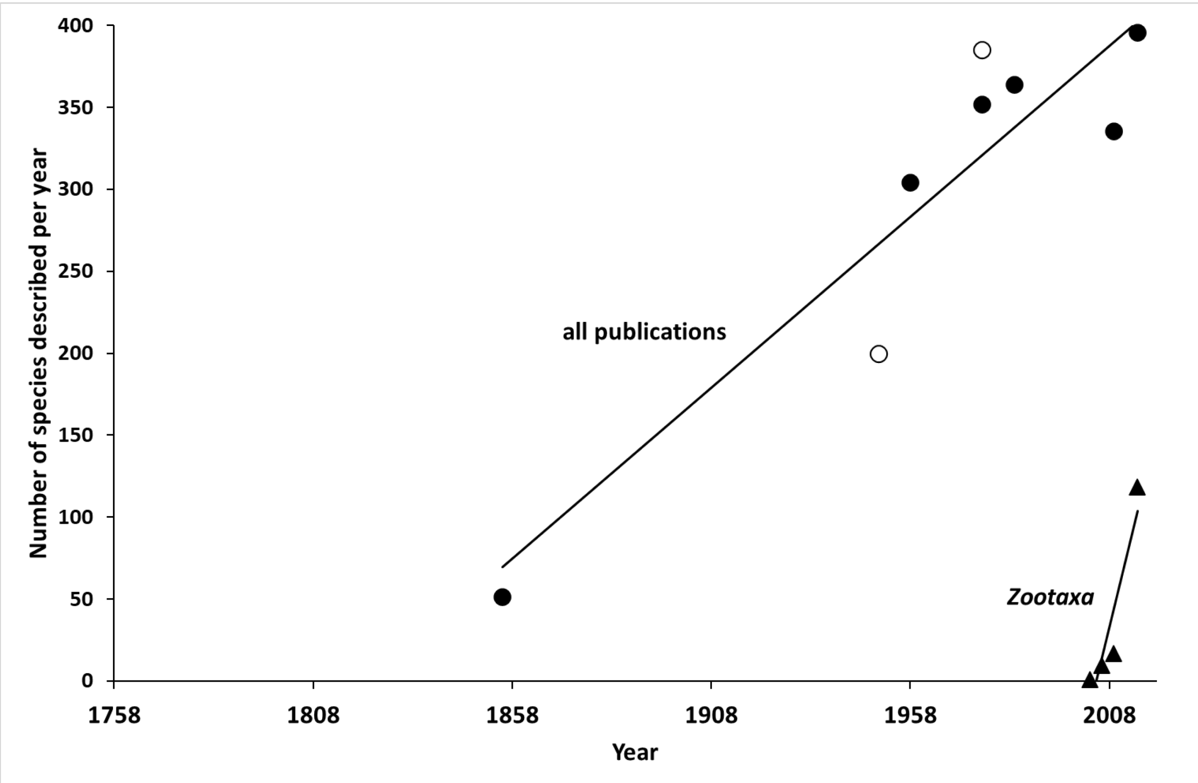

FIGURE 1. Descriptions of new nematode species per year. Circles are for all publications, triangles for the journal *Zootaxa* only. Filled symbols represent arithmetic mean rates per year for the period surrounding the point. Empty symbols represent estimates at the time. See text for full description. Trend lines are illustrative only.

Trends in the rate of nematode species and genus descriptions over time can be estimated thanks to some earlier summaries (Allen & Sher 1967, Hammond 1992, Hodda 2011, Hugot *et al*. 2001, Hyman 1951, Mayr *et* al. 1953, Stork 1993) (Figure 1). From the 3 nematode species named in the first formal binomial nomenclature (Linnaeus 1758) to the 10000 known in 1953 (Mayr *et al*. 1953) new nematode species descriptions therefore averaged about 50 per year for the nearly 200 first years of formal taxonomy. This figure of course obscures changes within the period, with an initially slower rate of species descriptions perhaps accelerating towards the end of the period. There were, however, periods within this time where large numbers of species were described in substantial monographs (e.g. Bastian 1865, Cobb 1920). By 1950, the total number of nematode species descriptions was estimated at about 200 per annum in the preceding few years (Hyman 1951). By 1966, the estimate for parasites of plants and free-living nematodes only was about 200 new species per annum (Allen & Sher 1967), which is about 300 species per annum if corrected for the estimated proportion of animal parasites not included (Hodda 2022a). Between 1993 and 2010, several estimates put the rate of new nematode species descriptions substantially above 300 new species per annum (Hammond 1992, Hodda 2011, Hugot *et al*. 2001, Stork 1993). The current estimate of total number of nematode species descriptions per year has increased to very nearly 400 new species per annum (Hodda 2022a). Thus it appears that the overall rate of species descriptions of nematodes is increasing, but only relatively slowly: there has been no explosion in new species descriptions thanks to genetic technologies.

TABLE 1. Approximate numbers of new species described from 2011 to 2019 (inclusive) relative to numbers of described species and estimated total species numbers for selected animal groups. All numbers approximate and rounded to allow for uncertainty in any estimate of species numbers (Chapman 2009, May 1988).

Taxonomic group	Described spp	Estimated total number of spp	New spp 2011–2019	New spp as % of described spp	New spp as % of total spp	References
Porifera	9,500	30,000	350	4	1.1	Hooper *et al*. 2021
Bryozoa	6,000	10,000	450	8	4.5	Bock & Gordon 2013, Gordon 1999, Gordon & Bock 2021
Annelida	20,000	30,000	1,600	8	5.3	Chapman 2009, Magalhaes *et al*. 2021
Tardigrada	1,500	15,000	200	13	1.3	McInnes *et al*. 2021
Nematoda	29,000	[1]500,000	3,800	13	0.8	Hodda 2021, 2022a
Opiliones	7,000	10,000	350	5	3.5	Coddington & Colwell 2001, Kury 2013, Perez-Gonzalez *et al*. 2021
Araneae	44,000	100,000	7,000	16	7.0	Jaeger *et al*. 2021, Zhang 2013
Acari	55,000	500,000	6,000	11	1.2	Skoracka *et al*. 2015, Zhang 2013, Zhang *et al*. 2021
Minor Insect orders [2]	12,000	30,000	450	4	1.5	Bernard & Whittington 2021, Stork 2018
Blattodea	7,600	28,000	250	3	0.9	Beccaloni & Eggleton 2013, Djernaes 2018, Stork 2018
Ephemeroptera	4,000	5,000	600	15	12.5	Jacobus *et al*. 2021
Odonata	6,000	7,000	500	8	7.1	Dijkstra *et al*. 2013, Paulson & Marinov 2021
Diptera	160,000	800,000	12,400	8	1.6	Whitmore *et* al. 2021, Stork 2018, Zhang 2013
Amphibia	8,300	20,000	1,400	17	7.0	Rivera-Correa *et al*. 2021
Mammalia	6,500	7,000	300	5	5.0	Burgin *et al*. 2018, Cordiero-Estrela *et al*. 2021, Fisher *et al*. 2018

The annual rate of new descriptions remains a very small proportion of the estimated total number of species—less than 0.1% of an estimated 500 000 to 1 million species (Hugot *et al*. 2001, Lambshead 1993). (Note that the values in Table 1 are for the period 2011–2019 and not annual rates.) If the estimates of the total number of nematode species are accurate, this equates to over a millenium to describe all species at the current rate, even for the lower estimate! (See below for further discussion of the total numbers of nematode species.)

1 Lowest estimate, see Hodda (2022a) and Hodda & Khudhir (2022) for discussion of higher estimates.

2 Including the insects Archaeognatha (Microcoryphia), Dermaptera, Embioptera, Siphonaptera, Zoraptera and Zygentoma, as well as the hexapod classes Protura and Diplura.

Because the recent classification includes authority and date for all valid nematode genera, the increase in number of genera and hence rate of proposal of nematode genera can be tracked more precisely than number of species (Figure 2). Using this data, the number of genera proposed has shown a steady increase, but with a notable temporary decrease in the decade from 1940 to 1950, and also a more recent, consistent trend to fewer proposals in the 3 decades since 1990 (Figure 2). While the earlier decrease is undoubtedly related to wars disrupting descriptive taxonomy during the decade, the cause of the recent decrease is less clear. It may be related to uncertainty in converting clades identified by molecular analyses into higher taxonomic groups (Dubois *et al*. 2021).

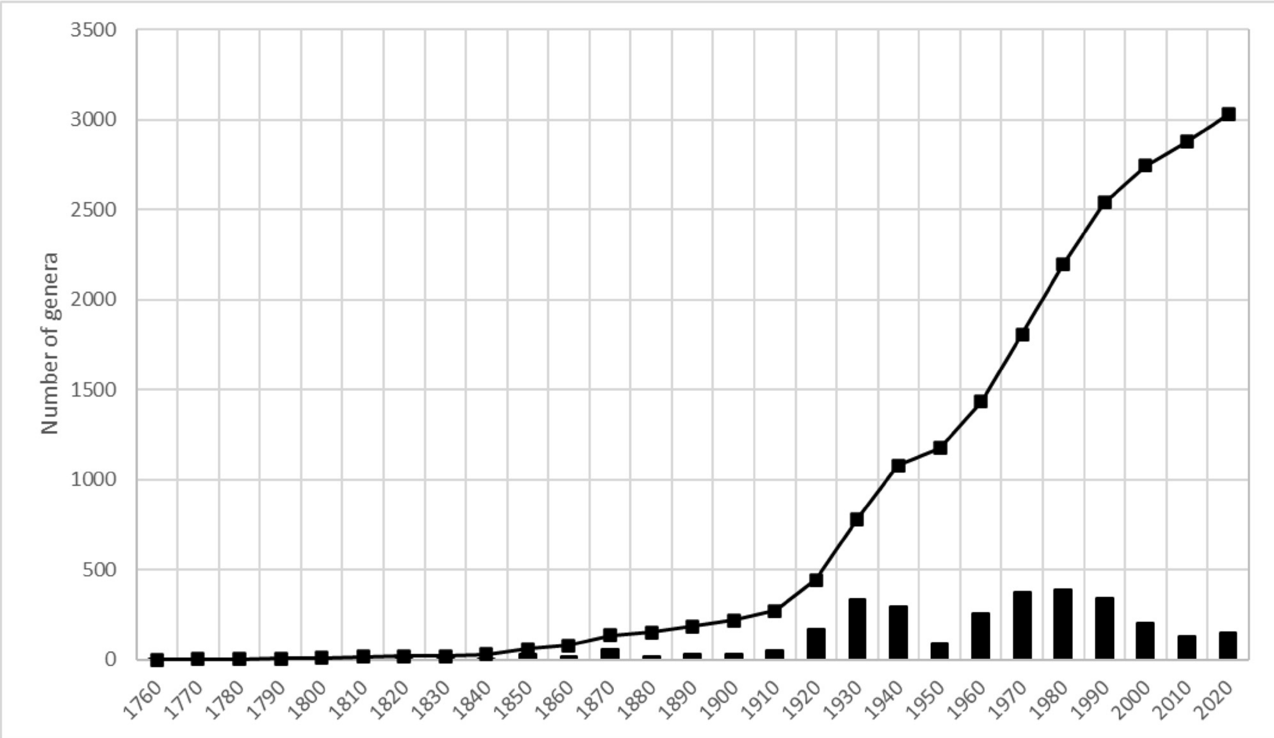

FIGURE 2. Proposal of new nematode genera per decade (columns) and total number of valid genera (points and line). The columns represent the total increase in the decade. The points and line represent the total number of valid genera at the end of the decade; i.e. the column for 2010 represents the genera added from the beginning of 2001 to the end of 2010, and the point for 2010 represents the number of genera at the end of 2010.

Sources of species descriptions

If the number of species described is not changing much, what does seem to be changing is the journals in which descriptions have been published. Summaries of publications describing nematodes in the journal *Zootaxa* (Hodda 2021, Xu *et al*. 2013, Zhao 2007), plus the current data, show a doubling of the rate of descriptions published in *Zootaxa* approximately every 3 to 4 years (Figure 1). This is after growing from 2 new species in the 3rd year of the journal in 2003, to 75 new species in 2020

Notwithstanding potential biases in some perceptions of *Zootaxa* as the only journal to publish species descriptions (Pinto *et al*. 2021), the publication seems to be responsible for an increasing proportion of new species descriptions (Figure 1). In the period from the last census (Hodda 2011) to the current one (Hodda 2022a), the journal *Zootaxa* has accounted for almost 20% of the total (over 600 species) (Hodda 2021). This proportion is increasing with some variation from year to year: in 2020 *Zootaxa* accounted for 25% of the total number of new nematode descriptions , which was just over 300. This is close to the proportion for the journal as a whole (Zhang 2021).

For genera proposed, *Zootaxa* has accounted for a slightly smaller but still substantial percentage (a total of 38 genera of the 285 proposed since 2000, or 13%). Although numbers of genera proposed per year are small and hence vary substantially from year to year, the proportion of genera published in *Zootaxa* seems to be growing as well: in 2020 *Zootaxa* published 4 of 11 new genera, or 36%.

The significance *Zootaxa* in documenting biodiversity has been discussed by several authors (Hodda 2021, Pinto *et al*. 2021, Zhang 2011, 2021).

New descriptions vs synonymizations

The current total number of valid species of nematodes in the latest census (over 28 000 in over 3000 genera) includes a substantial number of reinstatements of previously characterized but subsequently synonymized species and genera. Analysis of molecular data has often implied that older taxa often consist of multiple species, and that proposed species from different geographic regions which appear very similar and are hence often synonymized, are in fact often really different (Brandt *et al*. 2007, Derycke *et al*. 2009, Grosemans *et al*. 2016, Guden *et al*. 2018, Perez-Ponce de Leon & Poulin 2018). However, this has not always proved the case, and molecular evidence has indicated that some species are very widespread and variable, and hence have been described under multiple names that should indeed be regarded as synonyms (De Groote *et al*. 2017, De Oliviera *et al*. 2014, 2017). Overall, reinstatements of previous names have outnumbered synonymizations, but proposals of new species based on new specimens have vastly outnumbered changes involving existing names.

Distribution of new descriptions

In all publications since 2011 describing new nematode species, several trends in new species descriptions are apparent. These trends show that descriptions of new nematode species are often not a reflection of the true diversity of nematodes, but are heavily biased by geographic, economic and technical or methodological influences unrelated to the organisms themselves or their underlying diversity.

For example, most descriptions were from terrestrial habitats, freshwater aquatic environments or from terrestrial or freshwater aquatic hosts (2400 species). Only 30% of species were described from marine environments or hosts (about 1100 species). This is despite a much greater part of nematode phylogenetic diversity coming from marine habitats, as measured by the number of higher taxa (Hodda 2011, 2022a). Marine nematode diversity may be seriously underestimated (Brandt *et al.* 2007, Fonseca *et al*. 2010a, Hodda *et al*. 2009, Lambshead 2004, Lambshead & Boucher 2003). However, getting true estimates of the diversity of marine nematodes may be difficult because of the vast areas of coastline and ocean bed, and the logistic or methodological difficulties of sampling it (Hodda 1990, Hodda & Khudhir 2022, Lambshead & Hodda 1994). Marine nematodes were until recently underrepresented in molecular studies, too (Bik *et al.* 2010, Meldal *et al*. 2007).

The number of new species described seems strongly related to human resources applied to taxonomic effort. In the last few years, most new nematode species have been described from Asia, particularly the emerging economies of China and India (Table 2). By contrast, the fewest species by far were described from Africa, where nematological training and expertise remains sparse (Coyne *et al*. 2018, Wacekel *et al.* 2010). Relative to total surface of the earth or total land area, North America was also under-represented in new descriptions. One can only speculate on whether the underlying causes might be similar (because of little training in nematode taxonomy), or different (because of a much better-studied fauna meaning that there are fewer new species encountered). Notable also is that far more species were described from Australasia than would be expected from its scientific population (about 3% of the world's total overall: OECD 2011). This is related to several very active taxonomists having time to describe species in retirement freed from other commitments (Davies, Spratt, Smales). There are serious concerns that this situation will not continue, as there are few young people in training to replace them and succession planning has been limited (Hodda *et al*. 2017, 2019, Howie 2012).

Other phyla parasitic in vertebrates can have very different geographic distributions for new species descriptions (Poulin & Jorge 2019, Poulin *et al*. 2019), so the pattern of new species descriptions for nematodes may not be indicative of a more general trend.

On a continental scale, the geographic distribution of new nematode species descriptions is substantially different to both the land and total areas (including surrounding seas and oceans) (Table 2). Asia and Europe had a much larger proportion of species described than their areas, while the Americas and Africa had many fewer species described than their areas. The total proportion of species described from Australasia (14%) was close to the total area of land and water as a proportion of earth's surface (14%). However, water forms a large part of this area, including large parts of the South Pacific and Indian Oceans, and compared to the land area (6% of the total), the number of species described was very large because most of the new species descriptions were terrestrial rather than marine. Few new species have been described from Antarctica and surrounding waters, although the number of new species is substantial relative to the small number of known species from Antarctica and the estimated total number of species on and around that continent.

Of particular note is that several species were described, not from their presumed native location, but from quarantine interceptions in other places (apparently completely remote from the assumed origin of the specimens) (Table 2). In all of these cases, the original source of the specimens could not be positively identified, even though the new species could be positively described and diagnosed from the specimens intercepted. They may have come from the origin of the produce on which they were found, they may have come locally from the destination, or any place along the transport route of the produce. As the movement of plant and animal products has expanded, trade networks have become increasingly important in the dispersal of organisms generally (Banks *et al.* 2015). Likewise trade hubs may become increasingly important as centres where produce from many different places not otherwise sampled can be examined (Hodda *et al.* submittted). The implication of this is that finding new species some distance from their natural geographic range and habitat may become an increasing trend.

TABLE 2. Total number and % of described new species of nematodes from 2011 to 2019 listed by continent, together with their total area as a % of total earth's surface, ocean area as a % of earths total surface, and land area as a % of earth's total land area. Note that some new species were described from more than one continent.

Continent	new species described	% new species described	% total surface area of earth	Ocean as % of total area of earth	% total land area
Asia[1]	1672	47	22	9	30
North America[2]	330	9	19	14	17
South America[3]	416	12	17	13	12
Africa[4]	191	5	15	9	20
Australasia[5]	486	14	14	11	6
Europe[6]	439	12	8	6	7
Antarctica[7]	7	0	5	4	9
Trade [8]	19	1	??	??	??

[1] including adjacent seas and parts of the North Pacific, Indian and Arctic Oceans
[2] including adjacent seas and parts of the North Pacific, North Atlantic and Arctic Oceans
[3] including adjacent seas and parts of the South Pacific and South Atlantic Oceans
[4] including adjacent seas and parts of the South Atlantic and Indian Oceans
[5] including adjacent seas and parts of the South Pacific and Indian Oceans
[6] including adjacent seas and parts of the North Atlantic and Arctic Oceans
[7] including adjacent seas and parts of the Southern Ocean
[8] also included in total for origin of material where known, but not in total for place of interception

Ecological associations of new species

The description of new species was strongly biased by their life habits—whether they were free-living, or associated with vertebrates, invertebrates or plants. More free-living microbivorous or predatory nematodes were described than any other group, with nematodes associated with vertebrates having next most species described, and invertebrate- and plant-associated nematodes fewest species described (Table 3). This is roughly the pattern in the currently described species, but is vastly different to the estimated total number of species that really exist, where there are far more free-living species than other types (Hodda *et al.* 2009).

Significantly, the estimated total number of nematode species associated with invertebrates has increased as a result of extensive collecting and detailed molecular work concentrated on particular taxonomic groups of nematodes or hosts (Bartholomaeus *et al.* 2012, Davies *et al*. 2010a, b, 2012a, b, 2013a, b, 2014a, b, c, d, e, 2015, Giblin-Davis *et al.* 2014, Kanzaki *et al.* 2014, Zhao *et al.* 2013a, b, 2015). Similar increases in numbers of species have been observed in some nematode groups associated with particular vertebrates (Fenner *et al.* 2011, Justine & Iwaki 2014, Moravec & Ali 2014, Moravec & Barton 2015, Moravec & Diggles 2014a, b, 2015a, b, Moravec & Jirku 2014a, b, 2015, Moravec & Justine 2014a, b, 2015a, b, Moravec & Monoharan 2014a, b, Moravec & Van As 2015a, b, Moravec *et al.* 2014, 2015a, b, Purwaningsih & Smales 2010, 2011, 2014, Smales 2010, 2011a, b, c, 2012, 2013, 2014, 2015, Smales & Heinrich 2010, Spratt 2010, 2011,Weaver & Smales 2010, 2012). This highlights that the interests and areas of expertise of the most active systematists can have a strong influence on apparent diversity of particular groups, rather than the real biological diversity.

TABLE 3. Number and percentage of new nematode species described from 2011 to 2019 by gross ecological association.

Habitat	Species	percentage
free-living	1595	44
vertebrate-associated	1013	28
invertebrate-associated	447	12
plant-associated	535	15
all	**3590**	**100**

TABLE 4. Numbers of new species described from 2011 to 2019 in nematode genera with more than 5 species described, listed in decreasing order of number of newly-described species, with their classification and gross ecological association (f—free living; p—plant associated; i—invertebrate associated; v—vertebrate associated).

Genus	Order	f	p	i	v	new spp.	total spp in genus[1]
Philometra	Spirurida	0	0	0	1	[2]57	135
Bursaphelenchus	Panagrolaimida	0	1	1	0	36	135
Steinernema	Panagrolaimida	0	0	1	0	36	105
Fergusobia	Panagrolaimida	0	1	0	0	32	49
Aphelenchoides	Panagrolaimida	0	1	0	0	26	193
Xiphinema	Dorylaimida	0	1	0	0	25	255
Longidorus	Dorylaimida	0	1	0	0	24	159
Pristionchus [3]	Diplogasterida	1	0	0	0	[2]22	56
Cloacina	Rhabditida	0	0	0	1	19	140
Caenorhabditis [3]	Rhabditida	1	0	0	0	[2]18	38
Cucullanus	Spirurida	0	0	0	1	16	173
Sabatieria	Monhysterida	1	0	0	0	16	90
Schistonchus	Panagrolaimida	0	1	1	0	13	21
Daptonema	Monhysterida	1	0	0	0	12	153
Aporcelinus	Dorylaimida	1	0	0	0	11	25
Oscheius	Rhabditida	0	0	1	0	11	47
Procamallanus	Spirurida	0	0	0	1	11	195
Rhabdochona	Spirurida	0	0	0	1	10	159
Ditylenchus	Panagrolaimida	0	1	0	0	9	80
Paratylenchus	Panagrolaimida	0	1	0	0	9	170
Pratylenchus	Panagrolaimida	0	1	0	0	9	122
Trichuris	Trichocephalida	0	0	0	1	9	98
Deladenus	Panagrolaimida	0	0	1	0	8	32
Ektaphelenchoides	Panagrolaimida	0	0	1	0	8	30
Ficophagus	Panagrolaimida	0	1	1	0	8	16
Meloidogyne	Panagrolaimida	0	1	0	0	8	100

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TABLE 4. (Continued)

Genus	Order	f	p	i	v	new spp.	total spp in genus[1]
Oncholaimus	Oncholaimiida	1	0	0	0	8	121
Parapharyngodon	Spirurida	0	0	0	1	8	72
Rhabdias	Rhabditida	0	0	0	1	8	73
Syphacia	Spirurida	0	0	0	1	8	68
Tripylella	Tripylida	1	0	0	0	8	11
Aplectana	Spirurida	0	0	0	1	7	58
Aulolaimus	Mermithida	1	0	0	0	7	19
Hysterothylacium	Spirurida	0	0	0	1	7	115
Litinium	Ironida	1	0	0	0	7	13
Meteterakis	Spirurida	0	0	0	1	7	27
Phasmarhabditis	Rhabditida	0	0	1	0	7	18
Philometroides	Spirurida	0	0	0	1	7	32
Rotylenchus	Panagrolaimida	0	1	0	0	7	104
Sectonema	Dorylaimida	1	0	0	0	7	33
Trischistoma	Tripyloidida	1	0	0	0	7	16
Axonchium	Dorylaimida	1	0	0	0	6	37
Campylaimus	Monhysterida	1	0	0	0	6	23
Cosmocercoides	Spirurida	0	0	0	1	6	28
Crassonchus	Dorylaimida	1	0	0	0	6	6
Desmodora	Desmodoridae	1	0	0	0	6	72
Dichelyne	Spirurida	0	0	0	1	6	56
Dorylaimopsis	Monhysterida	1	0	0	0	6	26
Epacanthion	Enoplida	1	0	0	0	6	27
Geomonhystera	Monhysterida	1	0	0	0	6	33
Haliplectus	Plectida	1	0	0	0	6	25
Heth	Spirurida	0	0	0	1	6	44
Paramphimonhystrella	Monhysterida	1	0	0	0	6	9
Parasphaerolaimus	Monhysterida	1	0	0	0	6	9
Parodontophora	Monhysterida	1	0	0	0	6	36
Pseudaphelenchus	Panagrolaimida	0	0	1	0	6	6
Rhynchonema	Monhysterida	1	0	0	0	6	28
Ruehmaphelenchus	Panagrolaimida	0	0	1	0	6	8
Serpentirhabdias	Rhabditida	0	0	0	1	6	12
Tylencholaimus	Dorylaimida	1	0	0	0	6	52
Total 60		**24**	**12**	**10**	**17**	**687**	**4093**
% of total 2[4]		**40**[5]	**20**[5]	**20**[5]	**30**[5]	**20**[6]	**15**[7]

[1] Mean number of species per genus for the whole Nematoda is 9, with a median of 3 and a mode of 1 (under the classification of Hodda 2022a)

[2] not all species formally or conventionally described

[3] model organism with significance for knowledge of other organisms or basic biological processes

[4] % of total number of described nematode genera to end 2019

[5] % of number of nematode genera with more than 5 species described from 2011 to 2019; note figures for f, p, i and v add to more than 100% because some species fall into more than 1 category

[6] % of total number of new nematode species described from 2011 to 2019

[7] % of total number of all nematode species described at the end of 2019

Relationship of new descriptions with existing knowledge

The relationship between number of species described and the true species number within genera is difficult to untangle because the description of new species is heavily biased towards those genera with the most species already described. Just 2% of the total number of nematode genera together account for 20% of new descriptions (Table 4). This 2% includes 60 genera with more than 5 species described in the last 9 years, and all of the most speciose nematode genera are included in it, with the exception of *Helicotylenchus* (203 described species) (Table 4). The number of recently-described species in this 2% is considerably more than that expected if species descriptions were directly proportional to the number of species already described (15% of known species: Table 4). The large number of described species within these large genera could result from the effort being directed towards them, or else the substantial amount already known about them and the substantial taxonomic expertise developed in describing species. The taxonomic effort, knowledge and expertise could itself result from the genuinely substantial species diversity and the large number of species that really do exist.

The genera with most species newly recognized since 2010 also show heavy bias towards those with potential economic importance (Table 4). Of the 60 genera with more than 5 species described, only 40% were free-living, with 70% associated with plants, invertebrates or vertebrates. (Some genera are associated with more than one type of host.) The genus with the most species recognized was *Philometra*, parasites of fish. *Cucullanus*, another genus parasitic in fish, also had many species described. Plant parasites—genera *Bursaphelenchus*, *Aphelenchoides*, *Xiphinema*, *Longidorus*—have also had many species described. The former 2 genera are also associated with insect vectors, as is another genus having many species described—*Steinernema*. *Steinernema* is used for biocontrol of insects. Nematode genera used as model organisms—*Caenorhabditis* and *Pristionchus*—also had many species described recently (but see below for discussion of the form that this recognition has taken). Many free-living genera have had many species described, although the number is small relative to the large number and diversity of free-living genera and species thought to exist (see above). In some of the genera with many recent species descriptions, the large numbers of new species have been associated with only one or a few studies of limited geographic range (e.g. Siddiqi 2015).

Effort in discovering and describing vertebrate parasite species is not related to the diversity of potential hosts (Jorge & Poulin 2018).

Nature of species descriptions

Another notable trend has been recognition of species without traditional full descriptions (Bouket 2014, Dey *et al.* 2012, Felix *et al.* 2014, Kiontke *et al.* 2011). These studies presented molecular, cross-breeding, morphological and biogeographic studies providing strong evidence of reproductive isolation, infertile progeny, character divergence and geographic isolation. These are basic criteria defining separate species under the molecular, biological, phenotypic and ecological species concepts (Coyne *et al.* 1988, Mayden 1997, Mayr & Ashlock 1991, Wilkins 2003, 2009, 2011). Hence there can be little doubt that these are real evolutionary entities. However, there have been considerable lags between identification of many of these species and their full description and diagnosis. Many have yet to be produced and presented. (Such time lags are not restricted to nematodes (Bebber *et al*. 2010, Fontaine *et al*. 2012)). Perhaps we have reached a point where to make tangible gains in recognizing and documenting any significant portion of the vast global nematode diversity with forseeable resources, then more flexible methods of documentation and incomplete data will be all that is possible (De Queiroz 2007, Ereschefsky 2001, Lorenzen 1983, 1994, 1996, 2000, Pleijel 1999, Renner 2016). New criteria for species description, such as those proposed for recently proposed species of *Caenorhabditis* (Felix *et al*. 2014), may be required. Interim designations of sibling species which are distinct genetically, biogeographically and in host range, but are indistinguishable morphologically have used identifiers such as "*Caenorhabditis* sp. 5" in numerous publications for 10 years before formal—albeit non-conventional—description and naming (Felix *et al.* 2014, Huang *et al.* 2014, Stevens *et al*. 2019). Similar designations were used for another 15 species of *Caenorhabditis* for a considerable time before formal descriptions (Felix *et al.* 2014, Slos *et al*. 2017). Very recent studies of the model nematode genus *Pristionchus* have resulted in some rapid descriptions of many species based on morphology, morphometrics and genome-wide sequence analysis (Kanzaki *et al*. 2018). This practce is continuing, for example, *Rhabdias* sp.4 and *Rhabdias* sp.5 (Mueller *et al.*

2018), or *Anisakis typica* species complex sp.T (Eamsobhana *et al.* 2018). It may even be taking more indefinite forms, such as *Contracaecum* type II Genotype B or *Hysterothylacum* type IV genotype B & C (Shamsi *et al.* 2018) or *Cercopithifilaria* sp. II (Maia *et al*. 2017, Otranto *et al*. 2013a, b). There have even been synonymizations of informal names (for exmple for *Hysterothylacium* larval types I to XIV: Pantoja *et al.* 2016).

Some recent descriptions of *Caenorhabditis* species have, however, taken a more conventional approach (Ferrari *et al*. 2017, Slos *et al*. 2017).

Evolutionary relationships and species concepts have been studied intensively in the genus *Caenorhabditis* because it is a model organism. Discovery of cryptic species has been expected, with concomitant conceptual and logistic difficulties in providing the diagnosis or description required for the name to become available (Mueller *et al*. 2018, Palomares-Rius *et al*. 2014, Perez-Ponce De Leon & Poulin 2018). But the long-term use of informal identifiers is not limited to model nematodes. "*Contracaecum rudolphii* A"; also "B", "C", "D", "E" and "F" have been used widely for a long time (D'Amelio *et al.* 2012, Li *et al.* 2005, Mattiucci *et al.* 2002, Zhang *et al.* 2009). A similar situation has occurred with *Contracaecum osculatum* with at least 5 sibling species being referred to using single letter identifiers (D'Amelio *et al.* 1995, Nascetti *et al.* 1993, Orecchia *et al.* 1994). These identifiers are still being used currently 20 years later (eg Karpiej *et al.* 2014, Shamsi 2014, Skrzypczak *et al.* 2014). *Anisakis simplex* sp "A", "B" and "C" likewise have been used for many years before formal description of one of them (Mattiucci *et al.* 2014). Recently, *Cercopithifilaria* sp. I and *C.* sp. II have been proposed and used in multiple publications over several years (e.g. Otranto *et al.* 2011, 2012, Maia *et al.* 2017). Likewise in *Ditylenchus dipsaci* (Kuehn 1857) Filipjev 1934, of 6 new species identified in 2005, only 2 have been given formal names to date (Chizhov *et al.* 2010, Vovlas *et al.* 2011). Two females described in 1973 (Zullini 1973) were given formal names in 2019 (Pena-Santiago 2019). Informal identifiers have also been necessary when new undescribed species are known or suspected and need to be referred to before subsequent formal publication: when many new species are found or suspected, not all of them can necessarily be described in a single publication (eg Davies *et al*. 2010a, 2015).

Informal identifiers have also been used where material is sufficient for species diagnosis and description but insufficient for definitive diagnosis or placement in a genus (eg Nippostrongylinae sp. 1, 2, 3: Smales & Heinrich 2010, Smales 2014, or *Halomonhystera* sp. A and B: Leduc 2014, or *Fissicauda* sp.1,2: Durette-Desset *et al.* 2017). This may be quite frequent. Nematodes in many habitats display high spatial and temporal patchiness which makes obtaining enough specimens often problematic and impractical when operating with limited time and resources (Hodda 1990, Hodda & Traunspurger 2021, Hodda & Khudhir 2022). Except for a relatively few species, repeated sampling at the same place may infrequently locate the same species (Hodda 1981, Hodda & Khudhir 2022, Khudhir *et al*. 2022, Nicholas 2001, Nicholas & Hodda 1999). Likewise, sampling at adjacent places frequently does not result in re-collection of more than a few species in many habitats (Bernard 1992, Fonseca *et al*. 2010b, Gingold *et al*. 2010, Hodda 1990, Traunspurger & Michiels 2006, Venekey *et al*. 2010). Without a sufficient number of specimens, assessing the variation within putative new taxa and how it relates to other nematode taxa is often not possible.

What do nematode species tell us about evolution and species concepts?

There have been suggestions that among small organisms there are few true species. One suggestion is that small organisms are superabundant, can disperse with minimal energy cost suspended in the air or water or attached to drifting materials or other species, and can survive until they find suitable conditions (Costello & Wilson 2011, Costello *et al*. 2012, 2013, Finlay *et al*. 2001, Finlay & Fenchel 2004). This means there is constant mixing and few, widespread species. Nematodes fulfil all these criteria, being superabundant (Hodda & Davies 2019, Hoogen *et al*. 2019, Jairajpuri & Ahmad 1992, Platt 1994), able to disperse by wind, water or by using a vector organism (Banks *et al*. 2018, Fontaneto 2019, Kaya & Gaugler 1993, Kruitbos *et al*. 2009, Norton & Niblack 1991, Pena *et al*. 2011, Ptatscheck *et al*. 2018), and being able to survive for long periods if required (Gibbs 1982, Perry 1999, Wharton 1999, 2002). Although many nematodes are able to disperse by wind, water or biological vectors, it may be that many species do not (Hodda 1990).

Another suggestion is that high mutation rates and large population size mean that stable differences in fitness for different niches cannot evolve in different lineages for organisms smaller than 1mm body length, and hence species will not evolve (Rossberg *et al.* 2013). Most nematode species are less than 1mm long, meaning that conventional reproductively-isolated, genetically-distinct species should not exist under this theory.

The overwhelming evidence is contrary to both these theories. In at least some nematodes studied in detail, there are distinct groups based on molecular markers, reproductive isolation, morphological or biological differences and distribution. These are criteria used in most of the current species concepts, and they have been found in representatives of all types of nematodes: in the microbivorous free-living genera *Caenorhabditis, Micoletzkya* and *Pristionchus* (Cutter *et al*. 2019, Dey *et al.* 2012, Kanzaki *et al.* 2013, 2018, Kiontke *et al.* 2011, Ragsdale *et al.* 2013, Susoy & Herrmann 2014); in the mycetophagous plant- and insect-associated genus *Bursaphelenchus* (Abad *et al.* 1991, Beckenbach *et al.* 1999, de Guiran & Bruguier 1989, de Guiran & Ritter 1984, Fukushige 1991, Fukushige & Futai 1985, Kanzaki 2008, Lange *et al.* 2008, Mamiya 1986, Metge & Burgermeister 2008, Metge *et al.* 2008, Riga *et al.* 1992, Schauer-Blume 1990, Webster *et al.* 1990); in the obligate plant-parasitic genus *Globodera* (Chrisanfova *et al.* 2008, Fleming & Powers 1998a, b, Hoolahan *et al.* 2011, Picard & Plantard 2006, Picard *et al*. 2004); and in the vertebrate-parasitic genus *Ascaris* (Anderson 1995, 2001, Anderson *et al.* 1993, 1995, Criscione *et al.* 2007, Leles *et al.* 2012, Peng *et al.* 1998, 2005). It also applies in marine environments as well as terrestrial (De Ley *et al.* 1999, Derycke *et al.* 2009, Eyualem & Blaxter 2003, Fonseca *et al.* 2008, Tandigan De Ley *et al.* 2007). Detailed studies have found large-scale diversification in some nematode groups without genetic isolation (Susoy *et al*. 2016).

Although there are at least some clear groups, in nematodes the patterns of variation found in molecular, reproductive, biological, evolutionary, morphological, ecological and biogeographic characters can be far from simple. Some apparently similar groups prove on investigation to be clearly separated, and other apparently different groups on detailed investigation prove clearly the same, with most characteristics concordant. However, many groups are differentiated only partly, with their characteristics for differentiating species either inconsistent, contradictory, unclear or unknown. For example, in the plant-parasitic genus *Radopholus*, one species (*R. similis*) occurs worldwide but with clear allopatric host races which appear to be the same genetically (Kaplan & Opperman 1997, 2000, Kaplan *et al.* 1996, 1997, 2000). Other morphologically indistinguishable allopatric host races do appear to differ genetically and so are regarded as different species (*R. bridgei*, *R. daklakensis*, *R. duriophilus* and *R. arabocoffeae*: Nguyen *et al.* 2003, Siddiqi & Hahn 1995, Trinh *et al.* 2004, 2012, Uribe *et al.* 2010). Yet other morphologically indistinguishable host races are intermediate (Turaganivalu *et al*. 2013). There are other biogeographic differences as well (Marin *et al.* 1999). Similarly, in the other plant-parasitic genera *Ditylenchus* and *Xiphinema*, some groups which differ in hosts or morphology are genetically indistinguishable and therefore deemed conspecific, while other groups with indistinguishable host ranges are genetically distinct and therefore deemed separate species (De Luca *et al.* 2013, Douda *et al.* 2013, Gutierrez-Gutierrez *et al.* 2010, 2012, He *et al.* 2005, Kumari & Di Cesare 2013, Leles *et al.* 2012, Meza *et al.* 2012, Pedram *et al.* 2012a, b, Prior *et al.* 2010, Sakai *et al.* 2012, Subbotin *et al.* 2011, Vovlas *et al.* 2011). In deep-sea nematodes, some species appear to be very localized and have little intra-specific variation in morphology or genetics, while others are very widespread and have considerable morphological and genetic variation within species (Brandt *et al.* 2007, De Groote *et al*. 2017, De Oliviera *et al*. 2014, 2017, Derycke *et al.* 2008, 2013, Lambshead 2004, Lambshead & Boucher 2003, Zeppelli *et al.* 2011). At least some freshwater aquatic nematodes may be similar (genus *Chronogaster*: Ettema *et al.* 2000). In a mostly free-living, but opportunistically vertebrate-parasitic species (*Halicephalobus gingivalis* Stefanski 1954), intraspecific morphological variability in a single population of a single species started from a single individual can be greater than what is regarded as inter-specific variation (Anderson *et al* 1998, Fonderie *et al.* 2013, Nadler *et al.* 2003). Patterns of variability within the genera *Caenorhabditis*, *Pristionchus*, *Bursaphelenchus*, *Globodera*, *Radopholus*, *Ascaris* and *Trichuris* are similarly complex (*Caenorhabditis*—Crombie *et al*. 2019, Cutter *et al*. 2019, Dey *et al.* 2012, Ferrari *et al*. 2017, Kanzaki *et al.* 2012, 2013, Kiontke *et al.* 2011; *Pristionchus*—Ragsdale *et al.* 2013; *Bursaphelenchus*—Abad *et al.* 1991, Beckenbach *et al.* 1999, de Guiran & Bruguier 1989, de Guiran & Ritter 1984, Fukushige & Futai 1985, Kanzaki 2008, Lange *et al.* 2008, Mamiya 1986, Metge & Burgermeister 2008, Metge *et al.* 2008, Riga *et al.* 1992, Schauer-Blume 1990, Webster *et al.* 1990; *Globodera*—Alenda *et al*. 2013, Blanchard 2006, Boucher *et al*. 2013, Handoo *et al*. 2012, Lax *et al*. 2014, Madani *et al*. 2010, Montary *et al*. 2015, 2019, Thevenoux *et al*. 2019; *Radopholus*—Elbadri *et al.* 1999a, b, 2002, Haegeman *et al.* 2010, Hahn *et al.* 1996, Huettel & Yaegashi 1988, Huettel *et al.* 1984, 1986, Plowright *et al.* 2013, Valette *et al.* 1998; *Ascaris*—Cavallero *et al.* 2013, Iniguez *et al.* 2012, Liu *et al.* 2012; *Trichuris*—Xie *et al.* 2018). Comparative studies have demonstrated that the amount of genetic variation within single interbreeding populations or biological species varies considerably across Phylum Nematoda (Gibson & Fuentes 2014). Differences in the amount of genetic variation within species may in fact be inevitable, and result from different selective evolutionary pressures on each species. Parasitic species—particularly on vertebrates—may be more variable than other groups of nematodes, but there are clearly other, as yet unidentified, relationships (Gibson & Fuentes 2014, Perez-Ponce de Leon & Poulin 2018).

As a measure of the complexity of relationships among closely-related nematodes, and the issues this can raise in defining taxonomic entities, hybridization with various success rates has been observed between well-recognized species of several nematode genera (*Globodera*—Douda *et al*. 2014, Mugniery 1979, Mugniery *et al*. 1992, Thiery *et al*. 1996, 1997; *Nacobbus*—Anthoine & Mugniery 2006; *Aphelenchoides*—Cayrol & Dalmasso 1975, Dalmasso & Cayrol 1973, *Fergusobia*—Ye *et al*. 2007, *Anisakis*—Simsek *et al*. 2020, and *Haemonchus*—Santos *et al*. 2019). There is molecular evidence suggesting that several species of both *Meloidogyne* and *Caenorhabditis* have arisen from hybridization of 2 ancestral species (Lamelza *et al*. 2020, Schoonmaker *et al*. 2020). Hybridization may be important in speciation in many organisms (Abbot *et al*. 2013, Roux *et al*. 2016, Seehausen *et al*. 2014). Notwithstanding the apparent frequency of hybridization of putative species of nematodes, genetic barriers to hybridization have been identified in several genera (e.g. *Caenorhabditis*—Bundus *et al*. 2018, Cutter 2018 and *Mesorhabditis*—Launay *et al*. 2020).

Complex patterns of cross compatibility and incompatibility in what are often considered races within species are also known in several nematode genera (*Globodera*—Franco & Evans 1978; *Nacobbus*—Anthoine & Mugniery 2006; *Pratylenchus*—Mizukubo *et al*. 2003, Perry *et al*. 1980; and *Ditylenchus*—Ladygina 1969, 1970, 1972a, b, c, 1973, 1974, 1976a,b, 1978, 1982, Ladygina & Barabashova 1976).

Species definitions and boundaries

Defining species boundaries in nematodes is problematic because variation between individuals, populations, and reproductive, ecological or biogeographic groups is so complex (Bik *et al*. 2010, Thiery *et al*. 1997). But this situation is not limited to nematodes (Abbot *et* al. 2013, Carstens *et al.* 2013, Feder *et al.* 2012, Fujita *et al.* 2012, Lee 1998, Peccoud *et al.* 2009, Zhang *et al.* 2013). In other taxonomic groups as well the boundary between species, varieties, races and other sub-specific groups is a continuum as well (Barton 2001, Coyne & Orr 2004, Futuyma 2005, Mallet 2008, Seehausen 2004). Despite the uncertainties, the species is currently the basic unit for most studies of diversity, ecology and biology, as well as being used in biosecurity regulations and conservation planning. Hence, having a generally agreed concept of what is a species is important, even if this concept has to be a bit fuzzy. In this regard, the detailed studies on nematodes provide some of the best information available on which to base general models and concepts for other organisms (Cutter *et al*. 2019).

Although there are detailed studies of some species, nematode species descriptions based on detailed studies are not the norm (but see Felix *et al.* 2014, Hodda *et al.* 2014). The resources to investigate the details of biological, genetic, and ecological relationships of every putative species are generally not available, and are unlikely to be forthcoming any time soon. So a degree of uncertainty in the definition of most nematode species will remain, and the generally agreed concepts will need to be applied. A comprehensive cladistic phylogenetic analysis of free-living nematodes some years ago concluded that nematode classification was then an incomplete system, and was likely to remain so for some time (Lorenzen 1994). The present classifications show that the system is still incomplete for nematodes (Hodda 2022a). Even though over 28 000 valid species are recognized, and there are many more nematode species described but subsequently synonymized, this still represents only a small fraction of the estimated total number of species (Hugot *et al.* 2001, Hodda & Khudhir 2022). The task remains to describe as much of the huge nematode diversity as possible, even with the dual uncertainties of what is a nematode species and what is the taxonomic framework in which to place it evolutionarily. Too often nematode material is never recorded where specimens are unusual or rare, and the material never becomes available to scientists other than the collector (Khudhir *et al*. 2022). The tension between conservative approaches which only present taxonomic work that has a high degree of certainty as against presenting descriptions which are incomplete or uncertain (often because of a lack of material) was summarized recently by Payne (2015). Numerous examples of nematode taxa without full description and formal scientific name, but with an informal name and incomplete description testify to the issue in nematode taxonomy (eg Carta & Skantar 2014, Choudhury & Nadler 2016, Davies *et al.* 2015, De Oliviera *et al.* 2014, Kanzaki & Giblin-Davis 2014, Leduc 2014, Moravec & Barton 2015, Moravec & Jirku 2014a, Moravec & Manoharan 2014a, Moravec *et al.* 2016, Raymond *et al.* 2014, Smales 2015, Tchesunov *et al*. 2015, Thorne *et al.* 2017, Yong *et al.* 2015). There has also been a formal definition of what is a known species complex in the highly-studied model genus *Pristionchus* (Yoshida *et al.* 2018).

The number of nematode species

Recognition of the difficulty in defining species has led to concerns about taxonomic inflation. These concerns have been expressed for nematodes, particularly the plant parasites (Luc *et al.* 1987, Maggenti 1991, Maggenti *et al.* 1987, 1988), as well as in some charismatic vertebrate groups like birds, amphibians and mammals. In primates, the number of species has doubled since 1985 through elevation of subspecies to species level even though few new taxa have been discovered (Burgin *et al*. 2018, Fisher *et al*. 2018, Isaac *et al*. 2004). Taxonomic inflation may be less of an issue for nematodes than for more charismatic groups because new species have been overwhelmingly based on new material rather than just revision of old material as with primates. Some new species have been identified from existing material (primarily culture collections), but most new species of nematodes have resulted from collections in new locations, habitats or hosts, as well as more intensive collecting from places sampled inadequately previously. Re-sampling of previous collecting sites, as well as collections from new sites in similar habitats and collections in different habtats are all likely to result in previously undescribed nematode species being found (Hodda 1990, Hodda & Khudhir 2022).

Notable has been the recent description of nematodes from up to 9 Km below the Earth's surface (Borgonie *et al.* 2011). At the other end of the altitude range, nematode survival has been documented in space and high in the earth's atmosphere after disintegration of a space-ship re-entering earth's atmosphere (Szewczyk *et al*. 2005). Together, these findings extend the overall habitat envelope for nematodes, and supports the claim, made many years ago, that nematodes occur everywhere on earth: "if all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable… we would find its mountains, hills valleys, rivers, lakes and oceans represented by a film of nematodes. The ghostly outlines of all the plants, animals and humans would appear outlined by their nematode parasites…" (Cobb, 1914, p 472).

Nomenclatorial issues

The complexity of phylogenetic relationships in nematodes, together with their great diversity has also led to the suggestion of taxa above species and genus rank without taxonomic ranks, particularly in the species-rich Rhabditida (Sudhaus 2011). Such non-traditional approaches have been vigorously supported and equally vigorously disputed (Dubois *et al*. 2021, De Queiroz & Donohue 2001, 2013, Nixon & Carpenter 2000, Nixon *et al.* 2003, Platnik 2012, 2013). Higher taxa without ranks may be particularly useful in the largest nematode orders, the Spirurida, Rhabditida and Panagrolaimida. In these taxa the full range of traditional ranks has been required to reflect phylogeny, even with relatively conservative approaches assuming polytomies where evidence remains inconclusive or inconsistent (Hodda 2007, 2011, Hodda 2022a), but as the number of taxa known increases and the resolution improves, then the current number of ranks may prove inadequate. This does not seem to be necessary at the moment because, since previous synopses, there have been few studies or changes suggested to nematode classification above the family level (Hodda 2007, 2011). Several changes have been suggested to the composition of families, but these are relatively few. In few cases is there unequivocal, consistent genetic, morphological and other evidence to change families or resolve polytomies at higher levels of nematode classification. The concentration of new species descriptions in groups of economic, ecological or biological significance, rather than phylogenetic importance has not assisted resolving issues, notwithstanding initiatives to address this (Thomas 2007).

Conclusion

A corollary of the large number of new descriptions, uncertainty over exactly what does constitute a nematode species, and uncertainties in higher-level classification mean that revisions and synonymization will continue to be as necessary as new descriptions. Organization of the species and genera into classifications of higher taxa will increasingly be necessary to keep track of, and enable access to, nematode diversity. Continual refinement of these nematode classifications will need to continue if we are to reflect more and more accurately the great diversity and complexity of relationships among nematodes. In all this uncertainty, one thing is certain: nematode classification will continue to challenge science, as well as the International Code of Zoological Nomenclature and taxonomic system, with its intricacies. Despite all this, progress has been made, and continues to be made.

Acknowledgements

I thank Zhi-Qiang Zhang for the initial invitation to publish a classification of the entire Phylum Nematoda, colleagues at Australian National Insect Collection for discussions of classification and species concepts, and many taxonomic colleagues, for discusssions of the practicalities of species description and classification. I thank Mr W. Wanjura and Ms Manda Khudhir for help in counting taxa and sub-taxa, and Dr D. Huston and Ms M. Khudhir for assistance with proof reading.

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