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Whither Octochaetidae? - A review of its family status (Annelida: Oligochaeta)

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SUMMARY. Morpho-molecular evidence, based on recent rDNA analyses, is advanced for the phylogenetic retention of earthworm families Acanthodrilidae, Octochaetidae, Exiidae, and Megascolecidae *sensu* Blakemore (2000). Other options that receive some support are for the revival by Csuzdi & Zicsi (1994) of Benhamiinae Michaelsen, 1895/7 separate from meroic Octochaetidae Michaelsen, 1900, and possible restoration of Diplocardiinae Michaelsen, 1899 separate from holoic Acanthodrilidae Claus, 1880, both perhaps meriting elevation to family level. A terminal taxon, likely derived from Octochaetidae and defined by its further attainment of non-tubular prostates, is Caribbean Exxidae Blakemore, 2000. Resolution of the status or taxonomic rank within Megascolecidae Rosa, 1891 of North American tribe Argilophilini Fender & McKey-Fender, 1900 requires more information than is presently available. Alternatively, all these families may be cladistically telescoped into the basal Ocnodrilidae Beddard, 1891, although this would be 'uninformative' under the Code (ICZN, 1999) that "*may be equally applied to paraphyletic as to monophyletic groups*". Unlike all other groups that are 'acanthodriline', membership of Megascolecidae *s. stricto* depends upon possession of 'megascolecine' male pores, irrespective of character states of prostates, nephridia, guts, or setae. However, logically and tautologically, any morphological modification from an ancestral plesiomorphic state to a "transitional" or intermediate stage is naturally classed as a derived apomorphy. A new key is provided. [Keywords: Molecular-morphological phylogeny, Megascolecidae, Acanthodrilidae, Exxidae].

INTRODUCTION

"The family-level classification of the megascolecoid earthworms is in chaos"

[Fender & McKey-Fender (1990: 369) - for an overview of the dispute, these authors cite conflicting schemes of Gates (1959), Jamieson (1971), and Sims (1980)].

"Much breath and paper has been largely wasted arguing the appropriate rank of a group" [www.palaeos.com/Vertebrates/Lists/Cladograms/000Cladograms.html 2005]

The purpose of the current review is to explore options for consensus, using both deductive (morphological) and objective (molecular) evidence, in an historical and taxonomic context, of the suborders Lumbricina + Moniligastrida that may consist of fewer than 7 to greater than 20 families under various classifications currently espoused (see Reynolds & Cook, 1976: 1-2; 1981: 1; 1989: 1; 1993). Taxonomists have no general agreement about the composition of the superfamily MEGASCOLECOIDEA and most controversy revolves around elucidation and boundaries of Acanthodrilidae, Octochaetidae, and Megascolecidae.

Under the "Classical System" of Michaelsen (1900; 1921), which was largely confirmed yet simplified by Stephenson (1930), a megadrile section, consisting of earthworms corresponding to the suborder Lumbricina, resolved into 14 sub-families with the Megascolecidae comprising Acanthodrilinae, Megascolecinae, Octochaetinae, Ocnerodrilinae and Diplocardiinae. Working in New Zealand, Lee (1959) mostly recognized Stephenson's (1930) definitions but divided the Megascolecidae into just two subfamilies: the Acanthodrilinae (including the Ocnerodrilidae and Octochaetinae) with an 'acanthodriline' arrangement of male and prostatic pores, and the Megascolecinae with a 'megascolecine' arrangement i.e., one pair of male and prostatic pores united on 18 (irrespective of prostate form). However, Gates (1959: 257) refuted Lee and, despite being a constant critic of the Classical system, proposed a revised scheme in partial agreement with Michaelsen (1921) which re-elevated four of Stephenson's subfamilies to familiar status (all except Diplocardiinae). Despite sparse ontogenetical evidence of their supposed mesodermal origin, Gates (1959: 240) permitted only 'truly' racemose prostates in the Megascolecidae and he excluded all other non-racemose species, those "*with tubular glands, regardless of presence or absence of lateral branches from the axial lumen*", went into his (holoic) Acanthodrilidae and (meroic) Octochaetidae. Such interpretation was largely supported in a refined form by Sims (1966; 1980; 1982) using phenetic computer analyses and incorporating morphology of the ovaries, as initially proposed by Gates (1976), to ultimately advocate Ocnerodrilidae, Acanthodrilidae, Octochaetidae and Megascolecidae as separate taxa.

Gates' (1959) system as adopted by Sims (1980), was accessible and 'convenient', and appeared to have been widely accepted as the most pragmatic option (e.g. Parker, 1982; Easton, 1981: 35; 1984: 111; Sims & Gerard, 1985: 41; 1999, etc.). Yet it was found limited and flawed by several workers involved in revisions of species from various world families, including Blakemore (1994; 1997; 1999; 2000).

An intervening scheme, proposed by Jamieson (1971 and subsequently)

working from southeast Queensland, mainly just criticized Gates' obviously flawed system and was dismissive of differences in prostate form. Yet it too was restricted and based on syllogisms that allowed a relatively few actual instances of detailed descriptions of nephridial arrangements to account for placement of whole groups and to subsume three subfamilies (Ocnerodrilinae, Acanthodrilinae and Megascolecinae) into the Megascolecidae, sub-divided at tribal level on ultrastructural details of excretory nephridial structures. This scheme was critiqued and rejected in whole or part by several workers around the world (e.g. Easton, 1979; Sims, 1980; Sims & Gerard, 1985, 1999; Julka, 1988: 5, 368; Fender & McKey-Fender, 1990; Dyne & Wallace, 1994: 61; Reynolds & Righi, 1994; Csuzdi & Zicsi, 1994; Csuzdi, 1996: 349; Plisko, 2004; Wetzel, 2003, 2004), and presumably by any other authors citing either Octochaetinae/idae or Acanthodrilidae at the family level.

Rejection was due partly to its being based on negative (i.e., absent), or on seemingly "adaptive" characteristics of the nephridial system which are not only difficult to demonstrate as admitted by Jamieson (1974: 211), especially when absent, and which Easton (1979: 9, 17-18) and Sims (1980: 105) showed to be hampered by the paucity of available information for most species; and due partly to "artificial" groupings that incompatible with zoogeographical knowledge (e.g. Sims, 1980: 105; 1982: 284). Moreover, because the finer nephridial details of most species described from around the world are not known, and because determination of such details would now be difficult, if not impossible, to obtain (Gates, 1959: 252, 258; 1972: 24; Sims, 1980: 105), this scheme was impractical, did little to provide clarity, and was also found to have gross morphological groupings that were not mutually exclusive (e.g. Blakemore, 1994). Eventually, conclusive molecular analyses were applied that put the final "nail in the coffin" and, after 30 odd years, it was accepted by Dyne & Jamieson (2004) that their sub-familiar (or what they called suprageneric) tribal divisions were "*obsolete or restricted*" being based on "*highly homoplastic apomorphy of meronephridia*".

Throughout, Reynolds & Cook (1976; 1981; 1989; 1993) had maintained Acanthodrilidae, Octochaetidae, and Megascolecidae separately, but their concept differed to that of Michaelsen. These authors further combined Almidae (plus Biwadrilidae and Lutodrilidae?) in Criodrilidae, cited a dubious family "Diporochoetidae" [actually a lapsus for Lumbricidae (sub-)family Diporodrilidae Bouché, 1970], and added Lobatocerebridae Rieger, 1980 (mispelt and misattributed as "Labatocerebridae Reiger") that is, however, a Polychaeta. Monotypic Syngenodrilidae that is more often placed within the microdrile superfamily Alluroidoidea was omitted, but Alluroididae (misspelt "Allyroididae") was

retained under Lumbricina by Reynolds & Cook (1976: 2). These authors consistently endorsed Gates' pragmatic and 'convenient' incorporation of taxa with similar characteristics into family groupings in preference to Jamieson's contrived scheme.

However, one exceptional and “troublesome” species, *Exxus wyensis* Gates, 1959, disrupted an otherwise workable templet. This meroic species with an acanthodriline arrangement of male and prostatic pores complied with the Octochaetidae but, because it had racemose prostates, Gates (1959: 258) allowed it to introduce the acanthodriline state into his redefinition of the Megascolecidae, whereas Jamieson (1971) allowed it to introduce racemose prostates into his redefinition of the Acanthodrilidae. Neither of these options is acceptable.

Thus, Blakemore (1994; 1999; 2000) was obliged to independently re-evaluate the Classical concept of Acanthodrilidae and Megascolecidae and to maintain both separately depending primarily on the forms of the male pores and reproductive organs, and secondarily on the type of nephridia, while extracting from the Octochaetidae (or either of the previous two families where it had been artificially submerged by disparate authors) the genus *Exxus* that was placed in a new Neotropical family, Exxidae Blakemore, 2000, presently (Blakemore in prep.) comprising about nine species in two or three genera (see [Tab. 1](#)).

Contemporary revisions of the Octochaetidae by Csuzdi & Zicsi (1994), Csuzdi (1996; 1997; 2000) and Plisko (2004) re-established three subfamilies of Acanthodrilidae comprising an holoic Acanthodrilinae, and meroic Octochatinae plus Benhamiinae, with the latter sub-family having 2-3 pairs of extramural calciferous glands after segment 14. A review by James (2004a: 54, 55; fig. 3.1) retained Acanthodrilidae separately from Megascolecidae but, since neither Blakemore nor Csuzdi were cited, it is assumed this was based on Gates' (1959) now defunct concept rather than the more modern view. Recent additions to the family were proposed by Borges & Moreno (1991), Rodrigues & Fragoso (2002), Julka *et al.* (2004, 2005), and by James (2004b: 277 citing "Acanthodrilidae" in the title, "Megascolecidae" on page 278 yet describing *Dichogaster* species that belong in either Benhamiinae and/or Octochaetidae), similarly with these other papers it is unclear which version of "Octochaetidae" or "Acanthodrilidae" is supported. Moreover, a web-search for either taxon will yield several hundred hits, serving to demonstrate the lack of consensus for an inclusive Megascolecidae and, at the same time, illustrating the lack of stability and universality at family level for Oligochaeta systematics as required by ICZN (1999) that regulates taxonomic nomenclature from the sub-specific to the super-family levels.

METHODS

This review is based on surveys of the literature and reappraisal of recent morphological and molecular analyses, particularly by Blakemore (2000; 2002; 2005), Csuzdi (1994; 1996), Siddal *et al.* (2001), Plisko (2004), and Dyne & Jamieson (2004). Results are interpreted in a phylogenetic context under the requirements and recommendations of ICZN (1999). The inherited and current situation is presented, and options for future solutions are proposed and briefly discussed.

Previous classification schemes have tended to assume that presence of morphological states intermediate, or "transitional" between plesiomorphic (i.e., ancestral) and apomorphic (i.e. derived) lessen the facility by which some groups may be precisely divided. Whereas, under the present system, as initially advocated by Michaelsen (1907) and as supported by Blakemore (1994; 1999; 2000), choice is simplified by accepting that the logical and tautological division is really between plesiomorphic and "non-plesiomorphic" states. Thus the justifiable and pragmatic rationale behind the current and progressive species, genus, and family reviews is that ancestral states - those known to occur in 'primitive' taxa, such as tubular prostates (i.e., gland elongate with simple unbranched central), holoic nephridia (i.e., two per segment), and lumbricine setae (i.e., eight per segment), are considered plesiomorphic and **any derivation** from these are apomorphies (see also Stephenson, 1930: 711). This approach is strengthened, as reversion mutations back to 'primitive' states are not known to occur in earthworms. Even the supposed homoplastic reduction to a single pair of merioic 'micronephridia' in *Ramiella bishambari* (Stephenson, 1914) determined by Stephenson (1923: 397; 1930: 213, 233) were subsequently found by Gates (1972: 312) to be more numerous: in two or more ranks on each side in postclitellar segments.

Whereas the reproductive organs (that ensure propagation of species) are most definitive and relatively conservative, the "*well known dependence of the conformation of the alimentary tract on food and environment*" (Stephenson, 1930: 720) means that the degree of development of gizzards, calciferous glands, and of intestine often take secondary rank. Other bodily support organs such as the excretory nephridia are likely to be environmentally adaptive; for example, we observe nephridial reduction in species that secondarily acquire an aquatic habitat, and can anticipate opposite changes to conserve moisture (e.g. enteronephry, meronephry) in species subjected to desiccation. Thus, for *a priori* classification, the acanthodriline (and homologous microscolecine or balantine states) are plesiomorphic to the derived "non-acanthodriline", i.e.

megascolecine state; and states of prostates, nephridia, and guts are subordinate.

RESULTS

Rather restricted molecular phylogeny data by Dyne & Jamieson (2004), summarized here (Figs. 1 and 2), and conventional morphological considerations clearly support elevation and retention of Megascolecidae (viz. *Pontodrilus* through to *Amyntas*) separate from Acanthodrilidae (*Diplotrema* / *Diplocardia*) plus Octochaetidae. Moreover, division of holoic Acanthodrilidae and meroic Octochaetidae groups, the latter represented by genera *Octochaetus* and *Dichogaster* respectively for Octochaetinae Michaelsen, 1900 and Benhamiinae Michaelsen, 1895/7 (with nomenclatural priority deferred under ICZN, 1999: Art. 35.5 Example), appears justified. Elevation from within Octochaetidae of a family Exxidae Blakemore, 2000 for taxa with derived non-tubular prostates, seems reasonable on morphological grounds alone. The information is equivocal, but resurrection (and elevation?) of Diplocardiinae (*Diplocardia*) from within the Acanthodrilidae is not unsupported by the limited data available (Fig. 2 and [Tab. 2](#)). Overall, Ocnerodrilidae (*Eukerria*) is seen as a basal group, or most ancestral, of the taxa under consideration here.

The current system appears a natural progression from the Classical systematics of Michaelsen (1900), Stephenson (1930), and of Lee (1959), whereas intervening taxonomic schemes (of Gates and Jamieson) were diversionary - having unnatural groupings forced by overemphasis on details of prostates and/or adaptive (and often absent) ultrastructural minutiae of the nephridia; neither tenable on present results. Phylograms and tables (Figs. 1, 2; Tabs. 1, 2) present summaries and options for further resolution. A revised key to families and summary classifications are given in Appendices.

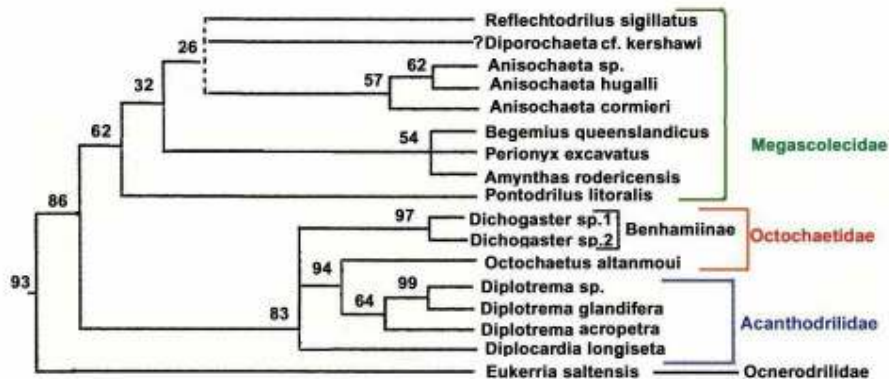


Fig. 1. Phylogram based on molecular analyses (modified and relabelled after Dyne & Jamieson, 2004: Fig. 3); families and species *sensu* Blakemore (2000, 2005).

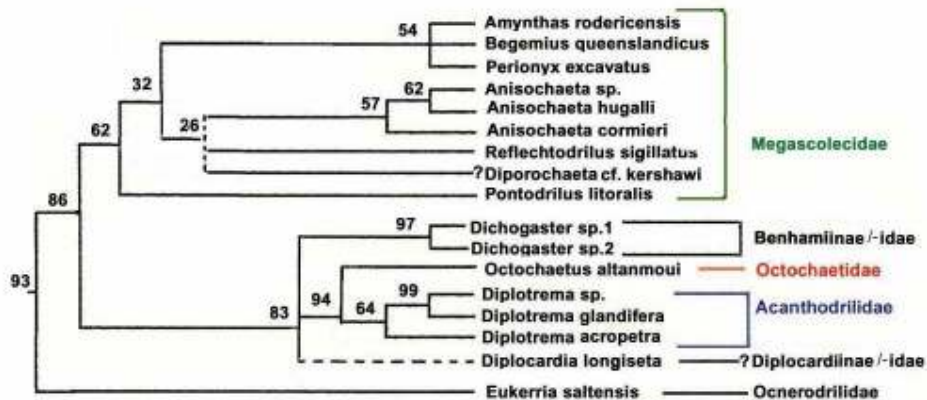


Fig. 2. Alternative classification that is not unsupported by the molecular phylogeny data as for Fig. 1 with 'weighting' to give hierarchy.

DISCUSSION

The phylogram derived from molecular data (Fig. 1) appears to vindicate the family classification of Blakemore (1994; 1999; 2000), despite relatively few species being included in the analysis and, assuming identifications were correct, none being actual type-species of their respective genus nor family. In contrast, Dyne & Jamieson (2004) used the same data to retain all taxa except *Eukerria* under Megascolecidae and to claim: “Evidence is reviewed supporting dismissal of the Acanthodrilidae and Octochaetidae *sensu* Gates (1959, 1972); the first was based on two symplesiomorphies (tubular prostates and holonephridia), the second on one symplesiomorphy (tubular prostates) and one highly homoplastic apomorphy (meronephridia)”, that

“*Ocotochaetidae* [sic] *sensu* Gates, and of recent attempts to resurrect it, is cladistically invalid”, and further that “*suppression of Gates' Octochaetidae ... is incontrovertible*” (although "Suppression" is actually a ruling enacted only by ICZN). But Dyne & Jamieson (2004) overlook the profound differences between a 'Hennigian Cladistic' and a 'Darwinian classification' (see Mayr & Bock, 2002). Moreover, they made no attempt to resuscitate remnants of Jamieson's (1971) defunct sub-familiar (or what they called 'supra-generic') tribal scheme defined mainly on ultrastructural consideration of nephridia, and were dismissive of family distinctions, such as Gates' (1959), based on various states of the male reproductive organs. Dyne & Jamieson (2004) yet compare mainly with an obsolete Gatesian classification, ignoring criticisms, e.g. by Easton (1979) and Sims (1980; 1982) as noted above, they fail to consider most recent family revisions by Csuzdi & Zicsi (1994), Csuzdi (1996; 2000), and, despite their results entirely supporting it, they completely ignore Blakemore (2000; 2002) [although Dyne & Jamieson (2004: 157) does cite a typing error in "Blakemore (2000)"].

Thus, after much diversion, it is timely in this Century to apply the molecular data to re-evaluation of the phylogenetic opinions provided under the 'Classical System' - as defined by Gates (1959; 1972), based on the solid foundations established in the last Century by Michaelsen, who named 1,083 species in a 53 year period to 1938, and by Stephenson, who himself described over 250 taxa, and who both did much to ensure stability in taxonomic nomenclature (see also Lee, 1994). Following the Classical system, the crucial division between the higher taxa considered here depends primarily upon the condition of the male pores: whether they are acanthodriline or megascolecine, and secondarily on nephridia, in which case the current molecular (DNA) results confirm that Megascolecidae is clearly separable from holoic Acanthodrilidae, and this in turn is distinct from meroic Octochaetidae: represented by *Octochaetus* in the subfamily Octochaetinae and by *Dichogaster* that is currently held in a subfamily Benhamiinae. Preliminary molecular evidence seems to indicate a schism (justified on the morphological basis of its gizzard duplication or combinations of other characters?) of Diplocardiinae/-idae (*Diplocardia*), but its closest relationships are indeterminable.

Stephenson (1923: 7, 316) had said: "*The sexual organs are the most important of all for systematic purposes*", and "*one of the great features in the evolution of the Megascolecinae has been the change in the prostate; and if this is not to be marked in our scheme of classification, the scheme will be comparatively useless; it will certainly fail to indicate what it ought*". Yet Gates' (1959: 240) ontogenetical starting point, that pheretima-like racemose prostates were from a 'mesodermal outgrowth' whereas tubular prostates were an 'ectodermal ingrowth', was obviously fatally flawed from the start as

the limited cases he cited (viz. by Stephenson and Ram, 1919, and Pickford, 1937, respectively) referred to samples from the families Megascolecidae and Acanthodrilidae that were already differentiated on the arrangements of their male pores. Had Gates (or anyone else) been able to demonstrate different ontogeny for tubular prostates in Megascolecidae (or for non-tubular prostates in what is now Exxidae), then there may have been some support. Yet derivation of non-tubular prostates in a species must be from an ancestor with the tubular sort, regardless of whether in an acanthodriline or a megascolecine taxon, and, although such a distinction is currently relevant only for membership of the Exxidae, it possibly has some basis for further sub-division within Megascolecidae *s. stricto* and possibly also within Diplocardiinae (as noted below).

Csuzdi & Zicsi (1994: 230) and Csuzdi (1996: 365) reviewed and placed in a revived subfamily Benhamiinae: Octochaetidae or Acanthodrilidae similar genera that were found “amphiatlantically”, they included the holoic genera *Pickfordia* Omodeo, 1958 and West African *Wegeneriella* Michaelsen, 1933 (non Amazonian *Wegeneriona* Cernosvitov, 1939). These holoic taxa (i.e. all except *Wegeneriona*) actually belong in Acanthodrilidae as redefined herein. Csuzdi (1996: 350-351) further redefined Acanthodrilidae to accept either the holoic (Acanthodrilinae *s. Csuzdi*) or meroic (Octochaetinae *s. Michaelsen*, 1900) states, but this was soon confounded by his rather contrived tribe 'Neogastrini' Csuzdi (1996: 363; 2000: 76) that allowed either state and is therefore unacceptable. Consequently, Csuzdi's two holoic 'Neogastrini' genera (amphiatlantic *Pickfordia* Omodeo, 1958 and African *Wegeneriella* Michaelsen, 1933) are re-allocated to Acanthodrilidae, and all other non-holic genera are presently allowed in Octochaetidae. Furthermore, Csuzdi's (1996: 365) definition of Megascolecidae with only 'Pheretima-type racemose prostates' is superseded by Blakemore (2000) that permits either tubular or non-tubular prostates in this family (see Fig. 1; Appendix 1).

South American *Wegeneriona* Cernosvitov, 1939 and *Neogaster* Cernosvitov, 1934 are now retained in Octochaetidae and, in answer to objections for these genera, apparently closely related to *Wegeneriella* and *Pickfordia*, respectively, being in separate families we must first reasonably accept that meroic nephridia are derived, thus any genus in Octochaetidae must have had an holoic ancestor (from a family such as Acanthodrilidae, whether still extant or not). Moreover, taxonomic grades are often parts of a partially revealed continuum that we classify somewhat arbitrarily into phylogenetic groups on best available information, thus we can expect closest similarities in taxa juxtaposed on either side of a natural divide. Stephenson (1930: 819) said "*A breaking up of the nephridia - the substitution of the [meroic] micronephridial for the [holoic] meganephridial condition of the ancestor - which is*

seen beginning in Howascolex, furnished the point of departure of the Octochaetinae".

Nevertheless, it is accepted that some definitions of Octochaetidae may yet inadvertently include polyphyletic taxa, perhaps requiring restriction of Octochaetidae to the New Zealand and Australian type-genus *Octochaetus* Beddard, 1893 (see Blakemore, 2004; 2005) and other allied genera; and subfamily Benhamiinae Michaelsen, 1895/7 restricted to its type-genus and similar taxa, may then, if sustainable, merit elevation to family level status. Restoration of some other synonyms of Octochaetidae (see Appendix 2) may also be considered. Such moves are deferred pending further morpho-molecular information of a more complete series of samples, ideally of the representative types of the type-species of the type-genera for each higher taxon.

Possible alternative options from the phylogramic data (Fig. 2 and [Tab. 2](#)) are equivocal, but appear to support resurrection (and elevation) of Diplocardiinae Michaelsen, 1899 separate from the Acanthodrilidae as per Michaelsen (1900: 122, 324), for polygiceriate North and Meso-American *Diplocardia* (and *Protozapotecia*, *Zapotecia* and possibly *Kaxadrilus*). This would be consistent with Gates (1977) who reasoned that *Diplocardia* was not particularly closely related to monogiceriate Australasian *Diplotrema*, and with Michaelsen (1900) who had Acanthodrilinae widely separated from Diplocardiinae and with Megascolecinae and Octochaetinae intervening (see [Tab. 1](#)). Just as Michaelsen's polygiceriate Diplocardiinae had naturally closer association to his meroic Trigastrinae, so now may a restored Diplocardiinae relate to Benhamiinae and possibly to Exxidae (cf. Octochaetinae *s. stricto* synonyms).

Some of the options noted above (and in Fig. 2 and [Tab. 2](#)) are tentative as more information is required for confirmation. For example, determination of the family affinities of *Kaxdrilus* Fragoso & Rojas, 1994 proposed for Meso-American species having a single gizzard (and calciferous-like glands) incorporating the two species from Mexico that James (1990) had provisionally placed in *Diplotrema*, or confirmation of enigmatic *Diplocardia michaelsoni* Eisen, 1899 and *D. udei* Eisen, 1899 [not "*D. udei* Gates, 1955" as cited by James (1995: 34)] that Michaelsen (1900: 324), Stephenson (1930: 370) and Gates (1959: 258) had noted with strictly non-tubular prostates (cf. Exxidae?). Pending further data, optimal stability is retained with the more certain arrangement shown in Fig. 1, and [Tab. 1](#) and keyed in Appendix 1.

Biogeographical distributions appear to show good correspondence with the current (and proposed optional) phylogenetic divisions. Acanthodrilidae *s. stricto* has a wide distribution, possibly attesting to its ancient pre-Gondwanan affinities, and currently includes endemic species in New Caledonia (e.g. type *Acanthodrilus*), New Zealand and Australia (e.g. *Diplotrema*), southern America and Africa (e.g. *Microscolex*,

Udeina), and Meso-America (e.g. *Diplocardia*, *Protozapotecia*, and *Zapotecia* that may better belong in a revived Diplocardiinae). For Octochaetidae, Gates (1972: 275) had said "*The vast oceanic discontinuities almost guarantee that the family is polyphyletic*"; its disjunct distribution was in New Zealand, India, Africa, Oceania, and Meso-America. However, separation off of Benhami-nae/-idea and related genera from the latter three regions may partially resolve this, leaving the residue of Octochaetidae *s. stricto* mainly confined to the Australasian region, with the long anticipated "missing-link" between octochaetids in New Zealand and India found recently with *Octochaetus ambrosensis* (Blakemore, 1997) and its allied taxa in Australia (Blakemore, 2000; 2005). It is enigmatic that Acanthodrilidae occurs on the Australian mainland (not Tasmania) and Americas and is especially dominant in South Africa, but is not known from India where Octochaetidae prevails. Perhaps during equatorial transit of the Indian sub-continent the Acanthodrilidae component was eliminated by climate or competition, perhaps with Moniligastridae, or antecedents merely evolved *in situ* to become Octochaetidae.

Megascolecidae *s. stricto* is still the dominant family in the Australasian and Oriental regions. Relatively 'primitive' North American Megascolecidae genera previously placed in *Plutellus* and *Megascolides* have now been put in nine genera (viz. *Arctiostrotus*, *Argilophilus*, *Chetcodrilus*, *Drilochaera*, *Driloleirus*, *Kincaidodrilus*, *Macnabodrilus*, *Nephralaxis*, and *Toutellus*) under tribe Argilophilini Fender & McKey-Fender, 1990 that is found only in the Pacific Northwest (see Fender, 1995: 54). Validity and taxonomic rank of a tribe Argilophilini within the Megascolecidae *s. stricto* is indeterminable on the morpho-molecular data presently available.

Is it justifiable to multiply Oligochaeta families? About 8,232 oligochaetes species are described in 804 genera of 38 families (data extrapolated from Wetzel, 2006), with about 30-40% comprising enchytraeid and aquatic microdrile cousins of 'true' earthworms that have at least 5,500 named species (Cs. Csuzdi, pers. comm.). In comparison, the greater number of taxonomists studying (for some reason) the marine Polychaeta has resulted in approximately 13,000 named taxa, although only 8,000 of these are considered reasonable species, and these are in 1000 genera and 82 families (Glasby & Fauchald, 2005). Thus actual species totals are approximately equivalent giving precedence for further taxonomic sub-division within the Oligochaeta.

Yet it is important to realize that all higher classification is speculative and, apart from specimens of representative species, the constructs of species, genera and families are intangible and hypothetical, proposed in order to conveniently place entities into manageable phylogenetic and hierarchical groupings. Most problematical are

entities close to perceived boundaries between groups (e.g. *Wegeneriella-Wegeneriona* and *Pickfordia-Neogaster* alluded to above, cf. Csuzdi 1993).

Moreover, reconciling a Linnean/evolutionary/systematic scheme with Cladistics is often impractical, if not impossible, due to different basic assumptions. This incongruence argument is succinctly put on Alan Kazlev/Toby White's *Palaeos* website by Dr R.K. Brummitt [<http://www.palaeos.com/Systematics/Cladistics/incompatable.html> July, 2005]: "*Linnaean classification without paraphyletic taxa is a logical impossibility. Every monophyletic genus in a Linnaean classification must be descended from something (probably a species) in a different genus, which must be paraphyletic. Similarly every monotypic family must be descended from a species in a genus in a different family. If one denies paraphyletic taxa, where do genera and families come from? Ultimately, one would end up sinking everything into its ancestral taxon, and the whole classification would telescope into its original taxon.... Put another way, all the species of a genus together equal the genus but all the offspring of a parent do not equal the parent.*"

The cladistic implication to merge all subsequent branches into the basal Ocnodrilidae (Fig. 1) is refuted on phylogenetic grounds (cf. Table 2), and for reasons as stated by Mayr & Bock (2002): "*A holophyletic clade encompasses a stem species and all of its descendants. A monophyletic taxon consists of descendants of the nearest ancestral taxon.... Furthermore, in no way is it valid to claim that Hennigian cladograms provide the foundation for understanding the evolution of biological organisms as these cladograms include only branching points (cladogenesis) and not the amount of evolutionary change (anagenesis)*".

Discussing molecular systematics methods, Mayr & Bock (2002) and Grant (2003) remind us that traditional morphological characters - the product of all ecological interactions and behavioural responses to the environment governed by large numbers of genes in the chromosomal genome, are usually quite reliable as opposed to narrow differences detectable in cytoplasmic organelles of the cell. Nevertheless, it seems that more information is needed from combinations of morphological and DNA studies of a greater series of representative specimens, preferably of the types, in order to get a definitive consensus, not only on the composition of earthworm families, but also the methodologies to test these. But taxonomists also need to remember that, academic speculation aside, there is a duty to provide workers in the field with well-considered, reliable and stable nomenclature and a practical system of classification. It is hoped the present contribution will help provide a base to stimulate constructive discussion and research in an appropriate direction along courses now

opened by the options proposed here, in order to answer the basic and simple question:
"To which family does this species belong?"

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REFERENCES

Selective – not all taxonomic citations presented here.

- Blakemore, R.J. (1994) "Earthworms of south-east Queensland and their agronomic potential in brigalow soils." PhD. Thesis, University of Queensland. Pp. 605 with the description of 75 species, including 80 figures.
- Blakemore, R.J. (1997) Two new genera and some new species of Australian earthworms (Acanthodrilidae, Megascolecidae: Oligochaeta). *Journal of Natural History*. 31: 1785-1848.
- Blakemore, R.J. (1999) The diversity of exotic earthworms in Australia – a status report. *Proceedings of "The Other 99%"*, edited by W. Ponder and D. Lunney, *Transactions of the Royal Zoological Society of NSW, 1999*. Pp 182-187. <http://biocollections.org/pub/worms/docs/Blakemore-eworms-Diversity-of-exotics.html>
- Blakemore, R.J. (2000) *Tasmanian Earthworms*. CD-ROM Monograph with Review of World Families. 'VermEcology', Kippax, Canberra, December, 2000. Pp. 800 including 222 figs. ISBN 0-646-41088-1.
- Blakemore, R.J. (2002) *Cosmopolitan Earthworms – an Eco-Taxonomic Guide to the Peregrine Species of the World*. VermEcology, PO BOX 414 Kippax, ACT 2615, Australia. Pp. 506 + including 80+ figs.
- Blakemore, R.J. (2005) *A Series of Searchable Texts on Earthworm Biodiversity, Ecology and Systematics from Various Regions of the World*. CD-ROM, YNU, Yokohama, Japan. [<http://bio-eco.eis.ynu.ac.jp/eng/database/earthworm/>].

- Borges, S.; Moreno, A. G. (1991) Nuevas especies del género *Trigaster* Benham, 1886 (Oligochaeta: Octochaetidae) para Puerto Rico. *Bollettino del Museo Regionale di Scienze Naturali - Torino*. 9(1): 39-54.
- Csuzdi, Cs. (1996) Revision der Unterfamilie Benhamiinae Michaelsen, 1897 (Oligochaeta: Acanthodrilidae). *Mitt. Zool. Mus. Berl.* **72**: 347-367.
- Csuzdi, Cs. (1997): Neue und bekannte Regenwürmer aus dem Naturhistorischen Museum, London (Oligochaeta: Acanthodrilidae). *Opusc. Zool. Budapest.* **29-30**: 35-47. [PDF](#)
- Csuzdi, Cs. (2000) A review of the Benhamiinae collection of the Natural History Museum, London (Oligochaeta: Acanthodrilidae). *Opusc. Zool. Budapest.* **XXXII, 2000**: 51-80. [In English].
- Csuzdi, Cs.; Zicsi, A. (1994) Revision der Gattung *Benhamia* Michaelsen, 1889 (Oligochaeta: Octochaetidae). *Revue suisse de Zoologie.* **101(1)**: 215-231.
- Dyne, G.R.; Jamieson, B.G. (2004). Native Earthworms of Australia II. (Megascolecidae, Acanthodrilinae). ABRS. CD-ROM. Pp. 200.
- Dyne, G.R.; Wallace, C.C. (1994). Biodiversity and conservation of the earthworm fauna of the wet tropics of Queensland's World Heritage Area. *Mem. Qld. Mus.* **36(1)**: 59-66.
- Easton, E.G. (1979). A revision of the 'acaecate' earthworms of the *Pheretima* group (Megascolecidae: Oligochaeta): *Archipheretima*, *Metapheretima*, *Planapheretima*, *Pleinogaster* and *Polypheretima*. *Bulletin of the British Museum (Natural History) Zoology.* **35(1)**: 1-128.
- Easton, E.G. (1981) Japanese earthworms: a synopsis of the Megadrile species (Oligochaeta). *Bulletin of the British Museum (Natural History) Zoology.* **40(2)**: 33-65.
- Easton, E.G. (1984) Earthworms (Oligochaeta) from islands of the south-western Pacific, and a note on two species from Papua New Guinea. *New Zealand Journal of Zoology.* **11**: 111-128.
- Fender, W. M. (1995) *Native earthworms of the Pacific Northwest: an ecological overview*. In P. F. Hendrix (editor): Ecology and biogeography of earthworms in North America. CRC Publishing, Boca Raton, Florida.
- Fender W.M.; McKey-Fender, D. (1990) Oligochaeta: Megascolecidae and other earthworms from western North America. In: D.L. Dindal (ed.) *Soil Biology Guide*. John Wiley & Sons, New York. Pp. 357-378.
- Gates, G.E. (1959) On a taxonomic puzzle and the classification of the earthworms. *Bulletin of the Museum of Comparative Zoology, Harvard.* **123(6)**: 229-61.

- Gates, G.E. (1972) Burmese Earthworms, an introduction to the systematics and biology of Megadrile oligochaetes with special reference to South-East Asia. *Transactions of the American Philosophical Society*. **62(7)**: 1-326. [Online via subscription here <http://links.jstor.org/journals/00659746.html>].
- Gates, G.E. (1976) On earthworm ovaries and their importance in megadrile systematics. I. *Megadrilogica*. **2(12)**: 1-2.
- Gates, G.E. (1977) More on the earthworm genus *Diplocardia*. *Megadrilogica*. 3(1): 1-48.
- Glasby, C.J.; Fauchauld, K. (2005) Polikey website. www.ea.gov.au/biodiversity/abrs/online-resources/polikey/index.html#history [Dec., 2005].
- Grant, V. (2003) Incongruence between cladistic and taxonomic systems. *American Journal of Botany*. 90:1263-1270. [www.amjbot.org/cgi/content/full/90/9/1263].
- ICZN (1999) *International Code of Zoological Nomenclature* (4th edition). International Trust for Zoological Nomenclature, c/o Natural History Museum, London. Pp. 306. [<http://www.iczn.org/iczn/index.jsp>].
- James, S. (2004a) Planetary Processes and Their Interactions with Earthworm Distributions and Ecology. In: *Earthworm Ecology* ed. (C. A. Edwards), CRC Press, Boca Raton. Revised 2nd Edition. Pp. 53-62.
- James, S. (2004b) Earthworms (Clitellata, Acanthodrilidae) of the mountains of Eastern Jamaica. *Organisms, Diversity & Evolution*. 277: 277-294.
- Jamieson, B.G.M. (1971) A Review of the Megascoleoid Earthworm Genera (Oligochaeta) of Australia. Part I - Reclassification and Checklist of the Megascoleoid Genera of the World. *Proc. R. Soc., Qld.* **82(6)**: 75-86.
- Jamieson, B.G.M. (1974) The indigenous earthworms (Oligochaeta: Megascolecidae) of Tasmania. *Bulletin of the British Museum (Natural History), Zoology*. **26(3)**: 201-328. [Cf. Blakemore, 2000].
- Julka, J.M. (1988) *The Fauna of India and the adjacent countries: Megadrile Oligochaeta (Earthworms) Family Octochaetidae*. Zoological Survey of India, Calcutta. Pp. 400.
- Julka, J.M., Blanchart, E.; Chapuis-Lardy, L. (2004) New genera and new species of earthworms (Oligochaeta: Octochaetidae) from Western Ghats, South India. *Zootaxa*. 486: 1-27. [<http://www.mapress.com/zootaxa/taxa/Annelida.html>].
- Julka, J.M., Ramanujam, S.N.; Lalthanzara, H. (2005) On a new species of earthworm genus *Eutyphoeus* (Octochaetidae: Oligochaeta) from Mizoram, India.

Megadrilogia. **10**: 69-72.

- Lee, K.E. (1959) *The Earthworm Fauna of New Zealand*. New Zealand Department of Scientific and Industrial Research, Wellington. Bulletin 130. Pp 486.
- Lee, K.E. (1994) Earthworm classification and biogeography: Michaelsen's contribution, with special reference to southern lands. *Mitteilungen aus dem Hamburg Zoologischen Museum und Institut*. **89(2)**: 11-21.
- Mayr, E.; Bock, W.J., (2002) Classifications and other ordering systems. *J. Zoological Systematics & Evolution*. **40(4)**: 169-194. [www.blackwell-synergy.com/doi/full/10.1046/j.1439-0469.2002.00211.x].
- Michaelsen, W. (1900) *Das Tierreich* Vol. 10: Oligochaeta. Friedländer & Sohn, Berlin. Pp. XXIX+575.
- Michaelsen, W. (1907) Oligochaeta in *Die Fauna Südwest-Australiens*. **1(2)**: 117-232. Jena: Gustav Fischer.
- Michaelsen, W. (1921) Zur Stammgeschichte und Systematik der Oligochäten, insbesondere der Lumbriculiden. *Archiv für Naturgeschichte, Berlin*. **86(8)**: 130-141.
- Parker, S.P. (1982) Lumbricina. In: "Synopsis and classification of living organisms." McGraw-Hill, New York. Pp. 55-61.
- Plisko, J.D. (2004) Review of the balantine genus *Udeina* Michaelsen, 1910 with descriptions of six new species in South Africa (Oligochaeta: Acanthodrilidae, Acanthodrilinae). *African Invertebrates*. **45**: 287-313.
- Reynolds, J. W.; Cook, D. G. (1976) *Nomenclatura oligochaetologica*. A catalogue of names, descriptions and type specimens of the Oligochaeta. Univ. New Brunswick, Fredericton, New Brunswick. Pp. 217.
- Reynolds, J. W.; Cook, D. G. (1981) *Nomenclatura oligochaetologica. Supplementum primum*. Fredericton, New Brunswick. Pp. 39.
- Reynolds, J. W.; Cook, D. G. (1989) *Nomenclatura oligochaetologica. Supplementum secundum*. New Brunswick Museum Monographic Series (Natural Science). No. 8: 1-37.
- Reynolds, J. W.; Cook, D. G., (1993) *Nomenclatura oligochaetologica. Supplementum tertium*. A catalogue of names, descriptions and type specimens of the Oligochaeta. New Brunswick Mus. Monogr. Ser. (Nat. Sci.). No. 9: 1-33.
- Reynolds, J.W.; Righi, G. (1994) On some earthworms from Belize, C.A. with the description of a new species (Oligochaeta: Acanthodrilidae, Glossoscolecidae and Octochaetidae). *Megadrilogica*. **5(9)**: 97-106.
- Rodrigues Aragonés, C.; Frago, C. (2002) Filogenia y biogeografía de *Cubadrilus*

- (Oligochaeta: Octochaetidae), un género nuevo de lombriz de tierra de Cuba. *Acta Zoologica Mexicana*. 87: 125-146. [<http://www.ecologia.edu.mx/azm/documentos/87/87-i.pdf>].
- Siddall, M.E., Apakupakul, K., Burreson, E. M., Coates, K. A., Erséus, C., Gelder, S. R., Källersjö, M.; Trapido-Rosenthal, H. (2001) Validating Livanow's Hypothesis: Molecular Data Agree that Leeches, Branchiobdellidans and *Acanthobdella peledina* form a Monophyletic Group of Oligochaetes. *Molecular Phylogenetics and Evolution*. 21: 346-351. [PDF](#) <http://research.amnh.org/~siddall/pub/livanow.pdf>
- Sims, R.W. (1966) The classification of the Megascolecoïd earthworms: an investigation of Oligochaete systematics by computer techniques. *Proceedings of the Linnean Society, London*. 177(2): 125-141.
- Sims, R.W. (1980) A Classification and the distribution of earthworms, suborder Lumbricina (Haplotaxida: Oligochaeta). *Bulletin of the British Museum (Natural History) Zoology*. 39: 103-124.
- Sims, R.W. (1982) Classification and distribution of the suborder Lumbricina (Haplotaxida: Oligochaeta). *Pedobiologia*. 23: 284-285.
- Sims, R.W.; Gerard, B.M. (1985) Earthworms. Keys and notes to the identification and study of the Species. *Synopsis of the British Fauna (New series)*. E.J. Brill, Leiden. No. 31. Pp. 171.
- Sims, R. W.; Gerard, B.M. (1999) *Earthworms: Notes for the identification of British species*. 4th Edition. Published for The Linnean Society of London and The Estuarine and Coastal Sciences Association by Field Studies Council, Montford Bridge, Shrewsbury, UK. Pp. 169.
- Stephenson, J. (1923) *The fauna of British India, including Ceylon and Burma. Oligochaeta* Taylor and Francis. London. Pp. 518.
- Stephenson, J. (1930) *The Oligochaeta*. Oxford University, Clarendon Press. Pp. 978.
- Wetzel, M. J. (2003; 2004; 2006) The Terrestrial Oligochaeta of Illinois - annotated checklist of species; and *Nomenclatura Oligochaeta* link: [\[http://www.inhs.uiuc.edu/cbd/collections/annelid/ilspecies.html\]](http://www.inhs.uiuc.edu/cbd/collections/annelid/ilspecies.html) 2003; www.inhs.uiuc.edu/~mjwetzel/TerrWoi.mjw.list.html 2004; <http://www.inhs.uiuc.edu/~mjwetzel/Nomen.Oligo.html> 2006].

Table 1. Progression of family classifications of the megadrile Earthworms

Michaelsen (1900)	Michaelsen (1921)	Stephenson (1930: 721)	Blakemore (2000/2005)
1. Moniligastridae	1. Moniligastridae	1. Moniligastridae	1. Moniligastridae
	2. Syngenodrilidae	A Syngenodrilinae	2. Ocerodrilidae
2. Megascolecidae	3. Megascolecidae	B Moniligastrinae	2a Malabariinae
A Acanthodrilinae	4. Acanthodrilidae	2. Megascolecidae	3. Acanthodrilidae
B Megascolecinae	A Acanthodrilinae	A Acanthodrilinae	?4. Diplocardiinae/idae
C Octochaetinae	B Octochaetinae	B Megascolecinae	5. Octochaetidae
D Diplocardiinae	C Diplocardiinae	C Octochaetinae	5a. Benhamiinae/idae
E Trigastrinae	D Trigastrinae	D Diplocardiinae	6. Exxidae
F Ocerodrilinae	E Ocerodrilinae	E Ocerodrilinae	7. Megascolecidae
G Eudrilinae	5. Eudrilidae	3. Eudrilidae	8. Eudrilidae
3. Glossoscolecidae	A Pareudrilinae	A Pareudrilinae	9. Glossoscolecidae
A Glossoscolecinae	B Eudrilinae	B Eudrilinae	10. Hormogastridae
B Hormogastrinae	6. Glossoscolecidae	4. Glossoscolecidae	11. Microchaetidae
C Microchaetinae	7. Hormogastridae	A Glossoscolecinae	12. Criodrilidae
D Criodrilinae	8. Microchaetidae	B Sparganophilinae	13. Sparganophilidae
4. Lumbricidae	9. Criodrilidae	C Microchaetinae	14. Lumbricidae
	10. Sparganophilidae	D Hormogastrinae	15. Almidae
	11. Lumbricidae	E Criodrilinae	16. Ailoscolecidae (inc. Komarekionidae)
		5. Lumbricidae	17. Lutodrilidae
			18. Biwadrilidae*
			19. Kynotidae*
			20. Tumakidae*

* Taxonomic groups yet to be extensively tested.

Table 2. Present and possible future classifications of MEGASCOLECOIDEA

Current (Blakemore 2000/2005)	Option 1	Option 2	Option 3
1. Ocnodrilidae (incl. Malabariinae)	1. Ocnodrilidae	1. Ocnodrilidae	1. Ocnodrilidae
2. Acanthodrilidae	A Ocnodrilinae	2. Acanthodrilidae	2. Acanthodrilidae
3. Octochaetidae (incl. Benhamiinae)**	B Malabariinae	A Acanthodrilinae	3. Octochaetidae
4. Exxidae	C Acanthodrilinae	B Diplocardiinae	4. Diplocardiidae*
5. Megascolecidae	D Octochaetinae	3. Octochaetidae**	A sub-family
	E Benhamiinae	A Octochaetinae	B sub-family
	F Exxinae	B Benhamiinae	5. Benhamiidae and/or Tigastrinae/idae***
	G Megascolecinae	4. Exxidae	6. Exxidae
		5. Megascolecidae	7. Megascolecidae*
			A sub-family
			B sub-family

*Diplocardiidae and Megascolecidae further division on characters such as tubular vs. non-tubular prostates, etc.. Option 1 not advocated, other Options pending more data.

** ICZN (1999: Art. 35.5; Example) states: "*If after 1999 a name in use for a family-group taxon (e.g. for a subfamily) is found to be older than a name in prevailing usage for a taxon at higher rank in the same family-group taxon (e.g. for the family within which the older name is the name of a subfamily) the older name is not to displace the younger name.*" Thus the older name BENHAMIINAE Michaelsen, 1985/7 does not displace the established OCTOCHAETIDAE Michaelsen, 1900.

*** Other options are restorations from synonymy in Octochaetidae (see Appendix 2).

APPENDIX 1

Revised Key to MEGASCOLECOIDEA (Options in braces)

1. Last hearts in 11; prostates tubular; calciferous glands or diverticula in 9 or 9-10 (Ocnerodrilinae) or absent (Malabariinae) **Ocnerodrilidae**
Last hearts after 11; prostates tubular or non-tubular; calciferous glands, if present, not just in 9 or 9-10 2
2. Male pores opening separately on 18 from pores of prostates in 17 and/or 19, or both male and prostatic pores on 17 or 19 (i.e. not combined on 18) 3
Male pores on 18 (or homeotic equivalent) combined with pores of a single pair of tubular or non-tubular prostates **Megascolecidae s. stricto**
3. Holoic; prostates always tubular, gizzard single or reduced **Acanthodrilidae**
[Holoic; prostates rarely non-tubular; gizzards multiple **Diplocardiinae/-idea**]
Meroic; prostates tubular or non-tubular; gizzards single or multiple 4
4. Prostates tubular **Octochaetidae**
 - 4a Calciferous glands 1-3 extramural pairs after reproductive organs, commencing in or after segment 14; (often multiple gizzards) **Benhamiinae**
 - 4b Calciferous glands, if present, before segment 14; (gizzard usually single) **Octochaetinae**Prostates non-tubular (i.e., racemose or tubuloracemose) ... **Exxidae** [Neotropical: Central America and Caribbean, no longer considered 'Australasian'; nine or ten known species in two or three genera. Type-genus *Exxus* Gates, 1959 often overlooked].

APPENDIX 2

Taxonomic summaries of Acanthodrilidae, Benhamiinae and Octochaetidae (non exhaustive)

Taxonomic Note: After Blakemore (1999; 2000; 2002), *Pontodrilus*, *Plutellus*, *Argilophilus*, and *Diporochoeta* are returned to Megascolecidae from Acanthodrilidae s. Gates. The genera *Megascolides* McCoy, 1878; *Scolioscolides* Gates, 1937; *Barogaster* Gates, 1939; monotypic *Priodochoeta* Gates, 1940: 116 (= *Diporochoeta*) and *Priodoscolex* Gates, 1940: 122; *Travoscolides* Gates, 1940: 137 (these latter three possible synonyms of *Megascolides*); and *Celeriella* Gates, 1958 are now transferred to Megascolecidae from Octochaetidae s. Gates, as their male and prostatic pores are combined on 18 rather than being acanthodriline cf. Gates (1972: 313) and Julka (1988).

Acanthodrilidae Claus, 1880 (restored *sensu* Blakemore, 2000; 2002 although Diplocardiinae/idae may merit separate status from Acanthodrilidae).

Type-genus *Acanthodrilus* Perrier, 1872; type-species *Acanthodrilus unguulatus* Perrier, 1872 from New Caledonia.

Synonymy after Michaelsen (1900: 122, 324), Blakemore (2002):

Acanthodrilinae (part.) Claus, 1880: 479; Vejdovsky, 1884: 63; Rosa, 1888: 9; Benham, 1890: 220; (+ Cryptodrilinae/idae part.) Beddard, 1891: 265; Rosa, 1891: 379; Beddard, 1895: 443, 516; (+ Diplocardiinae) Michaelsen, 1900: 32, 324; 1907: 138; 1922:58; Stephenson, 1923: 163; 1930: 820; Pickford, 1937: 98; Lee, 1959: 32.

Acanthodriiacea (Sippe = Clan, perhaps equivalent to current ICZN 'sub-tribe') Michaelsen, 1895: 23.

Microscolecini (lapsus?) Michaelsen, 1897: 25.

Diplocardiinae (sic) Michaelsen, 1899: 241.

Neodrilacea + Acanthodrilacea (part.) Lee, 1959: 35.

Acanthodrilidae (part.); Gates, 1959: 255; Sims, 1980.

Representative Genera (from Michaelsen, 1900; Csuzdi, 1996; Blakemore, 2005):

Hegesipyle Kinberg, 1867 (overlooked but available genus).

Acanthodrilus Perrier, 1872.

Microscolex Rosa, 1887 (syns. *Photodrilus*, *Deltania*, *Notiodrilus*).

Diplocardia Garman, 1888 [syns. *Geodrilus*, *Aleodrilus*, *Omahania*, *Naillenia*. Note: usually defined by paired oesophageal gizzards and (always?) lack of calciferous glands; species with non-tubular prostates may belong in a different group].

Rhododrilus Beddard, 1889 (syns. *Leptodrilus*, *Kayarmacia*).

Chilota Michaelsen, 1899.

Yagansia Michaelsen, 1899.

Diplotrema Spencer, 1900 (syn. *Eodrilus* Michaelsen, 1907. Note: two Mexican species placed in *Diplotrema* are now transferred to *Kaxdrilus*).

Pickfordia Omodeo, 1958.

Subgenus *Pickfordia*.

Subgenus *Omodeoscolex* Csuzdi, 1993.

Wegeneriella Michaelsen, 1933.

Parachilota Pickford, 1937.

Kaxdrilus Fragoso & Rojas-Fernandez, 1994.

Eodriloides Zicsi, 1998.

Plus approximately 30 other genera as listed by Blakemore (2002; 2005; and in prep.).

Benhami-inae/-idae Michaelsen, 1895/7 (a sub-family of Octochaetidae, possibly meriting separate family status, or merger in Octochaetidae)

Type-genus: *Benhamia* Michaelsen, 1889; with type-species *Benhamia rosea* Michaelsen, 1889 from Cote d'Ivoire tropical West Africa.

Synonymy from Michaelsen (1900: 330 of his Subfamily Trigastriinae that, according to Gates (1959: 256) disappeared when Stephenson (1930) then Michaelsen (1933) transferred the Indian *Eudichogaster* and the genera, *Trigaster*, *Eutrigaster*, *Dichogaster* and *Monogaster* to the Octochaetinae; also from Csuzdi & Zicsi (1994: 230); Csuzdi (1996; 2000):

Acanthodrilidae (part.) Rosa, 1888: 9; Typhaeidae (part.) Benham, 1890: 220;
Acanthodrilidae/-inae (part.) + Cryptodrilidae/-inae (part.) Beddard, 1891: 265;
Rosa, 1891: 379; Beddard, 1895: 443, 516.

Benhamiacea ("Sippe" = Clan, perhaps equivalent to current ICZN 'sub-tribe')
Michaelsen, 1895: 23.

Benhamini (sic); Michaelsen, 1897: 25.

Diplocardinae (part.) + Benhaminae (sic, part.); Eisen, 1900: 165, 208.

Trigastriinae (part.) Michaelsen, 1900: 330.

Benhamiinae (part.); Omodeo, 1958; Csuzdi & Zicsi, 1994; Csuzdi, 1996; 2000: 52.

Diagnosis emended from Csuzdi (1996: 351): Octochaetidae with duplicated oesophageal gizzards and 2-3 pairs of extramural, lamellar, calciferous glands beginning after segment 14. Csuzdi (1993: 351) allowed only species with 2-3 pairs of extramural calciferous glands after 14, however, Gates (1959: 244; 1972: 277) said common and widely peregrine *Dichogaster* species really have only a trilobed pair in segment 16 and, moreover, *Octochaetus* Beddard as originally described, and as by Stephenson (1930: 844) and Lee (1959) has a single gizzard with "*calciferous glands in the region of segments xv-xvii*". Thus the sub-family is not clearly differentiated morphologically apart from its polygicierate characteristic (cf. monogicierate members of *Monogaster* and perhaps *Millsonia* from Africa).

Representative Genera (partially from Csuzdi, 1996; 2000; and Blakemore, 2002):

Benhamia Michaelsen, 1889.

Dichogaster Beddard, 1888 [syns. *Microdrilus* Beddard, 1893 (type *Microdrilus saliens*), and *Balanta* Michaelsen, 1898 (type *Balanta ehrhardti*) in synonymy following Michaelsen (1900: 334), but *Millsonia* (type *M. nigra*) now removed (Csuzdi, 1996: 360)].

Subgenus *Dichogaster*.

Subgenus *Diplotheodrilus* Csuzdi, 1996.
Eutrigaster Cognetti, 1904.
Subgenus *Eutrigaster*.
Subgenus *Graffia* Csuzdi & Zicsi, 1991.
Millsonia Beddard, 1894 (sometimes misspelt "Milsonia").
Monogaster Michaelsen, 1915 (type-species *M. bidjimensis* Michaelsen, 1915 from Cameroon).
Wegeneriona Cernosvitov, 1939 [note: the major difference from the prior *Wegeneriella* Michaelsen, 1933 is the apomorphic attainment of meroic nephrida, this however is sufficient for family separation of these two genera; cf. Csuzdi (1995: 100)].
Agastrodrilus Omodeo & Vaillaud, 1967 [lacks gizzard].
Omodeona Sims, 1967.
Benhamiona Csuzdi & Zicsi, 1994.
Guineoscolex Csuzdi & Zicsi, 1994.
Monotheodrilus Csuzdi & Zicsi, 1994.
Neogaster Cernosvitov, 1934.
[And cf. *Trigaster* and *Eudichogaster* under Octochaetinae/-idae below].

Octochaet-inae/idae Michaelsen, 1900 (family or nominal sub-family)

Type-genus: *Octochaetus* Beddard, 1893; type-species *Acanthodrilus multiporus* Beddard, 1855 from New Zealand's South Island.
Synonymy after Michaelsen (1900: 318); Gates (1972: 275), Blakemore (2002):
Eudrilidae (part.) Vejdovsky, 1884: 63.
Eudrilidae (part.) + Acanthodrilidae (part.); Rosa, 1888: 9.
Typhaeidae (corr. of Typhoeinae, part.) + Acanthodrilidae (part.); Benham, 1890: 220.
Cryptodrilidae Beddard, 1890: 236 (part.).
Deinodrilidae + Acanthodrilidae (part.) + Cryptodrilidae (part.); Beddard, 1891: 265.
Acanthodrilinae (part.) + Cryptodrilinae (part.); Rosa, 1891: 379.
Perichaetini (part.) + Microscolecini (part.); Michaelsen, 1895: 23.
Cryptodrilidae (part.) + Acanthodrilidae (part.); Beddard, 1895: 443, 516.
Typhaeini? Michaelsen, 1897: 246.
Typhaeinae; Michaelsen, 1899: 242.
Octochaetinae (+ Trigastriinae) Michaelsen, 1900: 318.
Octochaetidae/-nae (part.); Stephenson, 1930; Pickford, 1937: 98, 605; Gates, 1959: 254; Lee, 1959: 32; 1972: 275; Sims, 1980.
Diagnosis emended from Csuzdi (1996); Blakemore (2000): Octochaetidae with single

gizzard (near 5); calciferous glands, present or absent. Csuzdi (1996: 351) had calciferous glands, if present, mostly between sexual organ segments (i.e. beginning before segment 14). However, monogiceriate *Octochaetus* has calciferous glands after 14, thus further review of Octochaetinae relative to Benhamiinae may be required (cf. *Trigaster*, *Eutrigaster*).

Representative Genera:

Octochaetus Beddard, 1892 [syns. *Cryptochaeta* Benham, 1950 (preocc. non *Cryptochetum* Rondani 1876 [Diptera] placed in synonymy by Lee, 1959: 104); *Neodiplotrema* Dyne, 1997 (placed in synonymy by Blakemore, 2004: 175)].

Howascolex Michaelsen, 1901 [type *Howascolex madagascariensis* Michaelsen, 1901 from Madagascar, now monotypic: other species from India separated off to subgenus *Gracevelynia* (now = *Ramiellona*) or to genera *Konkodrilus* and *Wahoscolex*].

And all other Octochaetidae genera endemic to New Zealand (see Lee, 1959; Blakemore, 2005), and India (see Julka, 1988; Julka *et al.*, 2004, 2005). The Cuban genus *Cubadrilus* Rodrigues & Fragoso, 2002 was stated to be very close to the Mexican *Zapatadrilus* James, 1991 (these authors showed this latter genus to be polyphyletic), indeed several species of both genera appear placeable in *Exxidus* (family Exxidae) that may be a senior synonym – pers. obs.. African *Monogaster* Michaelsen, 1915 now belongs in (Octochaetidae: Benhamiinae) according to Csuzdi (1996: 358).

Indian *Eudichogaster* Michaelsen, 1902 complies with Octochaetinae as currently defined. It was diagnosed by Stephenson (1923: 402) thus: Lumbricine. Two oesophageal gizzards. Calciferous glands in some of segments 10-13 as simple or paired sacs (not extramural). Meroic. Type *Benhamia indica* Beddard, 1896. Several species in the genus *Eudichogaster* [viz. *indica*, *poonensis* Fedarb (non *D. poonensis* Cognetti, 1910), and *parva*] were originally described as *Dichogaster* or *Benhamia*, and included under *Trigaster* (Trigastrinae) in the Terreich (Michaelsen, 1900).

Caribbean *Trigaster* Benham, 1886 also currently resides in Octochaetidae *s. stricto* but may actually be closer to Benhamiinae (and Exxidae?); several new taxa were described by Borges & Moreno (1991).

James (1991), Csuzdi & Zicsi (1994), and Csuzdi (1996) omit consideration of *Eudichogaster* in redefinitions of *Trigaster*, *Benhamia*, and *Eutrigaster*; separation of these genera was finally made on the basis of the calciferous glands (and gizzards): *Trigaster* (with three gizzards between 5-9) has none, *Dichogaster* and *Benhamia* (with gizzards in 5-6) and *Eutrigaster* (with gizzards 6-7) all have them in 15-17.