

Introductory Key to the Revised Families of Earthworms of the World

[Modified after Michaelsen (1900; 1907), Stephenson (1930), Sims (1980), Sims & Gerard (1995, 1999), Csuzdi (1996; 2000) and Blakemore (2000; 2002; 2005, 2006)].

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Introduction

“The family-level classification of the megascolecid earthworms is in chaos” – Fender & McKey-Fender, (Soil Biology Guide, 1990: 369) who, for an overview of the dispute, cite the conflicting schemes of Gates (1959), Jamieson (1971), and Sims (1980).

“Much breath & paper has been largely wasted arguing the appropriate rank of a group”. [<http://www.palaeos.com/Systematics/Cladistics/incompatable.html> July, 2005]

“Haeckelian phylogenies and Hennigian cladifications (= cladograms; see Glossary and Mayr, 1965) are quite different types of ordering systems from Darwinian classifications” - Mayr & Bock (2002: 170)

<http://www.blackwell-synergy.com/links/doi/10.1046/j.1439-0469.2002.00211.x/abs/>

Whereas Reynolds & Cook (1981: 1; 1989: 1; 1993) maintained Acanthodrilidae, Octochaetidae, and Megascolecidae, these authors cited a dubious family “Diporochoetidae” (actually a *lapsus* for Diporodrilidae Bouché, 1970 now a sub-family of Lumbricidae), and they added Lobatocerebridae Rieger, 1980 (misspelt and misattributed as "Labatocerebridae Reiger" that is, however, a Polychaeta). Many other families or Oligochaeta taxa at sub-familial level have been variously proposed and subsumed over the years, eg. Cryptodrilinae/-idae, Diplocardiinae, Argilophilini, etc..

Phylogenetic division based on morphology and behaviour as keyed below gains support from recent studies on underlying molecular characteristics, e.g. Siddal *et al.* (2001) who were the first to apply DNA data to studies of earthworm phylogeny, including *Lumbricus terrestris*, "*Pontodrilus litoralis (bermudensis)*" and *Eisenia fetida*.

In a recent review, James (2004: 54, 55; fig. 3.1) - as with Dyne & Wallace (1994) as reported in Blakemore (1997: 1788), retains “Acanthodrilidae” separately from “Megascolecidae” but he fails to cite Blakemore (2000) so we must assume this is based on Gates’ (1959) now defunct families concept rather than the more modern view. However, James (2004: 58) is inconsistent in further praising a scheme based on Jamieson’s equally defunct families concept that failed to recognize Acanthodrilidae (nor Octochaetidae) when he states: “a century of work by a small but dedicated group has

failed to resolve such fundamentals as the definitions of families (e.g., Sims 1980). To date, only Jamieson (1988) and Jamieson et al. (2002) have offered a rigorous analysis of this problem". And yet, ironically, this latter citation from a molecular analysis of only a few mostly non-type species seems merely to reinforce and support the system, with solid foundations in the Classical systematics of Michaelsen (1900, 1907) and Stephenson (1930), that was refined and updated in Blakemore (2000, 2002, 2005, 2006) and is presented in the summary key below.

Appendix 1 presents current consensus on revival of components of superfamily Megascolecoida and Appendix 2 explains synonymy of Komarekionidae in Ailoscolecidae (from Sims, 1980).

A further advantage of this key, as with Blakemore (2000; 2002), is to simplify the taxonomic process, without sacrificing phylogenetic relationships, in order to relieve taxonomists and field ecologists from the tedious requirements to obtain Scanning Electron Micrographs (SEMs) of modified setae (where present!), or a futile hunt for obscure (and often absent!) fine ultrastructural minutiae such as 'multiple preseptal nephrostomes' or 'stomate megameronephridium median to multiple astomate mircomeronephridia' in caudal segments, whether exonephric or not, and presumably in specimens that are not posterior amputees. Once these aberrations are dispensed with, then more reliance and importance is rightly placed on the condition of the less environmentally adaptive reproductive organs, internal and external structures that not only define specific taxonomic groups, but also allow resolution at all levels for the majority of species, whether they be recently described, or classical taxa that tended to have only a few "key" features characterized.

It is hoped this brief introduction and reference will benefit ecologists, field-workers, and novice students wishing to answer the simple and basic question:

"To what Family does this Species belong?"

Results

Introductory Key to the FAMILIES of Earthworms

Occasional species may have suppressed anteriors with segments 1 and 2 fused or aborted – this determined by setae on "first" segment, by internal septa, and by reproductive organs in other than the usual locations (i.e., testes in 10 and 11, ovaries in 13). Rarely supernumerary segments occur, eg. due to mutation or regeneration of specimens. In such cases, add (or subtract) counts to the segment numbers in the keys below. "Holoic" means a single pair of obvious, large holonephridia per segment and "Meroic" (or non-holoic) encompasses all other combinations which, for practical purposes, the novice need not discriminate into micro-meronephridia, mega-meronephridia, or what-have-you.

1. Clitellum usually formed from a single layer of cells in the region of the male pores; male pores on or before 12 (in segment immediately behind testis); macrolecithal, i.e., eggs large, yolky 2

Clitellum more than one cell thick; male pores after 12 (one or more segments behind testis); microlecithal (eggs smaller) 4

(Suborder Lumbricina also classed as Megadrili, the megadrile earthworms).

2. Testes and male funnels not intraseptal; male pores one or two pairs 3

Testes and male funnels in testis sacs suspended from preceding septa; male pores, one pair (rarely two pairs) on 10 or in 10/11 (or 11/12 and 12/13)

Moniligastridae [Oriental and Indian sub-region; Suborder Moniligastrida usually included in eco-taxonomic considerations along with the megadriles].

3. Male pores two pairs on 12, or on 11 and 12; (spermathecae one to three pairs in 6/7/8/9) **Haplotaxidae** [Haplotaxidae is usually classed with the microdriles; cosmopolitan distribution; aquatic or limnic, typically predatory. One species, *Haplotaxis gordioides* (Hartman, 1821) is widely distributed (e.g. in Europe and Champaign, Illinois) probably by transportation; and it is thought to be terrestrial, eg. it was abundant in European WWI trenches (Gates, 1972:59)].

Male pores one pair on 12; (spermathecae opening near 4/5, or 3/4 and 4/5) **Enchytraeidae** (Small white segmented ‘pot worms’; usually excluded from the megadriles and considered with microdriles; littoral, aquatic or terrestrial and frequently in moist forest soils; cosmopolitan distribution but uncommon in tropics).

4 (1). Prostatic glands, or ‘prostate-like’ bursae, discharging through or near male pores or on adjacent segments. (Note: abnormal specimens have aborted glands) 5

Prostatic glands absent and ‘prostate-like’ bursae, when present, not associated with the male pores 12

PROSTATES PRESENT

5 (4). Male pores posterior to segment 16 6

Male pores on segments 13, 15 or 16 11

6. Last hearts in 11; prostates tubular, calciferous glands or 'diverticula' typically in 9 or 9-10, or intramural spaces in some of 8-10 (Ocnerodrilinae), or absent (Malabariinae) **Ocnerodrilidae**

[Circumtropical but not Oriental/Australasian regions; found in Neo-Tropics, Africa; India; about 21 genera, a few species introduced elsewhere; often aquatic].

Last hearts posterior to segment 11; (calciferous glands, if present, not in 9 or 9-10) 7

7. Male pores opening separately from pores of two pairs of prostates in 17 and/or 19, usually male pores on 18, or male and prostatic pores combined or separate on 17 or 19 8

Male pores on 18 (or homeotic equivalent) combined with pores of a single pair of prostates, or on 17 and emerging from ducts of 'euprostates' 10

8. Holoic; (with prostates tubular), gizzard single or reduced **Acanthodrilidae**
(Gondwanan or Pangaeen?)

Holoic; (prostates always tubular?), gizzards multiple **Diplocardiinae/-idea** **
(Gondwanan or Laurasian?)

Meroic; (with prostates tubular or non-tubular) 9

9. Prostates tubular **Octochaetidae**
(Australasian, Indian, Oriental, Ethiopian, Neotropical)

9a. Calciferous glands 2-3 extramural pairs after reproductive organs,

commencing in or near segment 14; (often multiple gizzards) **Benhamiinae**

Michaelsen, 1895/7 (?Ethiopian, Neotropical)

9b. Calciferous glands, if present, not as above; (gizzard usually single)

Octochaetinae Michaelsen, 1900 (?Australasian, Indian, Oriental)

Prostates non-tubular (i.e., racemose or tubuloracemose) **Exxidae**

[Neotropical: Central America and Caribbean, no longer considered 'Australasian'; nine known species in two (or three?) genera. Note: family name by Blakemore (2000) with type-genus *Exxus* Gates, 1959].

10 (7). Male pores on 18, spermathecae present in pre-testicular segments; (prostates tubular to racemose, nephridia holoic or meroic, setae lumbricine to perichaetine) ... **Megascolecidae** (Pangaean?)

Male pores on 17, spermathecae absent from pre-testicular segments, as coelomic cavities combining with ovaries; ('euprostates' present, holoic, lumbricine)

Eudrilidae (Tropical Africa south of the Sahara; about 45 genera, one species introduced to other tropical areas).

11 (5). Body quadrangular; male pores on porophores **Criodrilidae**

[Southwestern Palaearctic: Europe, Middle East, Russia and Siberia to Pacific coast; Japan (*Biwadrilus*); *Criodrilus* introduced into (UK?) and USA and South America and possibly south India; only 2 or 3 species, mainly aquatic].

Body cylindrical; male pores in copulatory pouches **Kynotidae**

[Malagasian: Madagascar; 12 species in primary forests (*Kynotus*)].

PROSTATES ABSENT

12 (4). Oesophageal gizzard(s) or dilations present in pre-testicular segments
..... 13

Oesophageal gizzards or dilations absent from pre-testicular segments
..... 17

13. Extra-mural calciferous glands present 14

Extra-mural calciferous glands absent 15

14. Gizzard in 6; (supra-oesophageal vessel present) **Glossoscolecidae**

[Neotropical: Central, S. America, Caribbean; 200 species, a few species distributed and circumtropical in forest soils or near coast].

Gizzard in 7; (supra-oesophageal vessel absent) **Microchaetidae** [Terrestrial

in Africa especially South African grasslands (eg. *Microchaetus*), (cf. *Kynotus* in Madagascar). *Branchydrilus* Benham, 1888 is poorly known, monotypic for *B. benhami* Michaelsen, 1900: 463 with homeland unknown].

15 (13). Body quadrangular in section, at least in hind-body; (supra-oesophageal vessel present) **Almidae** [Tropical

equatorial (South America, Africa, Indo-Asia); 6 genera, 40 species, some possibly peregrine; aquatic in tropical East Africa (*Callidrilus*), India and Southeast Asia (eg. *Glyphidrilus*). Also limnic, amphibious, or limicolous or in caves in South and Central America, India]. [Note: the genus *Tritogenia* Kinberg, 1867 is meroic rather than holoic. *Glyphidrilus* was placed in

Microchaetidae by some earlier authors, but now is generally under Almidae].

Body cylindrical; (supra-oesophageal vessel absent) 16

16. Male pores paired on 15; (two or three oesophageal gizzards each restricted to a single segment in 6-8) **Hormogastridae**

[Mediterranean, 28 taxa in 4 genera; one species, *Hormogaster redii* Rosa, 1887 in Africa (Tunis and Algeria) and a single record of transport to North America (Gates, 1954; 1972: 61)].

Male pores paired on 22; (one or two oesophageal gizzards each occupying two segments) **Ailoscolecidae**

[Pyrenees and southeast USA, two genera both monotypic, viz. *Ailoscolex lacteospumousus* Bouché, 1969 and *Komarekiona eatoni* Gates, 1974]. [Note: Sims, (1980: 108) put American Komarekionidae Gates, 1974 in synonymy, but Reynolds & Cook, (1993) appear to have maintained it].

17 (12). Testes two pairs in 10 and 11; (intestinal gizzards, when present, in some or all of 17-25) 18

Testes ten pairs in segments 12-21; (intestinal dilations in 21-24) **Lutodrilidae**
(Louisiana southeast USA; riverine or limicolous; monotypic).

18. Intestinal gizzards (and calciferous glands) absent **Sparganophilidae**

(Nearctic, Neotropical: North and Central America, introduced into Europe; Single genus accommodating a dozen or more species; limnic or aquatic).

Intestinal gizzards present 19

19. Intestinal gizzards in or before 20; (calciferous glands present, male pores usually on 15 but some parthenogenic morphs of *Eiseniella tetraedra* have male pores displaced by several segment, most usually on 13 or 11) **Lumbricidae**
 [Holarctic: North America, Europe, Middle East, Central Asia to Japan; several species widely distributed; mostly terrestrial].

Intestinal gizzard in 25 (calciferous glands in 20, dorsal pores present) ... **Tumakidae**
 [Monotypic for *Tumak hammeni* Righi, 1995 from Venadillo (Tolima) Columbia, South America].

** Michaelsen (1900) diassociated his Megascolecidae subfamilies Acanthodrilinae (“A” on page 122) and Diplocardiinae (“D” on page 324) using a key similar to this:

1. Calciferous gland(s) or oesophageal poche(s) in 9 **Ocnerodrilinae**
 Calciferous glands or oesophageal pouches absent or not in 9 2
2. Two or three gizzards in front of testis segments (i.e. before 10 and 11) 3
 Gizzard, if present, single in front of testis segment 10 4
3. Holoic **Diplocardiinae**
 Meroic **Trigastrinae** (= **Benhamiinae**)
5. Vasa deferentia combined with prostatic pores exit on 18 **Megascolecinae**
 Vasa deferentia combined with prostatic pores exit on 18 6
6. Holoic **Acanthodrilinae**
 Meroic **Octochaetinae**

Michaelsen’s divisions seem insightful and phylogenetically valid, but merit elevation to family level plus addition of **Exxidae** - a derivation of **Trigastrinae** (= **Benhamiinae**).

Select References – full references and discussion in Blakemore (2000, 2002, 2006)

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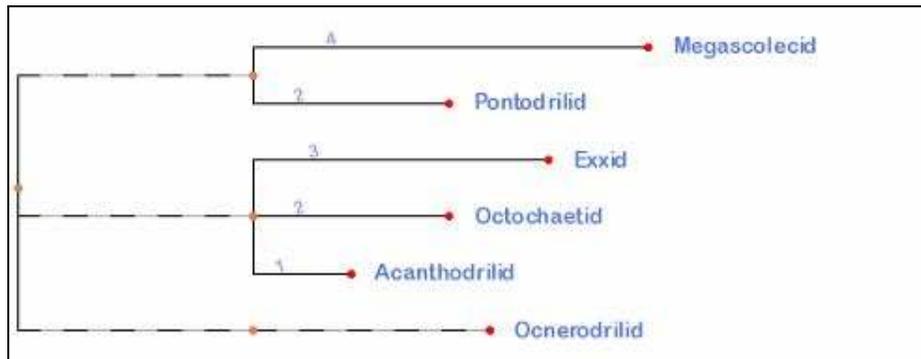
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Appendix 1

Phylogeny of Acanthodrilidae, Octochaetidae, Exxidae, & Megascolecidae revisited with recourse to non-molecular means – a summary of current consensus

"A Darwinian classification, by using two criteria, similarity and common descent leads to the recognition of classes (taxa) of similar entities.." ... "...almost any method of weighing is preferable to using unweighed characters"..."..morphological characters, the product of large numbers of genes, are usually quite reliable" - Ernst Mayr & W.J. Bock (2002: <http://www.blackwell-synergy.com/servlet>). [Other References above].

Key morphological characters - the product of ecological interactions and evolutionary time and expressed by combinations of genes, as found in type-species of type-genera of the families in the title are compared via weighting on basic characters in the more 'primitive' Ocerodrilidae. Phylogenetic position is attributed to similarity (or rather dissimilarity) and descent (or rather ascent), regardless of geographical proximity. Re-analysis again shows the Megascolecidae diagnosed only by its derived, non-acanthodriline male field, irrespective of any other character. Moreover, it is newly resolved into a sub-family with tubular prostates (and holoic nephridia), as found in tribe Argilophilini, (type American *Argilophilus marmoratus ornatus* Eisen, 1893) proposed (including meroic *Driloleirus*) by Fender & McKey-Fender (1990) - although this name competes for priority with Vejdovsky's (1884: 63) resurrected Pontodrilidae and Plutellidae (types Indo-australasian *Pontodrilus litoralis* Perrier, 1874 and Australian *Plutellus heteroporus* Perrier, 1873). The residue of megascolecoid species comply with sub-family Megascolecinae having derived non-tubular prostates (as for the Indian type *Megascolex caeruleus* Templeton, 1844). Further, secondary and subordinate division may be "convenient" within these two sub-families on basis of such features as holoic vs. non-holoic nephridia or lumbricine vs. non-lumbricine setae. Due possibly to the "well known dependence of the conformation of the alimentary tract on food and environment" (Stephenson, 1930: 720), the position within Octochaetidae [type N.Z. *Octochaetus multiporus* (Beddard, 1885)] of sub-family Benhamiinae, currently defined by its arrangement of calciferous glands, is not fully resolved; and neither is the status, validity nor extent of the polygiceriate Diplocardiinae sub-family of Acanthodrilidae (type New Caledonian *Acanthodrilus unguatus* Perrier, 1872). Support for the current phylogeny, using weighted morphology, is that the resulting tree (shown below) is an almost perfect fit for that pertaining to molecular analyses from Blakemore (2005: Fig. 1), with addition of the Exxidae (type *Exxus wyensis* Gates, 1959). Strict comparisons yet require DNA testing, ideally from (type-specimens of) the type-species.



Simple phylogram (above) composed from Fredslund, J. (2006). PHY·FI. *BMC Bioinformatics* (2006, 7: 315. <http://cgi-www.daimi.au.dk/cgi-chili/phyfi/go>) from basic morphological data of type-species (in table below), compared to molecular cladogram, not necessarily from types, (Fig. 1). Note position of *Pontodrilus litoralis* with respect to Megascolecidae and the possibility of restoring Pontodrili-nae/-idae Vejdovsky, 1884.

Taxa / Characters:	Hts >11	Non-acantho	Non-tubular	Non-holoic	(Sub)Family	WEIGHT
<i>Ocnerodrilus occidentalis</i> Eisen, 1878	0	0	0	0	OCNERODRILIDAE	0
<i>Acanthodrilus unguatus</i> Perrier, 1872	1	0	0	0	ACANTHODRILIDAE	1
<i>Octochaetus multiporus</i> (Beddard, 1885)	1	0	0	1	OCTOCHAETIDAE	2
<i>Exxus wyensis</i> Gates, 1959	1	0	1	1	EXXIDAE	3
<i>Pontodrilus litoralis</i> Perrier, 1874	1	1	0	0	PONTODRILINAE	2
<i>Megascolex caeruleus</i> Templeton, 1844	1	1	1	1	MEGASCOLECIDAE	4
					Weighting:- 0 = old; 1 = new.	

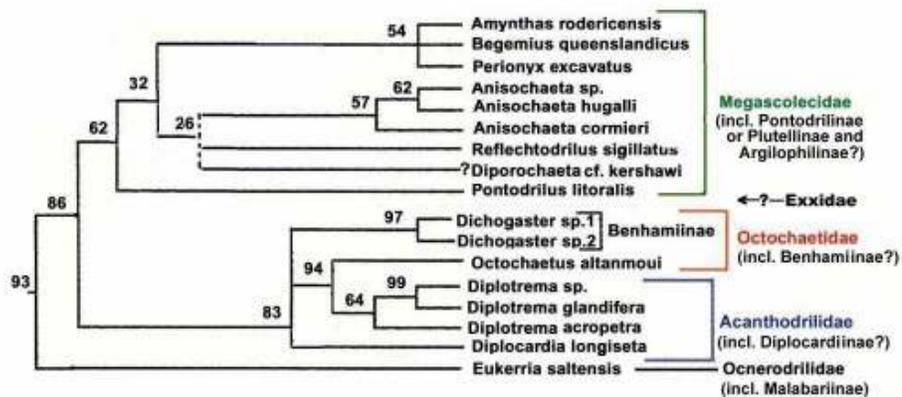


Fig. 1. Phylogram based on molecular analyses (modified and relabelled after Dyne & Jamieson, 2004: Fig. 3); families and species *sensu* Blakemore (2000, 2005).

***Appendix 2** - Sims' (1980: 108) reasons for synonymy of Komarekionidae in Ailoscolecidae, presented by him in a footnote:

"The similarities between *Ailoscolex* Bouché, 1969 and *Komarekiona* Gates, 1974 have not been recognized previously, possibly because of a printing error in Bouché's monograph (1972). In this work, the diagnosis of the family Ailoscolecidae included the statement "Glande de Morren presente" (p. 197), whereas in the account of the anatomy of *A. lacteospumosus* there is the conflicting statement "Glande de Morren absente" (p. 199). The absence of calciferous glands however, was previously established in the original descriptions of the family and species (Bouché, 1969: 526, 529 & 530)."

[End of Introductory Key to World Families of Earthworms].