



A proposed order-level classification in Oligochaeta (Annelida, Clitellata)

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Abstract

The purpose of our contribution is to propose a robust and practical order-level classification of the families of Oligochaeta, that is, non-leech Clitellata. The order level is mandatory in Linnaean rank-based classification and is also required in many internet-based biodiversity databases. However, it has received little attention in oligochaete systematics, and the few available order-level classifications of Oligochaeta no longer represent phylogenetic relationships adequately. Our proposal is based on corroborated molecular phylogenetic evidence and takes as benchmarks class level for Clitellata, subclass level for Oligochaeta and Hirudinea, and order level for Crassicitellata, the monophylum that includes most of the earthworm taxa. As a result, eleven orders are proposed: ALLUROIDIDA Timm & Martin, 2015; CAPILLOVENTRIDA Timm, **n. ordo**; CRASSICITELLATA Jamieson, 1988; ENCHYTRAEIDA Kasprzak, 1984; HAPLOTAXIDA Brinkhurst & Jamieson, 1971; LUMBRICULIDA Brinkhurst & Jamieson, 1971; MONILIGASTRIDA Brinkhurst & Jamieson, 1971; NARAPIDA Timm, **n. ordo**; PARVIDRILIDA Timm, **n. ordo**; RANDIELLIDA Jamieson, 1988; TUBIFICIDA Jamieson, 1978. This order-level classification is robust and easily adaptable to future insights into phylogenetic relationships.

Key words: Linnaean classification, order-level taxa, taxonomy, earthworms, aquatic oligochaetes

Introduction

Within the phylum Annelida, three major groups have traditionally been recognized, Polychaeta Grube, 1850, Oligochaeta Grube, 1850, and Hirudinea Savigny in Lamarck, 1818. From a phylogenetic point of view, Oligochaeta represents a derived lineage within Polychaeta (Struck *et al.* 2011), and the hirudineans have evolved from oligochaete ancestors (Michaelsen 1919). Hence, in phylogenetic classifications the first two groups are usually dismissed as paraphyletic; in handbooks and databases, however, Oligochaeta and Polychaeta are still maintained, from a perspective of evolutionary classification, or for reasons of practicality and tradition. Universally accepted is Clitellata (Michaelsen 1919), a monophyletic taxon that includes Hirudinea and all oligochaete taxa.

Oligochaeta was erected as an order (Grube 1850) and remained so for decades (e.g., Udekem 1855; Claparède 1862; Vejdvoský 1884; Beddard 1895; Michaelsen 1900, 1928; Stephenson 1930), with few exceptions (class level in Benham 1890 and Avel 1959). Its elevation to subclass level, below class Clitellata, by Brinkhurst and Jamieson (1971) was influential and widely followed. In contrast, the corresponding attempts of an order-level classification of subtaxa of Oligochaeta above family level (Avel 1959; Brinkhurst & Jamieson 1971; Brinkhurst 1982a,b; Timm 1981; Jamieson 1988) have remained controversial, and often the order level was simply ignored by systematists of Clitellata.

However, the order level is mandatory in Linnaean rank-based classification and is also required in taxonomic databases such as WoRMS (2021). Hence, the purpose of our contribution is to propose a robust and acceptable order-level classification of the families of Oligochaeta (= oligochaetous Clitellata), following three criteria: (1) We present order-level taxa that are monophyletic, as far as we know, and we accept non-monophyletic taxa only when the phylogenetic relationships are still unresolved. We attempt to represent as far as possible the most recent insights into Clitellata phylogeny (Erséus *et al.* 2020 and references therein). (2) The orders are supposed to represent meaningful and recognizable taxa. (3) We respect the general classificatory scheme of class Clitellata with subclasses Oligochaeta and Hirudinea such as appears in many internet sources on taxonomy or biodiversity (e.g., EoL, ERMS, wikispecies, WoRMS, see also Ruggiero *et al.* 2015a,b).

Our approach is motivated by the concern to deal with a situation that has become untenable given the most recent knowledge of phylogenetic relationships within Clitellata, and to take into account the requirements of current taxonomic databases. Our purpose here is therefore practical and not meant to cast the fine-grained phylogenetic branching pattern of Clitellata into a Linnaean hierarchical classificatory framework (comp. Jamieson 1988; see also Dubois *et al.* 2021). Actually, we have different opinions considering a future classification. Some of us hold that a phylogenetic classification should integrate the whole of Annelida, i.e., take into account the nested position of Clitellata within a subgroup (“Sedentaria”, Struck *et al.* 2011) of what still is named “Polychaeta” in spite of its evidently paraphyletic status, and that likewise “Oligochaeta” should be eliminated or considered synonymous with Clitellata. Others hold that Linnaean ranks are useful only in an evolutionary classification that allows paraphyletic groups, and that phylogenetic classification, to be effective, should abandon Linnaean ranks. That said, we all share an urge to resolve the problem of lacking an order-level classification of oligochaete Clitellata.

Historical account

The name Oligochaeta was first introduced by Grube (1850), for an order consisting of two families: Lumbricina and Naidea. Udekem (1855) and several subsequent authors accepted in general the taxon established by Grube, although sometimes with non-latinized names, while the number of families grew gradually. Oligochaeta was treated as a single order also in the monographs by Vejdovský (1884) and Beddard (1895). Michaelsen (1900) and Stephenson (1930) accepted the ordinal rank of Oligochaeta only by default, while dividing the group into (already numerous) families.

Michaelsen (1919) coined the class Clitellata, containing the two orders Oligochaeta and Hirudinea. Later, he subdivided Oligochaeta into the suborders Archioligochaeta (mostly small aquatic worms with chaetae variable in shape and number per bundle) and Neoligochaeta (mainly the earthworms plus some other taxa, all with simple, sigmoid and usually paired chaetae) (Michaelsen 1921). Ude (1929) rejected these two names referring to their unproven evolutionary sequence. Michaelsen’s dichotomous division of Oligochaeta was last used by Chekanovskaya (1981), who called the two orders Naidomorpha and Lumbricomorpha.

Later, Michaelsen (1929) suggested an alternative classification based on differences in the male reproductive apparatuses, in particular the position of the male pores in relation to the testes. This led to three suborders, named Oligochaeta plesiopora, Oligochaeta prosopora, and Oligochaeta opisthopora. The first group included the majority of smaller, often aquatic, oligochaetes with *male pores in the segment behind the testis segment* (the “plesiopore” condition); the second consisted of the single, aquatic, family Lumbriculidae, with *male pores within the testis segment* (“prosopore” condition); and the third group comprised the earthworms plus a few aquatic taxa, with *male pores several segments posterior to the testis segment(s)* (“opisthopore” condition). Stephenson (1930: 718ff.) considered these attempts to classify Oligochaeta above the family level unnecessary and not sufficiently backed by phylogenetic evidence; he listed the families directly below the order Oligochaeta without intergrading ranks. Avel (1959) accepted Michaelsen’s (1929) version with modifications: Oligochaeta was raised to a class, the suborders to orders, and the plesiopore group was subdivided, based on differences in the position of the spermathecae, leading to four orders, in scientific French: Plésiopores plésiothèques, Plésiopores prosothèques, Prosopores, and Opisthopores (Avel 1959). It should be noted that these classifications were meant to represent phylogenetic relationships, albeit not in a cladistic, Hennigian sense.

Brinkhurst (1971, 1982a,b, 1984) proposed a phylogenetic scenario of oligochaete taxa based on a hypothesized octogonadal ancestor with a plesiopore male reproductive system. (“Octogonadal” means two pairs of testes and

two pairs of ovaries in four consecutive segments.) From this condition, still present in some species of Haplotaxidae, all other conditions were considered to be derived. Based on this scenario, the first classification (Brinkhurst & Jamieson 1971; Brinkhurst 1982a) united all plesiopore and opisthopore taxa (i.e., those with male pores at least one segment posterior to the testes) in one order, Haplotaxida. It contained the bulk of all oligochaetes, small and large, aquatic and terrestrial. Two further orders were created for species with prosopore male pores (i.e., male pores and testes in the same segment), these were the aquatic Lumbriculida and the terrestrial Moniligastrida; the latter are earthworm-like forms much different from Lumbriculida. Later, Brinkhurst (1982b, 1984) reorganized the oligochaete taxa in four orders, Haplotaxida (now containing only Haplotaxidae), Lumbriculida (as before, with the single family Lumbriculidae), Tubificida (the bulk of small aquatic oligochaetes plus the amphibious Enchytraeidae), and Lumbricida (all earthworms plus Moniligastrida and the only opisthopore aquatic family, the Alluroididae). As a sidenote, Aeolosomatidae was excluded from Oligochaeta by Brinkhurst (1982b).

Timm (1981) also proposed a four-order classification of oligochaetes (without aeolosomatids, branchiobdellidans and leeches): Tubificida (corresponding to Naidomorpha sensu Chekanovskaya), Haplotaxida [consisting of Haplotaxidae, Alluroididae and the numerous earthworm families later recognized as the monophylum Crassicitellata (Jamieson 1988)], Moniligastrida and Lumbriculida (both with a single, nominate family). This was a combination of the systems of Brinkhurst and Jamieson (1971) and Chekanovskaya (1981). The leading hypothesis here was that the tubificidan (“naidomorph”) line with their diverse chaetae could not have descended from haplotaxid-like ancestors with paired chaetae, the latter considered as a synapomorphy of the “lumbricomorph” groups. Kasprzak (1984) adopted Timm’s proposal but placed two families, Enchytraeidae and Dorydrilidae, into respective orders of their own.

Jamieson (1988) presented and discussed in full detail a phylogenetic classification using Linnaean ranks. The underlying tree was the result of a morpho-cladistic analysis. The large asymmetry of the tree resulted in a high number of ranks, including subclasses, superorders, suborders, cohorts and superfamilies, which are not covered here. The number of orders in Jamieson’s system reached five: (1) Randiellida, with a single genus of uncertain position, and in sister-group position to the rest of the clitellates (as sub-class Randiellata), (2) Tubificida, including the bulk of aquatic families (then: Capilloventridae, Phreodrilidae, Tubificidae, Naididae, Opisthocystidae, Dorydrilidae) and the Enchytraeidae, (3) Lumbriculida, (4) Moniligastrida, and (5) Opisthopora (Alluroidina plus Crassicitellata, the latter including most of the earthworm families). The families Haplotaxidae and Tiguassidae were united in a presumably paraphyletic superorder Haplotaxidea, but an order rank taxon was not erected. Later, the same author integrated new insights of molecular phylogenetic analyses (Jamieson 2006) and presented a revised cladistic classification of Clitellata with indentations and symbols instead of Linnaean ranks to represent the hierarchy of taxa (ibid.: 260ff.). In a following chapter (ibid., 293 ff.), four orders were recognized, Tubificida, Haplotaxida *sensu stricto*, Moniligastrida, and Opisthopora; order level was not assigned to Randiellata and Lumbriculata, the latter a taxon with Lumbriculidae and Hirudinea as sister groups (Jamieson 1988).

Curiously, it was the three-order system (Brinkhurst & Jamieson 1971; Brinkhurst 1982a) that was used in databases like WoRMS (2021), where the order level is mandatory. However, this system is impractical and outdated. It unites many divergent families into one mega-order Haplotaxida, with the subsequent need to create sub-ranks such as suborders and super-families. Furthermore, it no longer represents phylogenetic relationships adequately (see below); this, however, is also true of the other proposals (Chekanovskaya 1981; Timm 1981; Brinkhurst 1982b, 1984; Kasprzak 1984; Jamieson 1988; Jamieson 2006). Modern authors usually ignore the order level and the corresponding taxa, such as Haplotaxida sensu Brinkhurst & Jamieson (1971); oligochaetes under study are introduced as, for example, “Oligochaeta: Naididae” (Corbi *et al.* 2015) or “Annelida, Clitellata, Tubificinae” (Ohtaka & Martin 2011). In general, the family level has always been less problematic and more explanatory than the order level in oligochaetous Clitellata.

Results and discussion

Molecular phylogenetic studies have greatly advanced our understanding of the phylogenetic relationships of oligochaete taxa. Figure 1 illustrates the current understanding of phylogenetic relationships among families of oligochaetous Clitellata, based on a recent phylogenomic study (Erséus *et al.* 2020). With the exception of Haplotaxidae, all families shown are currently considered as monophyletic, and so is Crassicitellata, the taxon that includes the

numerous families of true earthworms (21 families in Magalhães *et al.* 2021, not listed here). Our proposal of order-level taxa in Oligochaeta is based on this tree, with the accepted order-level of Crassicitellata as benchmark. The proposal is further conditioned by the asymmetric tree topology and the derived position of Crassicitellata, which together leads to a system where each order comprises not more than one or two families. As a sidenote, it should not go unnoticed that the tree in Erséus *et al.* (2020) neatly reflects the early concept of Archiologochaeta and Neologochaeta (Michaelsen 1921, 1928), with the latter nested in the former.

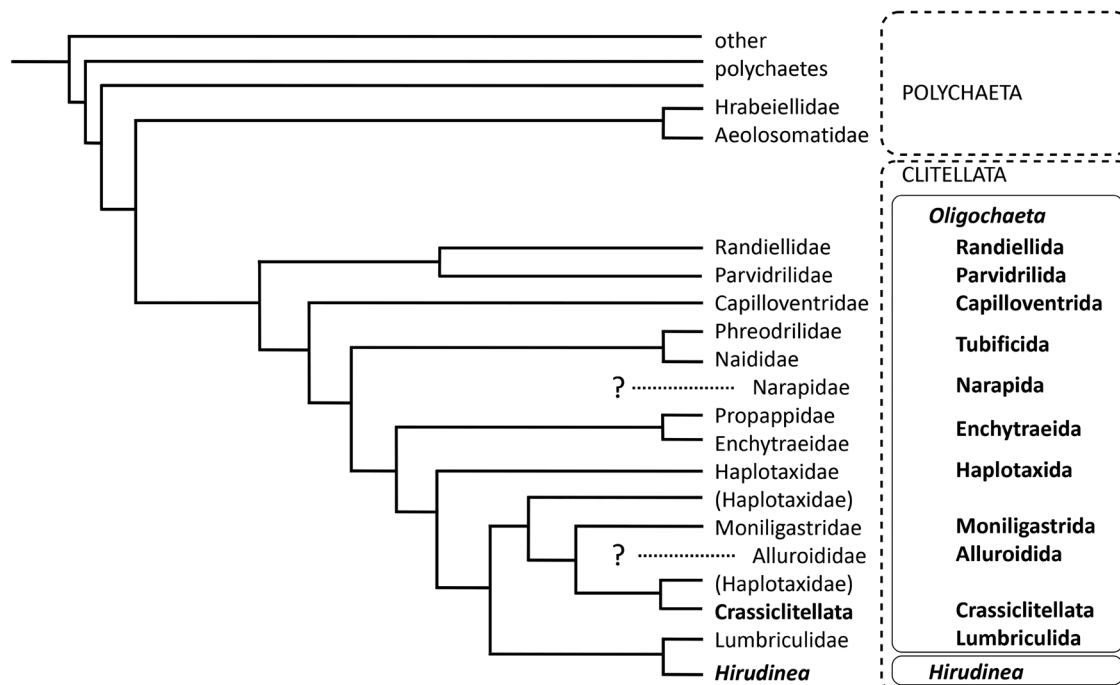


FIGURE 1. Phylogenetic relationships of families of Oligochaeta (=oligochaetous Clitellata), schematized after Erséus *et al.* (2020), and corresponding proposals of order-level taxa, printed in bold regular. Taxa with question mark were not investigated in Erséus *et al.* (2020) for lack of DNA data. Broken line boxes and words in capital letters: class level, continuous line boxes and words in bold italics: subclass level. The polyphyletic Haplotaxidae appears three times; the name without brackets represents the position of the type species, *Haplotaxis gordioides* (Hartmann in Oken, 1819). For further explanations, see text.

Closely related to Crassicitellata are five families, Moniligastridae, Alluroididae, Haplotaxidae, Tiguassuidae, and Syngenodrilidae. The latter two are not shown in Fig. 1. Haplotaxidae is polyphyletic (Erséus *et al.*, 2020) and will be split into different families (Martinsson *et al.*, forthcoming). Closely related to Haplotaxidae is the monospecific Tiguassidae, but DNA data are not yet available. Moniligastridae are earthworms that lack the opisthoporous male pore condition and also a multi-layered clitellum, the latter an apomorphy of Crassicitellata. Alluroidids are opisthoporous aquatic worms, similar in other respects to some taxa of Haplotaxidae; each is placed in an order of its own here. Syngenodrilidae, representing one species, which itself was described on a single specimen (Smith & Green 1919), has been associated with either Moniligastridae (Stephenson 1930) or Alluroididae (Michaelsen 1928; Brinkhurst & Jamieson 1971). Molecular data of Alluroididae and Syngenodrilidae are lacking; the latter is provisionally included in Alluroidida here.

Lumbriculidae, a species-rich group of prosoporous aquatic oligochaetes, is the sister-group of Hirudinea (Martin 2001), the latter a taxon considered to include three orders, the true leeches, named Hirudinida (Siddall *et al.* 2001), and the leech-like Acanthobdellida and Branchiobdellida; the latter was previously accommodated in Oligochaeta. The fact that taxa of different rank are sister-groups (order Lumbriculida and subclass Hirudinea) is odd from a perspective of phylogenetic (= cladistic) classification but acceptable in evolutionary classification (see Mayr & Ashlock 1991: 122), and maintained here for practical reasons. Included in Lumbriculida is the monotypic Dorydrilidae, a doubtful family with close but unresolved relationships to Lumbriculidae. Hrabě (1984) includes *Dorydrilus* in Lumbriculidae, a view supported by molecular data (Achurra *et al.*, forthcoming).

Enchytraeidae is a species-rich and ubiquitous taxon whose monophyly has been confirmed (Erséus *et al.* 2010a). The few species of the monotypic Propappidae were initially considered as primitive aquatic members of Enchytraeidae (Michaelsen 1916, 1928) but later accommodated in a family of their own (Coates 1986). The sister-group relationship of Propappidae and Enchytraeidae (Marotta *et al.* 2008) does not have strong molecular support (Erséus *et al.* 2020) but both families share a distinctive character, an extreme forward-shift of the spermathecae. As a sidenote, this character was reflected in Avel's (1959) "Plésiopores *prosothèques*" (italics by us).

Naididae as represented in Fig. 1 is a mega-taxon of aquatic oligochaetes, result of the fusion of the two species-rich families Naididae and Tubificidae into one family after recognizing that the former was polyphyletic, the latter paraphyletic, and that both together are monophyletic (Envall *et al.* 2006); the new comprehensive family, into which later the species-poor Opistocystidae were fused as well (Erséus *et al.* 2010b), received the name Naididae for reasons of nomenclature (Erséus *et al.* 2008). However, some systematists maintain Tubificidae in their traditional circumscription and accommodate the rest of Naididae *sensu* Erséus *et al.* (2008) in four different families (see below). The sister-group relationship of Phreodrilidae and Naididae *s.l.* (i.e., *sensu* Erséus *et al.* 2008) is supported by similarities of the male reproductive apparatuses.

Three small aquatic oligochaete families, each with a single genus, are very different genetically and in the structure of their reproductive system, and they are now considered as derived from the ancient clitellate stem (Erséus *et al.* 2020): Capilloventridae, Parvidrilidae (both bearing dorsal hair chaetae like most Tubificida, but also ventral, a unique feature among oligochaetes) and Randiellidae (externally resembling Enchytraeidae). The monospecific family Narapidae is another taxon of unclear position; it has simple genitalia (possibly a derived feature) and lacks chaetae, but molecular data are unknown. Each of these families deserves establishment of a separate nominal order, which so far has been formally proposed only for Randiellidae (Jamieson 1988). We suggest order level also for Parvidrilidae, even though it may form a monophyletic group with Randiellidae (see Erséus *et al.* 2020, p. 625); both families are very different in the reproductive structures and chaetal equipment (comp. Erséus & Strehlow 1986; Martínez-Ansemil *et al.* 2012).

Proposal of order-level classification of Oligochaeta. In formal faunistic databases such as WoRMS; World Distribution of the Aquatic Oligochaeta (Timm 2021), etc., one must find all taxa in their "boxes" at the main levels of the taxonomic hierarchy. We propose the following, practical system of the subclass Oligochaeta (= oligochaetous Clitellata) with 11 orders (in alphabetic order here), most of them consisting of small and aquatic worms. The numerous families of the order Crassicitellata (majority of the earthworms, see James & Davidson 2012; Magalhães *et al.* 2021), are not listed here. Dates of authorship of some families have recently been corrected (Van Haaren *et al.* 2021), following the rules of ICZN (1999). At the order level, where the rules of ICZN do not apply, authorship and date refer to the reference where, to the best of our knowledge, for the first time a taxon has been erected at order level with the spelling as given below.

Alluroidida Timm & Martin, 2015

Family Alluroididae Michaelsen, 1900 (amphibious, mainly freshwater)

Family Syngenodrilidae Smith & Green, 1919 (terrestrial?; one genus, one species)

Capilloventrida Timm, *n. ordo*

Family Capilloventridae Harman & Loden, 1984 (freshwater, marine)

Crassicitellata Jamieson, 1988

at least 21 families of true earthworms (mostly terrestrial)

Enchytraeida Kasprzak, 1984

Family Propappidae Coates, 1986 (freshwater)

Family Enchytraeidae d'Udekem, 1855 (mostly terrestrial, also freshwater, marine)

Haplotaxida Brinkhurst & Jamieson, 1971

Family Haplotaxidae Michaelsen, 1900 (freshwater, polyphyletic)

Family Tiguassidae Brinkhurst, 1988 (freshwater, one genus, one species)

Lumbriculida Brinkhurst & Jamieson, 1971

Family Lumbriculidae Claus, 1872

(including also the former Dorydrilidae Cook, 1968—mostly freshwater; sister group of the subclass Hirudinea Savigny in Lamarck, 1818; the latter with orders Acanthobdellida Livanow, 1905, Branchiobdellida Holt, 1963 and Hirudinida Siddall *et al.*, 2001)

Moniligastrida Brinkhurst & Jamieson, 1971

Family Moniligastridae Claus, 1880 (terrestrial and earthworm-like)

Narapida Timm, **n. ordo**

Family Narapidae Righi & Varela, 1983 (freshwater, one genus, one species)

Parvidrilida Timm, **n. ordo**

Family Parvidrilidae Erséus, 1999 (freshwater, one genus)

Randiellida Jamieson, 1988

Family Randiellidae Erséus & Strehlow, 1986 (marine, one genus)

Tubificida Jamieson, 1978

Family Naididae Ehrenberg, 1831

*Family Pristinidae Lastočkin, 1921

*Family Opistocystidae Černosvitov, 1936

*Family Tubificidae d'Udekem, 1855

Family Phreodrilidae Beddard, 1891

* included in Naididae s.l. in phylogenetical classification (see Erséus *et al.* 2008)

Side note. As a result of literature studies, authorship of the following taxon names was changed as follows (see also Van Haaren *et al.* 2021): Hirudinea Savigny in Lamarck, 1818, previously cited as Hirudinea Lamarck, 1818 or Savigny, 1822. *Haplotaxis gordioides* (Hartmann in Oken, 1819), previously cited as *Haplotaxis gordioides* (Hartmann, 1821).

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