PAPBA 1795/1
ISSN : 1388 - 5545

Nematology, 2001, Vol. 3(3), 199-208

Forum article

Biodiversity in helminths and nematodes as a field of study: an overview

Jean-Pierre HUGOT [1,*], Pierre BAUJARD [2] and Serge MORAND [3]

[1] *Muséum National d'Histoire Naturelle, Institut de Biosystématique, 55 rue Buffon, 75231 Paris cedex 05, France*
[2] *IRD, Laboratoire de Nématologie, B.P. 1386, Dakar, Sénégal*
[3] *Université de Perpignan, Laboratoire de Biologie Animale, 66860 Perpignan cedex, France*

Received: 17 August 1999; revised: 19 February 2000
Accepted for publication: 22 September 2000

Summary – Despite their potential negative effects, parasites may be used as targets for biological conservation and studies on the evolutionary and ecological impact of parasitism. These purposes serve to increase our knowledge on the species diversity of parasites. In the present paper we try to precisely define the composite zoological group currently designated as 'helminths' and to address the question of how many known species there are in the different clades of parasitic worms, as compared with the other major groups described in the Animalia. The relationships between helminthology and nematology are discussed. Finally, the question of how to improve the organisation of research in these different fields of study is briefly considered. The Nematoda seems to be the group which needs the greatest effort in the future. This supposes that specialists in nematode taxonomy are numerous enough to maintain a substantial effort. The necessary taxonomical effort is weakened by the distribution of the fields of study between helminthology and nematology, something which is inadequate from a zoological, as well as from a logical, point of view. The study of nematode zoology would certainly improve if nematology could emerge as an undivided speciality. One of the prior goals in such a unified field of study would be an exhaustive inventory of the nominal living species. A cooperative effort will also be needed to found the basis of a general classification of the phylum Nematoda. Finally, a clarification and a standardisation of the terminology is also needed.

Keywords – biodiversity, helminthology, nematology, species inventory, taxonomy.

Interest in the ecology and evolution of host-parasite relationships is growing (Poulin, 1998). Many have recognised that parasites have the potential to regulate host population, host community and even food web stability (Grenfell, 1992; Morand *et al.*, 1996; Morand & Arias-Gonzalez, 1997; Poulin, 1998). Also, parasites are presumed to play a major role in the evolution of host life history traits and host behaviour (Hamilton & Zuk, 1982; Hochberg *et al.*, 1992; Loehle, 1995). Recent studies have tried to interpret the patterns of parasite species richness among several groups of hosts, including birds, mammals and fishes (Bush *et al.*, 1990; Poulin 1995; Gregory *et al.*, 1996; Sasal *et al.*, 1997; Morand & Poulin, 1998). It was also hypothesised that parasite diversity is linked to their specificity towards their hosts (Brooks & McLennan, 1993b, pp. 115-116). Reconstructions of evolutionary scenarios were proposed to explain the common history of host and parasite associations (Page, 1995). In some cases, these reconstructions illustrate the phenomenon of close coevolution with cospeciation (Brooks & Glen, 1982; Hugot, 1988, 1999).

All of these questions are closely related to our knowledge of parasite species diversity (Bush *et al.*, 1995). Within the entozoan parasites the so-called 'parasitic worms' or 'helminths' are the most abundant. However, estimates of the number of parasite species are difficult to obtain (Poulin, 1996). This difficulty is considered to be partly linked to the rapidly decreasing number of systematicians able to complete and organize our knowledge on the taxonomy of these groups (Lambshead, 1993; Coomans, 2000; De Ley, 2000). On the other hand, this deficiency also partly results from the fact that the different fields of study with which they are concerned are not precisely, nor logically outlined. In the following account, we *i*) try to precisely define the different zoological groups which are designated as helminths; *ii*) address the question of how many known species there are in the different clades of parasitic worms, in relation to other major

* Corresponding author, e-mail: hugot@mnhn.fr

© *Koninklijke Brill NV, Leiden, 2001*

Fonds Documentaire IRD
Cote : Bx 26034 Ex : 1

Fonds Documentaire IRD
010026034

groups described in the Animalia; *iii*) give special attention to the relationships between helminthology and nematology. Finally, the question of how to improve the organisation of research in these different fields of study is addressed.

Material and method

TAXONS CONSIDERED IN THIS WORK

All the groups analysed in the *Helminthological Abstracts* and the *Nematological Abstracts* are considered herein. Data concerning the origins of the terminology were found in Camus (1783) and Moulé (1911).

CLASSIFICATIONS

The classification of the Metazoans in Fig. 1 is based on the cladogram of the invertebrates major taxa given by Meglitsch and Schram (1991), but modified to add the vertebrates. Those groups which are considered to be within the remit of helminthology are in bold and shifted to the right. The general classification of the nematodes (Fig. 2) is based on Gadea (1973), Andrássy (1976), Adamson (1987), and Anderson (1988), as synthesized by Brooks and McLennan (1993b, p. 350), and modified as follows: the nematode groups where adults are parasites of invertebrates are added after Poinar (1977); the Tylenchida are developed following Fortuner and Raski (1987) and Luc *et al.* (1987). As this classification is not the result of any analytical approach it must be considered schematic and conditional. It is an empirical way we have chosen to sketch the groups, not a scientific assessment. However, this classification generally fits with the recent work published by Blaxter *et al.* (1998, 2000), the major exception being the Enopliomorpha which was not recognized as a monophyletic group by the last authors. But, as Blaxter *et al.*'s work displays a basal polytomy between the different groups which are combined in the Enopliomorpha of Fig. 2 and a monophyletic group corresponding with the Chromadorimorpha of the same figure, we have chosen to maintain the basal dichotomy proposed in previous classifications.

HOW MANY SPECIES ARE THERE ON THE EARTH? (TABLE 1)

The numbers on the left half are after Hoffman (1982), Strathman and Slatkin (1983), Meglitsch and Schram (1991) and Stork (1993) for invertebrates, and after May (1988), Hammond (1992), Wilson and Reeder (1993) and Chauvet and Olivier (1993) for vertebrates, with the exception of the Urochordata, after Monniot (pers. comm.). The numbers on the right half are after Meglitsch and Schram (1991) for the Pentastomida, Annelida and Nematomorpha, after Golvan (1994) for the Acanthocephala, after Brooks and McLennan (1993a, b) and Vaucher (pers. comm.) for the parasitic platyhelminths. For free-living Nematoda, the evaluation is after Andrássy (1992), (unpubl.) and Lambshead (1993); for the phytoparasitic Nematoda, after Baujard (unpubl.). For the zooparasitic Nematoda, the estimated number of known species has been compiled from books and (or) recent taxonomic revisions: Yamaguti (1961), Rubzov (1977), Poinar (1978), Adamson and Van Waerebeke (1985), Anderson (1992), Hunt (1996a, b), Morand *et al.* (1996). The numbers for the Strongylida are after Durette-Desset (pers. comm.); within the Strongylida the Trichostrongylina which represents 35% of the species in the order and 90% of the species described during the last 25 years have been distinguished. The numbers for the Oxyurida are after a database in which we have computed all the species described in this order; the Oxyurida parasites of vertebrates or invertebrates are distinguished. In Table 1, groups and numbers in italic are considered to be in the field of helminthology. Groups and numbers in bold are totals and sub-totals. 'Animalia' is the sum of all groups. '*Helminths*' is the sum of the central right column plus the Nematomorpha. *Platyhelmintha* is the total of the Aspidobothrea, Digenea, Monogenea, Cestodaria and free-living flat worms. Nematoda is the total of all the nematodes. Within the Nematoda, the subtotals in bold distinguish either the free-living, or parasites of plant, invertebrates or vertebrates; *free-living marine* includes the Trefusiida, Enoplida, Monhysterida and Chromadorida; *free-living terrestrial* includes 50% of the Triplonchida, 95% of the Dorylaimida together with the Leptolaimida and 90% of the Rhabditida; *parasite of plants* includes 50% of the Triplonchida, 5% of the Dorylaimida, the Tylenchida and the Aphelenchida; *parasite of invertebrates* includes the Mononchida, Mermithida, Myenchida, Sphaerulariida, Hexatylida, Drilonematida, Rhigonematida, 10% of the Rhabditida, and the Diplogasterida and Rhabdiasida with the exception of 91 species considered to be parasites of vertebrate hosts; *parasite of vertebrates* includes the Dioctophymatida, Trichinellida, Muspiceida, Ascaridida, Spirurida, Strongylida (including the Trichostrongylina) and Oxyurida (in which the parasites of vertebrates and invertebrates were distin-

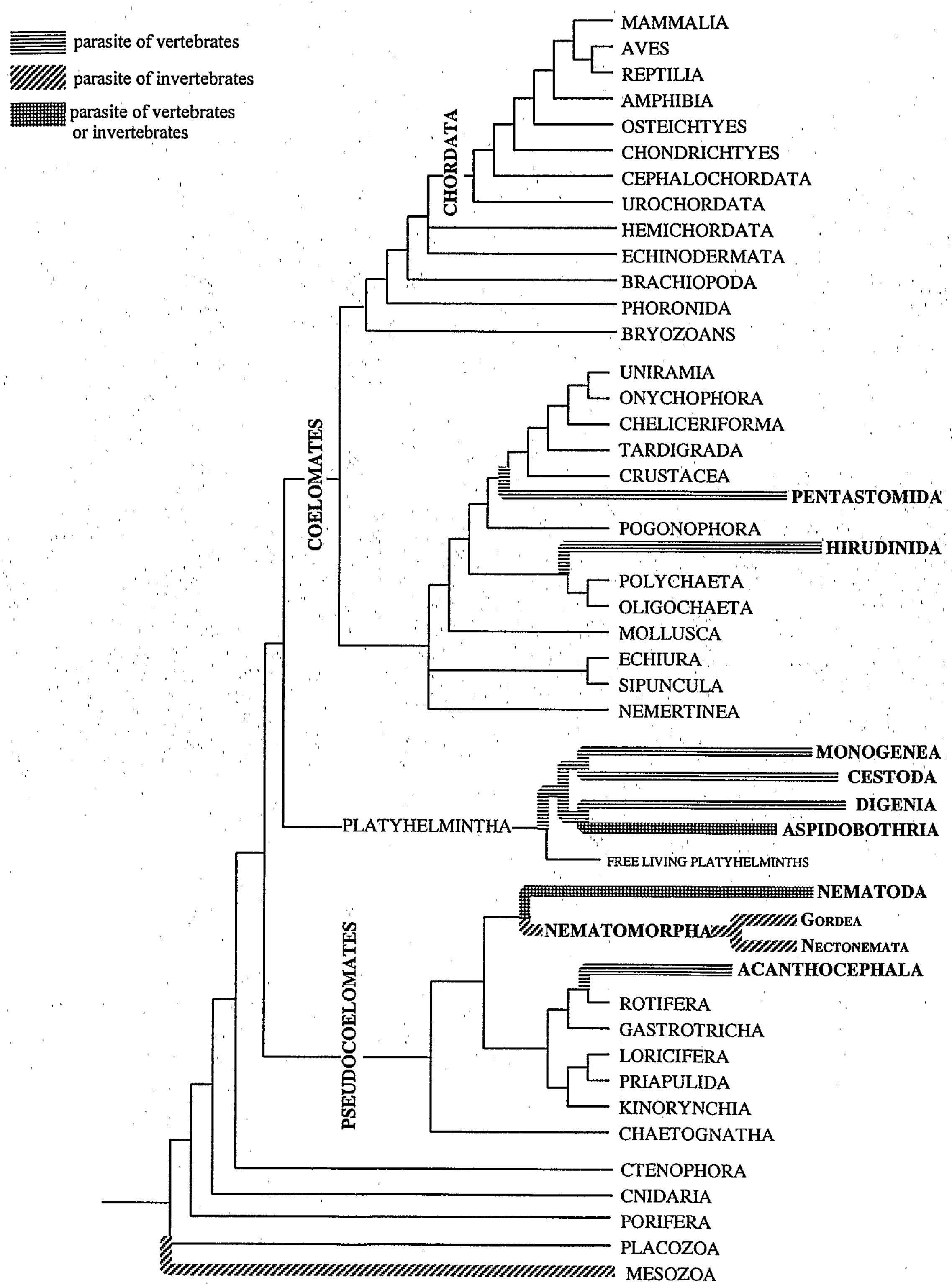

Fig. 1. *The helminths in the animal kingdom. General classification of the Metazoan after Meglitsch and Schram (1991), modified.*

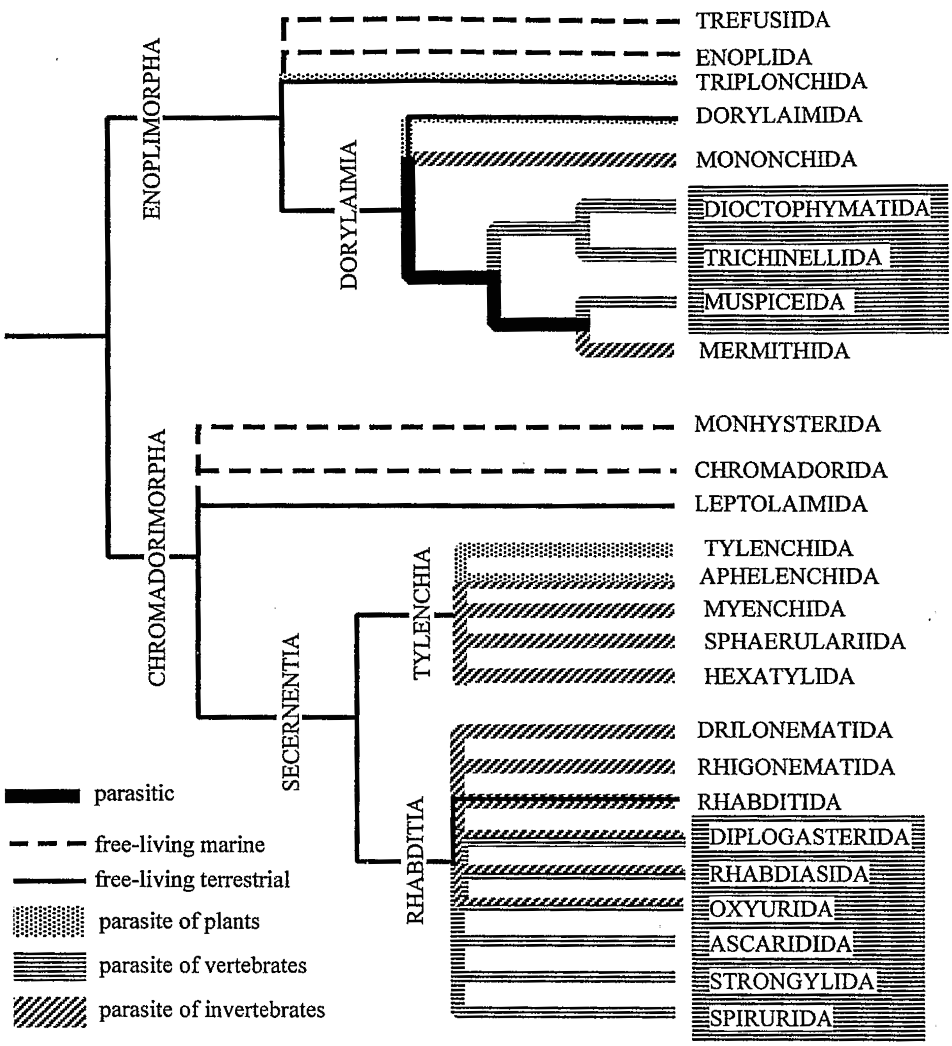

Fig. 2. *General classification of the nematodes after Brooks and McLennan (1993b), modified.*

guished); *zooparasitic* is the sum of the nematode parasites of animals.

Results and discussion

What is a worm?

'Worm' is generally used for naming all those animals crawling, wriggling and swarming with a depreciative understanding: weak, despicable, parasite, pest, rotten, corrupted ..., 'worm' was derived into wormy and worm-eaten. In the Latin translations of Aristotle, until the 18th century the references in zoology, 'worm' was used for all white-blooded animals without articulate antennae, as opposed to insect: white-blooded animals with articulate antennae. Together worm and insect covered all those animals which we now distinguish as invertebrates. The title of the chair created for Lamarck in the French Muséum d'Histoire Naturelle in 1793, and called: 'Insecta, Worms and Microscopic Animals' still reflects this ancient subdivision of the animal kingdom. Since that time successive improvements in our knowledge have resulted in either segregation of some 'worms' into distinct new phyla, or the classification of some others in their respective group, as insects, molluscs, arthropods, *etc.* Even today various animals are still called 'worms', either invertebrates, insect larvae (woodworm, silkworm, Cayor's

Table 1. *How many species are there on the Earth? Groups and numbers in italic are considered to be in the field of helminthology. Groups and number in bold are totals and sub-totals.*

	Estimated species	
	known	living
MAMMALIA	4637	?
AVES	9040	?
REPTILIA	6300	?
AMPHIBIA	4975	?
OSTEICHTYES	18 150	?
CHONDRICHTYES	843	?
CEPHALOCHORDATA	63	?
UROCHORDATA	3500	4000
CHORDATA	**47 508**	
MYRIAPODA	17 000	>60 000
INSECTA	950 000	10 000 000
UNIRAMIA	**967 000**	to 100 000 000
ONYCHOPHORA	75	?
CHELICERIFORMA	65 000	750 000
TARDIGRADA	550	1000
CRUSTACEA	75 000	150 000
OTHER ARTHROPODS	**140 625**	
HEMICHORDATA	100	⩾150
ECHINODERMATA	8000	?
BRACHIOPODA	330	400-500
PHORONIDA	13	20
BRYOOZOANS	4500	?
POGONOPHORA	120	500
MOLLUSCA	50 000	150 000
ECHIURA	130	?
SIPUNCULA	320	330
NEMERTINEA	800	>3000
OTHER COELOMATES	**64 313**	
ROTIFERA	1800	2500
GASTROTRICHA	450	⩾1000
LORICIFERA	50	100
PRIAPULIDA	15	20
KINORYNCHYA	150	500
CHAETOGNATHA	70	115
CTENOPHORA	80	130-500
CNIDARIA	10 000	?
PORIFERA	5000	10 000
PLACOZOA	1	?
MESOZOA	85	500
OTHER INVERTEBRATES	**17 701**	
ANIMALIA	**1 290 489**	
HELMINTHS	*23 670*	
NEMATODA	**26 646**	**1 000 000**

	Estimated species		
	known	parasitic on vertebrates	living
ACANTHOCEPHALA		***1141***	?
POLYCHAETA	8000		12 000
OLIGOCHAETA	3000		?
HIRUDINEA		*500*	?
ANNELIDA	**11 500**		16 000
NEMATOMORPHA	**275**		?
PENTASTOMIDA		***100***	?
free living platyhelminths	110		?
ASPIDOBOTHRIA		*50*	?
DIGENEA		*8000*	?
MONOGENEA		*3000*	?
CESTODEA		*2520*	?
PLATYHELMINTHA	**13 680**	***13 570***	20 000
TREFUSIIDA	70		?
ENOPLIDA	1600		?
TRIPLONCHIDA	200		?
MONONCHIDA	500		?
DORYLAIMIDA	1695		?
DIOCTOPHYMATIDA		*50*	?
TRICHINELLIDA		*384*	?
MUSPISCEIDA		*9*	?
MERMITHIDA	750		?
MONHYSTERIDA	900		?
CHROMADORIDA	1500		?
LEPTOLAIMIDA	3650		?
TYLENCHIDA	3400		?
APHELENCHIDA	570		?
MYENCHIDA	3		?
SPHAERULARIIDA	281		?
HEXATYLIDA	19		?
DRILONEMATIDA	90		?
RHIGONEMATIDA	150		>10 000
RHABDITIDA	1390		
DIPLOGASTERIDA	971	*91*	
RHABDIASIDA	47		
OXYURIDA (invertebrates)	211		2000
OXYURIDA (vertebrates)		*498*	1000
ASCARIDIDA		*1200*	?
SPIRURIDA		*2700*	?
STRONGYLIDA		*3427*	?
(TRICHOSTRONGYLINA)		*(1212)*	?
free-living marine	**4070**		?
free-living terrestrial	**6611**		?
total free-living	**10 681**		>500 000
parasite of plants	**4105**		?
parasite of invertebrates	**3501**		?
parasite of vertebrates		***8359***	?
zooparasitic	**11 860**		

worm), adult insects (glow-worm), annelids (earthworm), platyhelminths (tapeworm), or vertebrates (slow-worm).

WHAT IS AN HELMINTH?

In an extensive survey of parasitology in the ancient Greek and Latin literature, Moulé (1911) reviewed the diverse terms used for naming the Entozoa: the intestinal parasites. Three different words were used by the Greeks. The less specific was (theria) which principally designated 'wild animal', or more generally 'animal', but was also used for naming the intestinal worms: 'Intestinal worms (το θηεριωδες) are especially abundant at fall' (Hippocrates, *Epidemics*, Liv. II, §3). The closest approximation to our widespread 'worm' was probably σχωληξ (scolex), which generally designated insect larvae, but was also used by Hippocrates reporting on intestinal parasites of horses: 'Worms (σχωληχες) severely disturb horses and are not easily cured' (*Hippiatria*, Liv. II, ch. 26). 'Helminth', spelled ελμινθες ελμινζ or ελμιζ and translated *elminthes, elmintes* or *elmins* in French, was used by Aristotle '(*Peri ta zoa Istoriai*', Liv. V, ch. 19) for those worms which, following the translation by Camus (1783), '... grow in the faeces of animals, either before or after the faeces have been released from their gut. These are three kinds, the flat worms (ελμινθες πλατειαι), the round worms (ελμινθες στρογγυλαι) and the ascarids (ασχαριδες). These kinds can particularly be found in the human body'. Aristotle also spoke of helminths in the dogs, the fishes and the sponges: 'The sponge (σπογγος) supplies in its body small animals which are worms (ελμινθες)' ('*Peri ta zoa Istoriai*', Liv. V, ch. 14, §5). And Camus commented: 'Hippocrates also referred to the ascarids in his 'Epidemics', ... (where) ... he spoke of the round worms and flat worms'. This was confirmed by Moulé (1911) who also reported that the subdivisions proposed by Hippocrates and Aristotle were later endorsed by Dioscorides, Galen and Oribase.

This clearly suggests that of the different words used for naming worms, 'helminth' very soon designated worms living in the digestive tract of humans and animals, and thus was allied with the general concept of parasitism. In addition, subsequent to this word being used the concepts of 'flat helminth' and 'round helminth' also arose, later giving birth to the still available: 'platyhelminth' and 'nemathelminth'.

WHAT IS A NEMATODE?

Moulé (1911) translating Hippocrates ('Epidemics', Liv. II, sect. 1, §11) thought that 'ascarids' was probably first used for naming oxyurid nematodes parasitic in humans: 'The ascarids (αι ασχαριδες) revile at night' and, '... at the end of the intestines another illness can be observed: some small animals similar to worms living in the putrescent meat appear which are named ασχαριδες'. Elsewhere ('Diseases of girls', Liv. II, sect. 5) he gave medicine: 'When, on a woman, arise ascarids (ασχαριδες) either on the genital tract or the anus'. Moulé also referred to Galen: 'The ασχαριδες are short and tiny, as are the σχωληξ. Very often they are in the rectum of children, especially before they have reached puberty'. These symptoms clearly deal with enterobiasis. However, our common ascarid (*Ascaris lumbricoides*), had already been recognised, but unexpectedly was called ελμινθες στρογγυλαι (elmintes strongylid), a name which well identified its rounded cylindrical shape and also matched with Galen's description of symptoms: 'The round worms (ελμινθες στρογγυλαι) which generate in the upper parts of the digestive tract, sometimes climb upward through the stomach aperture and generate cough'.

As ascarids (ασχαριδες) and strongylids (στρογγυλαι) were gradually used for naming particular kinds of round worms it became necessary to create a new word for categorising the round worms as a whole: 'nematode' derives from νημα, νηματος, thread, slender with a cylindrical shape, from the Greek: νεω 'I spin', 'I weave'. It is a recently derived word: its first use cited by Cottez (1980) is in Rudolphi (1803) as nematoides (νηματῶδης), later giving birth to nematode (Boiste, 1839) and nemathelminth (Larousse, 1874).

HOW MANY HELMINTHS, HOW MANY NEMATODES AND HOW MANY ANIMALS ARE THERE ON THE EARTH?

Table 1 gives an estimate of how many species have been described in the animal kingdom. When available the estimated number of living species is also given. On the right half are those phyla which, partly or as a whole, deal with helminthology (in italic) and (or) nematology. In the central right column are given the estimated number of species parasitic in vertebrate hosts. On the left half are the other phyla. On the left side of Fig. 3 are represented the different components of the helminths with estimates of how many species have been described in each subgroup. For comparison the same information is given on

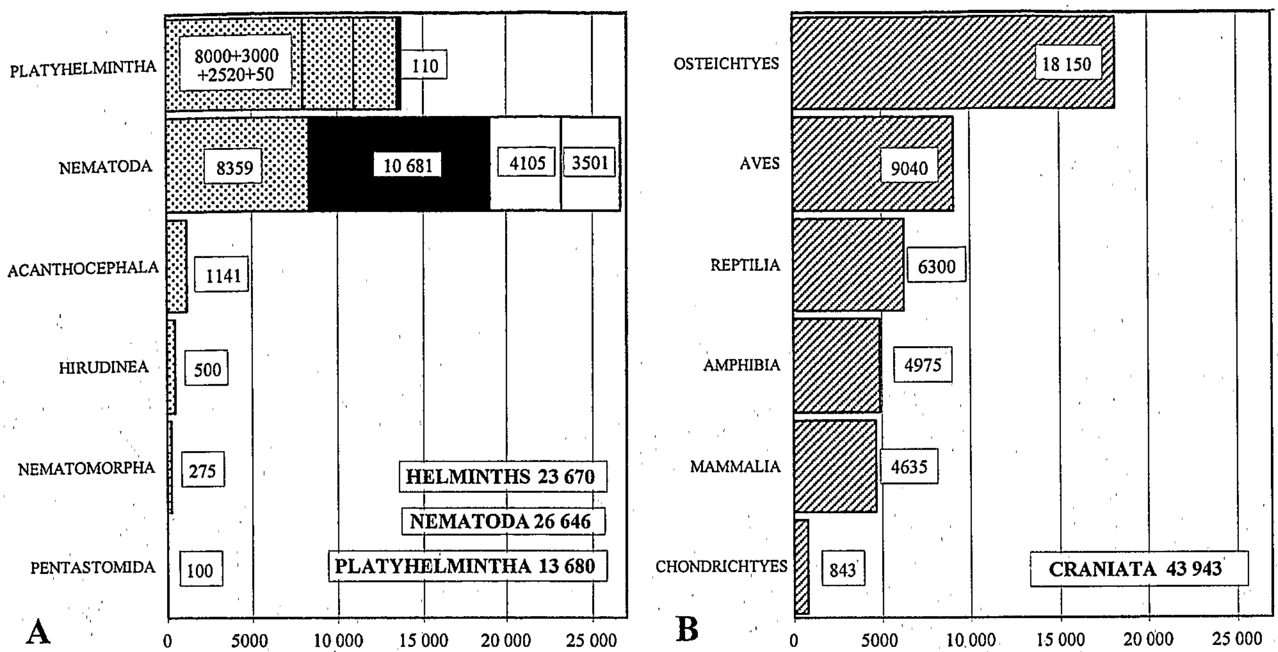

Fig. 3. *A: Histograms of the different groups in the helminths (large dotted blocks), following the number of described species, decreasing from top down. For the Platyhelmintha and the Nematoda the free-living species also have been represented (black blocks). For the Platyhelmintha the different subgroups have been figured from the left to the right: Digenea, Monogenea, Cestodea and Aspidobothria. For the Nematoda, these species which are parasitic on plants (4105) or invertebrates (3501) have been represented by thin dotted blocks. B: Histograms of the different groups in the Craniata, following the number of described species, decreasing from top down.*

the right side of the Fig. 3 for the different components of the Craniata. The helminths *sensu lato* represent 23 670 species with two major subgroups: the Platyhelmintha with 13 570 species and the vertebrate parasitic Nematoda with 8359 species. However, the Nematoda as a whole, with 26 646 species, represents one of the most abundant groups in the animal kingdom with more species than the Osteichtyes, and as many as the Tetrapods (Aves, Reptilia, Mammalia and Amphibia) put together. As a monophyletic group, the Nematoda represent one of the most diversified phyla within the Animalia with 8359 species parasitic in vertebrate hosts (as much as the Mammalia plus the Amphibia), 10 681 free-living species (more than the Aves), 4105 species parasitic in plants (as much as the Amphibia), 3501 species parasitic in invertebrate hosts.

ARE WE FAR FROM MAKING GOOD ESTIMATES OF SPECIES RICHNESS?

When considering the number of estimated living species in the Nematoda, which May (1988) evaluated at 1 000 000 and Hammond (1992) at 500 000, they could be the second most important group beneath the Arthropods. By comparison, the highest evaluation for the estimated number of living Platyhelmintha given by Brusca and Brusca (1990) is much lower; about 20 000 species. If we accept the lower estimate of 500 000 species, only 5.3 % of the living species in the Nematoda have been described. Hammond (1992) gave an average number of 364 new nematode species per year listed in the *Zoological Records* between 1979 and 1988. Comparing our 26 546 described species with the 10 000 described species given by Mayr *et al.* (1953) gives about the same result, with an average number of 385 new nematode species per year. Thus, if the estimation given by Hammond (1992) turns out to be an accurate approach to reality, and if the descriptions are still produced following the same rhythms, about 1300 years will be necessary to achieve an extensive record of the living species of Nematoda.

Conclusion

From antiquity until the 18th century, most of the naturalists also being physicians, zoological taxonomy and parasitology nomenclature often merged. The present situation, in which the parasitic 'worms' are distributed between the study fields of both helminthology and nematology, still reflects the history of parasitology in dealing with both medicine and zoology. This results in a confused arrangement where 'worm' has no exact sense in zoology, and from a cladistic point of view has no sense at all, and 'helminth' has no zoological significance, if one considers the taxonomic groups analysed in the *Helminthological Abstracts* (Fig. 1), and generally designates endoparasitic invertebrates on humans and animals. However, helminthology *i*) also includes the Monogenea, which are ectoparasites, and the Hirudinida which Meglitsch and Schram (1991), consider to be predators; *ii*) does not consider the Mezozoa (Fig. 1) and those nematodes which became adapted to endoparasitism in other invertebrates (Fig. 2), the former being ignored as parasites, the latter being considered to be a constituent of nematology together with phytoparasitic, free-living and predator nematodes; *iii*) conversely includes the Nematomorpha, the larvae of which parasitise arthropods, the adults being free-living; *iv*) is already split into different domains where experts on flatworms rarely interact with experts on roundworms.

Nematology *sensu stricto* is restricted to the study of free-living nematodes, phytoparasitic, entomoparasitic and predatory nematodes plus those zooparasitic nematodes whose hosts are invertebrates. This is a nonsense from a zoological point of view, because *i*) nematodes are now recognised as a natural group (Anderson, 1988; Meglitsch & Schram, 1991; Aguinaldo *et al.*, 1997; Blaxter *et al.*, 1998), probably the second largest one in the animal kingdom immediately behind the arthropods, when considering the number of described and estimated unknown species (Table 1, Fig. 3); *ii*) this situation generates an artificial partition of specialists into separate fields, each ignoring one another, and probably explaining why no satisfactory classification of the phylum as a whole has been achieved; *iii*) because nematodes doubtless became parasitic several times independently (Anderson, 1988, 1991; Blaxter *et al.*, 1998, 2000), this also results in a dichotomy within those nematode subclasses or orders which are partly free-living and partly parasites of plants or (and) animals, the most absurd example being the Oxyurida where families dealing with invertebrate hosts are considered in the field of nematology, and those where the hosts are vertebrates in the field of helminthology.

Many studies stress the evolutionary and ecological impact of parasitism (Bush *et al.*, 1995). Despite their potential negative effects, parasites may also be used as biological targets for various aspects of biological conservation (Gardner & Campbell, 1992). These purposes, as well as medical and veterinary studies on epidemiology and pathogenicity, should increase our knowledge on the species diversity of parasites. The necessary taxonomical effort is weakened by the distribution of the fields of study between helminthology and nematology. This is inadequate from a zoological as well as from a logical point of view and appears inefficient from a scientific point of view.

If one compares the number of estimated living species with the number of species which have already been described, the Nematoda is the group needing the greatest effort in the future (Lambshead, 1993; Coomans, 2000). This supposes that specialists in nematode taxonomy are numerous enough to maintain a substantial effort during the following years (Ferris, 1994; Coomans, 2000). The study of nematode zoology would also improve if nematology emerged as an undivided speciality (De Ley, 2000). One of the prior goals in such a unified field of study would be an exhaustive inventory of nominal living species. A cooperative effort will also be needed for founding the basis of a consensual classification of the phylum Nematoda (De Ley, 2000). Finally, a clarification and a standardisation of the terminology is also needed. This is necessary for easy communication between the specialists of the different groups. This is essential if tools of determination have to be proposed by the identifiers in nematology to the rest of the community, in the near future (Diederich *et al.*, 2000).

Acknowledgements

We thank O. Bain, G. Boucher, M.C. Durette-Desset, M. Luc, C. Monniot, A. Petter and C. Vaucher for giving us their own estimate of how many species there are in the groups they are respectively interested in.

References

ADAMSON, M.L. (1987). Phylogenetic analysis of the higher classification of the Nematoda. *Canadian Journal of Zoology* 65, 1478-1482.

ADAMSON, M.L. & VAN WAEREBEKE, D. (1985). The Rhigonematida (Nematoda) of Diplopoda: reclassification and its cladistic representation. *Annales de Parasitologie Humaine et Comparée* 60, 685-702.

AGUINALDO, A.M.A., TURBEVILLE, J.M., LINFORD, L.S., RIVERA, M.C., GAREY, J.R., RAFF, R.A. & LAKE, J.A.

(1997). Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature* 387, 489-493.

ANDERSON, R.C. (1988). Nematode transmission patterns. *Journal of Parasitology* 74, 30-45.

ANDERSON, R.C. (1992). *Nematode parasites of vertebrates. Their development and transmission.* Wallingford, UK, CAB International, 578 pp.

ANDRÁSSY, I. (1976). *Evolution as a basis for systematization of nematodes.* London, UK, Pitman Publishing, 287 pp.

ANDRÁSSY, I. (1992). A short consensus of free-living nematodes. *Fundamental and Applied Nematology* 15, 187-188.

BLAXTER, M.L., DE LEY, P., GAREY, J.R., LIU, L.X., SCHELDEMAN, P, VIERSTRAETE, A., VANFLETEREN, J.R., MACKEY, L.Y., DORRIS, M., FRISSE, L.M., VIDA, J.T. & THOMAS, W.K. (1998). A molecular evolutionary framework for the phylum Nematoda. *Nature* 392, 71-75.

BLAXTER, M.L., DORRIS, M. & DE LEY, P. (2000). Patterns and processes in the evolution of animal parasitic nematodes. *Nematology* 2, 43-55.

BOISTE, P.C.V. (1839). *Nomenclature complète d'histoire naturelle. Dictionnaire universel de la langue française. X^th^ edition* (revised by C. Nodier). Paris, France, Lecointe & Pougin, 149 pp.

BROOKS, D.R. & GLEN, D.R. (1982). Pinworms and primates: a case study in coevolution. *Proceedings of the Helminthological Society of Washington* 49, 76-85.

BROOKS, D.R. & MCLENNAN, D.A. (1993a). Comparative study of adaptive radiations with an example using parasitic flatworms (Platyhelminths, Cercomaria). *American Naturalist* 142, 755-778.

BROOKS, D.R. & MCLENNAN, D.A. (1993b). *Parascript. Parasites and the language of evolution.* Washington & London, Smithsonian Institution Press, 429 pp.

BRUSCA, R.C. & BRUSCA, G.J. (1990). *Invertebrates.* Sunderland, MA, USA, Sinauer, 550 pp.

BUSH, A.O., AHO, J.M. & KENNEDY, C.R. (1990). Ecological *versus* phylogenetic determinants of helminth parasite community richness. *Evolutionary Ecology* 4, 1-20.

BUSH, A.O., CAIRA, J.N., MINCHELLA, D.J., NADLER, S.A. & SEEDS, J.R. (1995). Parasitology year 2000. *Journal of Parasitology* 81, 835-842.

CAMUS, A.G. (1783). *Histoire des animaux d'Aristote avec la traduction françoise, suivie de notes.* Paris, France, Dessaint, 850 pp.

CHAUVET, M. & OLIVIER, L. (1993). *La biodiversité enjeu planétaire.* Paris, France, Sang de la Terre, 415 pp.

COOMANS, A. (2000). Nematode systematics: past, present and future. *Nematology* 2, 3-7.

COTTEZ, H. (1980). *Dictionnaire des structures du vocabulaire savant. Eléments et modèles de formation.* Paris, France, Le Robert, 515 pp.

DE LEY, P. (2000). Lost in worm space: phylogeny and morphology as road maps to nematode diversity. *Nematology* 2, 9-16.

DIEDERICH, J., FORTUNER, R. & MILTON, J. (2000). Genisys and computer-assisted identification of nematodes. *Nematology* 2, 17-30.

FERRIS, V.R. (1994). The future of nematode systematics. *Fundamental and Applied Nematology* 17, 97-101.

FORTUNER, R. & RASKI, D.J. (1987). A review of Neotylenchoidea Thorne, 1941 (Nemata: Tylenchida). *Revue de Nématologie* 10, 257-267.

GADEA, E. (1973). Sobre la filogenia interna de nematodos. *Publicaciones del Instituto de Biología Applicada, Barcelona* 54, 87-92.

GARDNER, S.L. & CAMPBELL, M.L. (1992). Parasites as probes for biodiversity. *Journal of Parasitology* 78, 596-600.

GOLVAN, Y. (1994). Nomenclature of the Acanthocephala. *Research and Review in Parasitology* 54, 135-205.

GREGORY, R.D., KEYMER, A.E. & HARVEY, P.H. (1996). Helminth parasite richness among vertebrates. *Biodiversity Conservation* 5, 985-997.

GRENFELL, B.T. (1992). Parasitism and the dynamics of ungulate grazing systems. *American Naturalist* 139, 907-929.

HAMILTON, W.D. & ZUK, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science* 218, 384-387.

HAMMOND, P.M. (1992). Species inventory. In: Groombridge, B. (Ed.). *Global diversity, status of the earth's living resources.* London, UK, Chapman & Hall, pp. 17-39.

HOCHBERG, M.E., MICHALAKIS, Y. & DE MEEÛS, T. (1992). Parasitism as a constraint on the rate of life-history evolution. *Journal of Evolutionary Biology* 5, 491-504.

HOFFMAN, R.L. (1982). Diplopoda. In: Parker, S.P. (Ed.). *Synopsis and classification of living organisms.* New York, NY, USA, McGraw Hill, pp. 689-724.

HUGOT, J.-P. (1988). Les nématodes Syphaciinae parasites de rongeurs et de lagomorphes. Taxonomie. Zoogéographie. Evolution. *Mémoires du Muséum National d'Histoire Naturelle, Paris, Série A, Zoologie* 141, 1-153.

HUGOT, J.-P. (1999). Primates and their pinworm parasites: the Cameron hypothesis revisited. *Systematic Biology* 48, 523-546.

HUNT, D.J. (1996a). *Travassosinema thyropygi* sp. n. (Nematoda: Travassosinematidae) from a spirobolid millipede from Vietnam with SEM observations on *Heth imias* Spiridonov 1989 (Nematoda: Hethidae). *Fundamental and Applied Nematology* 19, 7-14.

HUNT, D.J. (1996b). A synopsis of the Rhigonematidae (Nematoda), with an outline classification of the Rhigonematida. *Afro-Asian Journal of Nematology* 6, 137-150.

LAMBSHEAD, P.J.D. (1993). Recent developments in marine benthic biodiversity research. *Oceanis* 6, 5-24.

LAROUSSE, P. (1874). *Grand dictionnaire universel du 19e siècle*, Paris, France, 986 pp.

LOEHLE, C. (1995). Social barriers to pathogen transmission in wild animal populations. *Ecology* 76, 326-335.

LUC, M., MAGGENTI, A.R., FORTUNER, R., RASKI, D.J. & GERAERT, E. (1987). A reappraisal of Tylenchina (Nemata)

1. For a new approach to the taxonomy of Tylenchina. *Revue de Nématologie* 10, 127-134.

MAY, R.M. (1988). How many species are there on the Earth? *Science* 241, 1441-1449.

MAYR, E., LINSEY, E.G. & USINGER, R.L. (1953). *Method and principles of systematic zoology*. New York, NY, USA, McGraw-Hill, 471 pp.

MEGLITSCH, P.A. & SCHRAM, F.R. (1991). *Invertebrate zoology (3rd edition)*. London, UK, Oxford University Press, 623 pp.

MORAND, S. & ARIAS GONZALEZ, E. (1997). Is parasitism a missing ingredient in model ecosystems? *Ecological Modeling* 95, 61-74.

MORAND, S., IVANOVA, E.S. & VAUCHER, C. (1996). *Dicelis keymeri* n. sp. (Nematoda: Drilonematidae) from the earthworm *Octalasium pseudotranspadanum* Zicsi. *Proceedings of the Helminthological Society of Washington* 63, 19-23.

MORAND, S. & POULIN, R. (1998). Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* 12, 717-727.

MOULÉ, L. (1911). La parasitologie dans la littérature antique. II. Les parasites du tube digestif. *Archives de Parasitologie* 15, 353-383.

PAGE, R.D.M. (1995). Parallel phylogenies: reconstructing the history of host-parasite assemblages. *Cladistics* 10, 155-173.

POINAR, G.O. JR (1977). *CIH keys to the groups and genera of nematodes parasites of invertebrates*. Farnam Royal, Slough, UK, Commonwealth Agricultural Bureaux, 43 pp.

POINAR, G.O. JR (1978). Associations between nematodes and oligochaetes (Annelida). *Proceedings of the Helminthological Society of Washington* 45, 202-210.

POULIN, R. (1995). Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monographs* 65, 283-302.

POULIN, R. (1996). How many parasite species are there: are we closest to answers? *International Journal for Parasitology* 26, 1127-1129.

POULIN, R. (1998). *Evolutionary ecology of parasites*. New York, NY, USA, Chapman & Hall, 212 pp.

RUBZOV, I.A. (1977). *Aquatic Mermithidae of the fauna of USSR. Volume 1* (Translated from Russian). New Delhi, India, Amerind Publishing Co., 280 pp.

RUDOLPHI, C.A. (1803). Neue Beobachtungen über die Eingeweidewürmer. *Archieven für Zoology und Zootomie, Braunschweig* 3, 1-32.

SASAL, P., MORAND, S. & GUEGAN, J.-F. (1997). Determinants of parasite species richness in Mediterranean marine fish. *Marine Ecology Progress Series* 149, 61-71.

STORK, N.G. (1993). How many species are there? *Biodiversity Conservation* 2, 215-232.

STRATHMAN, R.R. & SLATKIN, M. (1983). The improbability of animal phyla with few species. *Paleobiology* 9, 97-106.

WILSON, D.E. & REEDER, D.M. (1993). *Mammal species of the world. A taxonomic and geographic reference, 2nd edition*. Washington DC, USA, Smithsonian Institution Press, 1206 pp.

YAMAGUTI, S. (1961). Systema Helminthum. *Volume III, Part I: The nematodes of vertebrates*. London, UK, Interscience Publishers Ltd, 679 pp.