SYSTEMATICS OF ANIMAL PARASITES

Mariaux, Jean
Muséum d'histoire naturelle, CP 6434, CH-1211 Geneva, Switzerland

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Contents

Summary

Parasitic associations are extremely frequent, and parasitism as a mode of life has evolved in almost all groups of organisms. It is estimated that nearly half of the known animal taxa are parasitic during part or the whole of their life. Except for medical and veterinary aspects, this incredibly rich component of our biodiversity is little studied and most frequently omitted from surveys and inventories, despite its crucial role in the functioning of ecosystems. In this chapter, a systematic survey of animal (but not plant, unicellular or microbial) parasites is presented, reviewing both classical groups and lesser-known forms. No special emphasis is placed on veterinary, medical or otherwise economically important taxa, and all true parasite groups are presented globally. The most important of them are the Platyhelminthes (flatworms), including the flukes and tapeworms; the nematodes (roundworms); and the arthropods, including the insects, mites and crustaceans. Smaller groups, such as the acanthocephalans, gastropods, leeches and all other animal phyla with typical parasites, are also introduced. In most cases, a brief report of the taxon's characteristics and diversity is given, together with information on its peculiarities – anatomical or ecological - directly linked to its parasitic life-style. Some examples are also included. Particular emphasis is given to the taxonomic organization and the phylogenetic position of the cited organisms, with the aim of this work being an entry point for, and a reference source to, acquiring further information on animal parasites.

> "*But to a small subset of human beings parasites are glorious creatures, no less part of Darwin's tangled bank than organisms more acceptable to anthropocentric idealization.*"
> D. Brooks & D. McLennan, *Parascript*, 1993

1. Introduction and Scope

Parasitism has appeared many times during the course of animal evolution, and probably well over 100 times in the history of life (Poulin, 2011). Today, almost all of the recognized metazoan phyla include members that have selected parasitism as a mode of life. Thus, although parasites are often difficult to observe, they are in fact omnipresent, and much more diverse than usually suspected.

This contribution aims at surveying and briefly introducing this diversity, following the lines of biological systematics. In order to maintain some homogeneity, only animal parasites of other animals will be presented and other important groups of parasitic organisms, such as protozoans, fungi or plants, will not be considered here. Similarly phytoparasitic animals will also be excluded from this review.

In the same way, and despite the fact that biological categories are sometimes difficult to define precisely, only "true" parasites will be listed, and organisms with different types of symbiotic relationships, such as mutualists, will not be treated here.

The exact nature of a parasitic association is often difficult to establish, and despite our rather clear appreciation of the various types of symbiotic relationships known to occur (Poulin, 2011), the interpretation of many specific cases remain challenging. In this context, we define parasitism as a lasting heterospecific interaction in which one of the partners (the parasite) is dependent on the resources of the other (the host) (but see chapter 10). This interaction can last for the whole or only part of the parasite's life, and the resources offered by the host can be diverse, but the interaction will be at the physiological level (and not, for instance, merely phoretic).

As far as possible, a complete systematic survey of animal parasites will be presented, meaning that no special emphasis will be given to taxa of particular medical or veterinary significance. Even though economically important parasites are much better known than forms found in wild and poorly studied hosts, the latter are more numerous than the former. Obviously, a complete morphological description of each group goes far beyond the scope of this text; however, some information on important characters, either morphological or ecological (life cycles) associated with the taxa, are presented wherever deemed appropriate.

2. Zoological Classification and References

The major groups of animals (phyla) are rather well defined and hypotheses for explaining their evolutionary relationships in many cases exist. However, these hypotheses are, by nature, subject to constant refinements, making nomenclature instable. This is even truer for the relatively poorly known groups of organisms to which many parasites belong. As a consequence, no single nomenclatural reference can be used for all the taxa considered below, and appropriate references will be given for each of them separately.

As the aim of this text is to present a general overview of parasite diversity, we avoid giving details on lower taxonomic levels of the groups considered. In most cases only major taxa will be introduced and a few specific examples given. In accordance with good taxonomic practice, the authors of each taxon cited will be mentioned after its first occurrence.

3. Parasites Biology

Like all living organisms, parasites show a number of adaptations and specializations to their particular mode of life. These are extremely diverse and will not be detailed here.

It is however important to remember that these adaptations occur at both morphological and physiological levels. They can concern the locomotory (often reduced), attachment (often developed), digestive, sensorial or physiological (specialized) or immunological (efficient) systems, as well as, of course, reproduction. The latter is typically very efficient and frequently allows for a considerable production of eggs and/or juveniles. The most typical adaptation to parasitism is, however, in the selection of extraordinarily specialized, often complicated and sometimes surprisingly original life cycles (despite the fact that these life cycles can be reduced to a limited number of fundamental scenarios (Poulin, 2011)). One should indeed remember that the most challenging task of a parasite is to insure access to a new host for its descendants. The conjunction of this obvious goal and the constraints of a living environment have led to the development of various strategies, involving for example the use of additional hosts for the transmission of larval forms or even the induction of behavioral modifications in the hosts for increasing the reproductive success of the parasites. Many examples of both of these types of adaptations can be found in textbooks (e.g. Cheng, 1986; Bush et al., 2001) or in more specialized references (e.g. Combes, 2001; 2005; Poulin, 2007).

4. The Diversity of Animal Parasites

Some groups of animals, such as flatworms or roundworms are well known for their parasitic mode of life. This is especially so for the several representatives of these groups which commonly infest humans. Others, such as acanthocephalans, are only known by specialists, but are remarkable in their adaptations to parasitism and represent classical examples of obligatory parasites. Finally, some other groups, such as crustaceans or mollusks, which are well known for being free-living, have only a few lineages that have evolved a parasitic life style. Globally, parasitic taxa are known from almost all animal phyla and it is estimated that possibly a third to a half of the known animals are parasitic during a whole or part of their life. In term of parasitic species numbers, the most important groups are the Arthropoda (400,000), Platyhelminthes (>20,000) and the Nematoda (16,000). Other important groups are the Mollusca (7,000), the spiny-headed worms (Acanthocephala) (1,200) and the Annelida (1,000), whereas the remaining animal parasites are distributed in many other phyla (de Meeûs & Renaud, 2002; Chapman, 2009). These figures are obviously only minimal approximates, as neither the complete diversity nor the exact biology of most groups is known.

5. Platyhelminthes Gegenbaur, 1859

The flatworms form one of the major groups of parasitic animals. About 80% of the over 23,000 known species are parasites. Trematodes, tapeworms and monogeneans are exclusively parasites and represent the largest groups of flatworms. Together they form the Neodermata Ehlers, 1985, which is characterized by a number of ultrastructural features, especially a unique type of tissue covering the body of adults, i.e. syncytial neodermis. Besides these major groups of parasites, a few taxa among the free-living platyhelminths, the so-called "Turbellaria", have also evolved a parasitic life style. The higher systematics of flatworms is still a matter of contention; although most of the larger groups are identified, some of their relationships remain uncertain (Ehlers, 1985; Littlewood et al. 1999a; 1999b; Littlewood & Bray, 2001).

Flatworms are cosmopolitan and live in all type of habitats, but the majority are marine. Adults can be found on or in all groups of vertebrates, and their larvae use a diversity of vertebrates and/or invertebrates as intermediate hosts. A few groups of flatworms are especially well known because they parasitize humans; however, these are not really representative of the diversity of the phylum, as most parasitic platyhelminths are found in or on fishes.

5.1. Parasitic « Turbellaria »

The name 'Turbellaria' is commonly used for all non-neodermatan flatworms, although the group is widely recognized as being polyphyletic. This also usually implies that these non-neodermatan forms are free-living, which is not always the case, since several turbellarians exhibit various types of symbiotic association, the exact nature of which is often difficult to determine. The 'Turbellaria' consists of many lineages, to which we should add the acoels, whose systematic position is still very uncertain. Most of these lineages include some symbiotic forms, which are usually associated with marine invertebrates, such as echinoderms, crustaceans or mollusks. However, it is likely that only a few of them can be considered as true parasites, and even these exhibit little or no morphological modification associated with this life-style (Jennings, 1971). The systematics of the group is not fixed, but the system of Tyler et al. (2006-2010) is adopted here.

Acoela Uljanin, 1870. Whether these mysterious, very simple and tiny worms belong to the Platyhelminthes is contentious. They have been considered as an independent basal lineage within the Bilateria, flatworms and even a member of the Deuterostomia (Egger et al., 2009; Philippe et al., 2011). Several taxa are probably parasitic, or at least endocommensal, in sea urchins or echinoids. Some species are closely associated with corals (e.g. *Waminoa* Winsor, 1990), but their exact impact on their host is not clear.

Rhabdocoela Meixner, 1925. A number of families in this group harbor parasitic forms: the Graffillidae Graff, 1904 and Provorticidae Beklemischev, 1927 are parasites of lamellibranch mollusks and other flatworms. The Umagillidae Wahl, 1910 is a rather large group of more than 50 species, which are essentially associated with holothurians and echinoids. Many of them are considered commensals, but parasitism is known in some genera, such as *Syndesmis* François, 1886 in echinoderms. Specimens of the monotypic Acholadidae Hickman & Olsen, 1955 live encysted in a starfish.

Temnocephalida Blanchard, 1849. About 150 species are known. These small worms (a few mm long) are characterized by a posterior adhesive disc and anterior tentacles, which are obvious attachment organs. They live on freshwater crustaceans hosts, mostly in Australia and South America, but are also known to occur on mollusks and turtles. The nature of the interaction of temnocephalids with their hosts is unclear but most seem to be commensals rather than parasites.

Fecampiida Rohde, Luton & Johnson, 1994. These might be a sister group of the Neodermata. The Fecampiidae Graff, 1903 comprise three genera and about 20 species. All of them are endoparasites of crustaceans or annelids. Members of *Kronborgia* Christensen & Kanneworff, 1964 are unusual for turbellarians by being dioecious.

Prolecithophora Karling, 1940. Also known as the Alloeocoela, this group consists of a few marine parasitic forms in the families Cylindrostomatidae Reisinger, 1924 and Hypotrichinidae Bresslau, 1928. They are usually found in lamellibranchs, although species of *Ichthyophaga* Lesson, 1843 parasitize fishes.

5.2. Cestoda Rudolphi, 1808

The cestodes are exclusively endoparasites, lack a gut and consist of two subclasses: the smaller "Cestodaria" monozoic forms, with about 25 known species, and the much larger, Eucestoda (tapeworms or true cestodes) which are mainly segmented, with over 5,000 species. The latter is formed of about 16 orders (Khalil, Jones & Bray, 1994; Caira & Jensen, 2010). Cestodes infest all classes of vertebrates, except for primitive jawless fishes (Agnatha Cope, 1899). They are particularly diversified in bony fishes, selachians and homeotherms but less common in reptiles and amphibians. The phylogenetic classification of the group is still not fully resolved, despite many recent attempts. However, the present consensus is for the eucestodes from homeotherms to be derived within the class, whereas cestodarians and eucestodes from bony fishes are basal (Littlewood & Bray, 2001; Waeschenbach et al., 2007).

5.2.1. "Cestodaria"

The Cestodaria is a paraphyletic group retained here for the sake of convenience. It belongs to the Neodermata and is closely related to the true tapeworms. It comprises two small groups of fairly different animals: the Amphilinidea and the Gyrocotylidea. Both groups are small and of no economic importance. They share a typical ten-hooked larva (Rohde, 1994).

Amphilinidea Poche, 1922. Only 8 species are known. They are large unsegmented, leaf-like worms, reaching 10–30 cm in length. Amphilinideans possess an anterior attachment organ; parasitize the body cavity of chondrosteans (sturgeons), teleosts and turtles; and use crustaceans as intermediate hosts.

Gyrocotylidea Poche, 1926. This group comprises about 15 known species and are found in chimaeras (Holocephali). Gyrocotylideans possess an anterior muscular attachment organ and a posterior so-called "rosette". The unsegmented adult lives in the spiral intestine of the fish and can reach, in some species, more than 16 cm in length. Their larva is known as a lycophore, but their exact life cycle remains unknown

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Bibliography

Amin, O. M. (1987). Key to the families and subfamilies of Acanthocephala, with the erection of a new class (Polyacanthocephala) and a new order (Polyacanthorhynchida). *Journal of Parasitology* 73: 1216-9. [This is a concise and practical key of the acanthocephalans up to the subfamilial level, allowing for an overview of the taxonomic structure of the phylum].

Anderson, R. C. (2000). *Nematodes parasites of vertebrates: Their development and transmission*. CABI Publishing, Wallingford, UK. [The most important synthesis on life-cycles of nematodes of vertebrates].

Anderson, R. C., Chabaud, A. G. & Willmott, S. (2009). *Keys to the nematode parasites of vertebrates*. Archival volume. CABI Publishing, Wallingford, UK. [These keys are among the most used references for nematodes identification. They were initially published in separate volumes between 1974 and 1983].

Bleidorn, C., Podsiadlowski, L., Zhong, M., Eeckhaut, I., Hartmann, S., Halanych, K. M. & Tiedemann, R. (2009). On the phylogenetic position of Myzostomida: Can 77 genes get it wrong? *BMC Evolutionary Biology* 9: 150. [A discussion of the evolutionary relationships of myzostomids using a multi-genes approach].

Boeger, W. A. & Kritsky, D. C. (1993). Phylogeny and revised classification of the Monogenoidea Bychowsky, 1937 (Platyhelminthes). Systematic *Parasitology* 26: 1-32. [A major morphological revision of the monogeneans].

Boeger, W. A. & Kritsky, D. C. (2001). Phylogenetic relationships of the Monogenoidea. In Littlewood, D. T. J. & Bray, R. A. (Eds.). *Interrelationships of the Platyhelminthes*. (pp. 92-102). Taylor & Francis, London. [This paper discusses the family relationships of the Monogenea as well as the position of the class within the Platyhelminthes].

Boero, F. & Bouillon, J. (2005). Cnidaria and Ctenophora. In Rohde, K. (Ed.). *Marine parasitology*. (pp. 177-82). CABI Publishing, Wallingford, UK. [A short but well organized report on the diversity of parasitic sponges, listed by host group].

Boxshall, G. (2005). Copepoda, in Rohde, K (Ed), *Marine parasitology*. (pp. 123-138). CABI Publishing, Wallingford, UK. [A synthetic summary of the biology of parasitic copepods in a marine environment].

Bray, R. A. (2008). Introduction and key to superfamilies. In Bray, R. A., Gibson, D. I. & Jones A. (Eds.). *Keys to the Trematoda*. Vol 3. (pp. 1-5). CABI Publishing and Natural History Museum, London. [This chapter summarizes the taxonomic scheme retained in the 3 volumes of this series and offers a key to the major groups of trematodes].

Brooks, D. R. & McLennan, D. A. (1993). *Parascript. Parasites and the language of evolution*, Smithsonian Institution Press, Washington. [An essay on the comparative approach and the evolution of parasites].

Bush, A. O., Fernandez, J. C., Esch, G. W. & Seed, J. R. (2001). *Parasitism: The diversity and ecology of animal parasites*. Cambridge University Press, Cambridge. [One of the few recent textbooks with a comprehensive coverage of the field].

Caira, J. & Jensen, K. (2010). A survey of tapeworms of vertebrate bowels of the earth. h t t p s : / / s ites . google . com / site / tapewormpbi / home [Accessed Aug. 2011]. [This is the result of a worldwide and on-going collective effort to survey the diversity of cestodes].

Canning, E. U. & Okamura, B. (2004). Biodiversity and evolution of the Myxozoa. *Advances in Parasitology* 56: 43-131. [A reference to understand the evolution of the myxozoans, with detailed accounts of their biology and structure].

Chapman, A. D. (2009). *Numbers of living species in Australia and the world* (2nd ed.). Australian Biological Resources Study, Canberra. [This is one of the reliable synthetic sources for obtaining numerical biodiversity data. It is also available on line for free].

Cheng, T. C. (1986). *General parasitology*. Academic Press Inc., Orlando. [A very comprehensive textbook covering the diversity of parasites].

Chervy, L. (2002). The terminology of larval cestodes or metacestodes. Systematic *Parasitology* 52: 1-33. [This important paper is the result of a collaborative effort attempting to fix the terminology of cestode larvae].

Combes, C. (2001). *Parasitism: The ecology and evolution of intimate interactions*. University of Chicago Press, Chicago. [A fascinating survey of host-parasite interactions, and of parasites adaptations to their particular mode of life].

Combes, C. (2005). *The art of being a parasite*. University of Chicago Press, Chicago. [An excellent and easily readable essay on the biology of parasitism]

Crompton, D. W. T. & Nickol, B. B. (1985). *Biology of the Acanthocephala*. Cambridge University Press, Cambridge. [Although not very recent this book remains a reliable and complete source of information on acanthocephalans].

De Ley, P. & Blaxter, M. L. (2002). Systematic position and phylogeny. In: Lee, D. L. (Ed.). *The Biology of Nematodes*. (pp. 1-30). Taylor and Francis, London. [This contribution introduces a revised classification of the nematodes, based on morphological and molecular characters].

De Ley, P. & Blaxter, M. L. (2004). A new system for Nematoda: Combining morphological characters with molecular trees, and translating clades into ranks and taxa. *Nematology Monographs and Perspectives* 2: 633-653. [A development and update of the previous reference].

De Meeûs, T. & Renaud, F. (2002). Parasites within the new phylogeny of Eukaryotes, *Trends in Ecology and Evolution* 18: 247-251. [This is a very interesting contribution allowing us to appreciate the diversity and importance of parasites within animals and plants. Numerical data on their abundance are also provided].

Egger, B., Steinke, D., Tarui, H., De Mulder, K., Arendt, D., Borgonie, G., Funayana, N., Gschwentner, R., Hartenstein, V., B. Hobmayer, Matthew, H., Hrouda, M., Ishida, I., Kobayashi, C., Kuales, G., Nishimura, O., Pfister, D., Rieger, R., Salvenmoser, W., Smith, J., Technau, U., Tyler, S., Agata, K., Salzburger, W. & Ladurner, P. (2009). To be or not to be a flatworm: The acoel controversy. *Plos One* 4: e5502. [This paper is an attempt to place the acoels in the tree of life using a large dataset of new molecular and developmental characters].

Ehlers, U. (1985). *Das phylogenetische System der Plathelminthes*. Gustav Fischer Verlag, Stuttgart. [A major contribution to the systematics of flatworms and one of the first with a phylogenetic approach].

Franc, A. (1968), Sous-classe des Prosobranches, In Grassé, P.P. (Ed), *Traité de Zoologie. Tome 5. Fascicule 3. Gastéropodes et Scaphopodes.* (pp. 40-324) Masson et Cie, Paris. [This older reference is among the rare ones that contains a detailed account of the diversity of parasitic gastropods].

Gaud, J. & Atyeo, W. T. (1996). Feather mites of the world (Acarina, Astigmata): The supraspecific taxa. *Annales du Musée Royal de l'Afrique Centrale. Sciences Zoologiques* 277: 1-193. [A taxonomic reference for these little studied mites].

Gibbons, L. M. (2010). *Keys to the nematode parasites of vertebrates: Supplementary volume*. CABI Publishing, Wallingford, UK. [This volume complements the above-mentioned classical keys of Anderson et al (2009)].

Gibson, D. I., Jones, A. & Bray, R. A. (Eds.). (2002). *Keys to the Trematoda*. CABI Publishing and Natural History Museum, London. [The first of 3 volumes that represent a major multi-authors effort to describe the diversity of trematodes].

Hallan, J. (2005). Synopsis of the described Arachnida of the world. Texas A&M University. h t t p : / /i nsects . tamu . edu / research / collection / hallan / Acar i / 0ReportHi . htm [Accessed Aug. 2011]. [This very complete coverage of mites diversity is provided with estimates of species numbers. Each taxon is checked by a specialist and in most cases complete systematic references, including synonyms are provided].

Hallan, J. (2007). Synopsis of the described Nematoda of the world. Texas A&M University. h t t p : / / insects . tamu . e du / r esearch / collection / hallan / Nematoda / Family / 0 NematodaIndex0 . h tm [Accessed Aug. 2011]. [See above, equivalent entry for nematodes].

Hugot, J. P., Baujard, P. & Morand, S. (2001). Biodiversity in helminths and nematodes as a field of study: An overview. *Nematology* 3: 199-208. [A discussion on the diversity of helminths, including numerical data on their abundance].

Jennings, J. B. (1971). Parasitism and commensalism in the Turbellaria. *Advances in Parasitology* 9: 1-32. [One of the rare comprehensive reviews of these poorly studied organisms].

Kearn, G. C. (2004). *Leeches, lice and lampreys: A natural history of skin and gill parasites of fishes*. Springer, Dordrecht. [This original and very complete contribution focuses on the ectoparasites of fishes].

Khalil, L. F., Jones, A. & Bray, R. A. (1994). *Keys to the cestode parasites of vertebrates*. CABI Publishing, Wallingford, UK. [Since its publication, this book is the major reference on cestode diversity and systematics. The key goes down to the genus level].

Kuchta, R., Scholz, T., Brabec, J. & Bray, R. A. (2008). Suppression of the tapeworm order Pseudophyllidea (Platyhelminthes: Eucestoda) and the proposal of two new orders, Bothriocephalidea and Diphyllobothriidea, *International Journal for Parasitology* 38: 49-55. [A paper introducing the formal splitting of the classical Pseudophyllidea into 2 new taxa].

Littlewood, D. T. J. & Bray, R. A. (2001). *Interrelationships of the Platyhelminthes*, Taylor & Francis, London. [This book details the contributions presented during a major conference on the evolution of Platyhelminthes that was held in 1999 in London].

Littlewood, D. T. J., Rohde, K., & Clough, K. A. (1999a). The interrelationships of all major groups of Platyhelminthes: Phylogenetic evidence from morphology and molecules. *Biological Journal of the Linnean Society* 66: 75-114. [This is an attempt to understand the phylogeny of both the free living and parasitic flatworms. It uses various character sources, including molecular].

Littlewood, D. T. J., Rohde, K., Bray, R. A. & Herniou, E. A. (1999b). Phylogeny of the Platyhelminthes and the evolution of parasitism. *Biological Journal of the Linnean Society* 68: 257-287. [This paper deals with evolution of the flatworms, with an emphasis on their life-history].

Maggenti, A. (1981). *General nematology*. Springer-Verlag, New York. [A textbook that clearly introduces nematode biology].

Martin, J. W. & Davis, G. E. (2001). *An updated classification of the recent Crustacea.* Science Series, Natural History Museum of Los Angeles County 39: 1-132 [A reference checklist for crustaceans systematics].

Olson, P. D., Cribb, T. H., Tkach, V. V., Bray, R. A. & Littlewood, D. T. (2003). Phylogeny and classification of the Digenea (Platyhelminthes: Trematoda). *International Journal for Parasitology* 33: 733-55. [An important molecular phylogeny of the trematodes based on small and large rRNA genes].

Philippe, H., Brinkmann, H., Copley, R. R., Moroz, L. L., Nakano, H., Poustka, A. J., Wallberg, A., Peterson, K. J. & Telford, M. J. (2011). Acoelomorph flatworms are deuterostomes related to Xenoturbella. *Nature* 470: 255-8. [A new hypothesis on acoeles evolution and phylogenetic relationships].

Poulin, R. (2007). *Evolutionary ecology of parasites* (2nd ed.). Princeton University Press, Princeton, NJ. [This is an important contribution on the evolution of parasitism from an ecological perspective].

Poulin, R. (2011). The many roads to parasitism: A tale of convergence. *Advances in Parasitolology* 74: 1-40. [A synthetic overview on the evolution of parasites, including a comparison of their life cycles].

Price, R. D., Hellenthal, R. A., Palma, R. L., Johnson, K. P. & Clayton, D. H. (2003). *The chewing lice: world checklist and biological overview*. Illinois Natural History Survey Special Publication 24: 1-501. [This is a major reference for the group, with keys to the genera and a host-parasite checklist].

Riley, J. (1986). The biology of pentastomids. *Advances in Parasitology* 25: 45-128. [A complete review of our knowledge of the tongue worms, including taxonomical and phylogenetic aspects].

Rohde, K. (2005). *Marine parasitology*. CABI Publishing, Wallingford, UK. [This is a comprehensive coverage of the role and importance of parasites in the marine environment. Very complete and accessible, even for a non specialist].

Rohde, K. (1994). The minor groups of parasitic Platyhelminthes. *Advances in Parasitology* 33: 145-234. [This review summarizes an impressive amount of data on the lesser known groups of Neodermata and parasitic Turbellaria].

Rouse, G. W. (2005). Polychaeta (bristle worms). In Rohde, K. (Ed.). *Marine parasitology*. (pp. 193-6). CABI Publishing, Wallingford, UK. [A short account of the diversity and biology of parasitic polychaetes].

Tyler, S., Schilling, S., Hooge, M., & Bush, L. F. (2006-2010). Turbellarian taxonomic database. Version 1.6 h t t p : / / turbellaria . umaine . edu [Accessed Aug. 2011]. [An up to date reference on Turbellarian systematics].

Waeschenbach, A., Webster, B. L., Bray, R. A. & Littlewood, D. T. (2007). Added resolution among ordinal level relationships of tapeworms (Platyhelminthes: Cestoda) with complete small and large subunit nuclear ribosomal RNA genes. *Molecular Phylogenetics and Evolution* 45: 311-25. [The largest effort to date to elucidate cestode phylogeny with molecular characters].

Walter, D. E. & Proctor, H. C. (1999). *Mites: Ecology, evolution and behavior*. University of New South Wales Press and CABI Publishing, Wallingford, UK. [A very complete and easily accessible synthesis on the biology of mites].

Biographical Sketch

Jean Mariaux, born in 1960. Received MSc in 1984, PhD in 1991 both from the University of Neuchâtel, Switzerland. Postdoctoral researcher 1991-1992, Laboratory of Molecular Systematics, Smithsonian Institution, Washington D.C., USA. Currently Curator, Dept. of Invertebrates, Museum of Natural History of Geneva and Titular Professor, Dept. of Genetics and Evolution, University of Geneva, Switzerland.