

The major megadrile families of the World reviewed again on their taxonomic types (Annelida: Oligochaeta: Megadrilacea)

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Abstract. A critique of recent clado-molecular phylogenies notes shortcomings of starting materials, methods applied, and, therefore, their conclusions; hence this review. A new group, Exquisiclitellata, is newly defined as those ‘non-crassiclitellate’ members of the superorder Megadrilacea (*viz.*, Moniligastridae Claus, 1880, plus Alluroididae Michaelsen, 1900 and Syngenodrilidae Smith & Green, 1919). Support for restitution and elevation of American Diplocardiinae Michaelsen, 1900 and Argilophilini Fender & McKey-Fender, 1990 are again raised. ICZN priority requires revival of *Typhoeus* Beddard, 1883 over synonym *Eutyphoeus* Michaelsen, 1900 and the sub-family Typhoeinae (corr. of Typhaeinae Benham, 1890) is re-established. Hoplochaetellinae sub-family nov. is proposed as a development of Octochaetidae s. lato in India. Wegeneriellinae sub-fam. nov. accommodates the holoic members of a restricted Neogastrini Csuzdi, 1996 from W. Africa and S. America. Caribbean family Exxidae Blakemore, 2000 and related Trigastrinae Michaelsen, 1900 are both retained. A contingency table of Megascolecidae s. stricto sub-families and types is presented with some revived and a few new sub-families proposed, particularly from Australasia. These are Diporochaetinae, Megascolidesinae, Celeriellinae, and Woodwardiellinae sub-fams. nov. Synonymy of Perichaetidae Claus, 1880 over Megascolecidae Rosa, 1891 is deferred for reasons of nomenclatural stability. For the large African family Eudrilidae Claus, 1880, a new sub-family, Polytoeutinae, is advanced and the status of abandoned Teleudrilini Michaelsen, 1891 and overlooked Hippoperidae Taylor, 1949 are noted.

Keywords. Earthworm family classification, taxonomic nomenclature, molecular phylogeny, primary types, synonyms.

INTRODUCTION

Megadrile oligochaetes now number about 7,000 named taxa (Csuzdi 2012, and pers. comm. June, 2013). Plus an estimate is of approximately 3,000 aquatic microdriles (exact figures are unavailable) to give a total for Class (or Order) Oligochaeta of *ca.* 10,000 taxa. Twenty years ago Reynolds & Cook (1993) listed 7,254 Oligochaeta species (terrestrial megadriles plus aquatic microdriles), in 780 genera and 36 families, since increased to *ca.* 40 families (Blakemore 2000, Plisko 2013). In comparison, totals for marine Polychaeta are of about 13,000 names – although only 8,000 of these were considered reasonably valid – in 1,000 genera and 82 families (these data from Dr Chris Glasby: <http://www.ea.gov.au/biodiversity/abrs/online-resources/polikey/index.html#history> accessed Dec. 2006). Thus the polychaete workers have allocated roughly the same number of species into

more than twice the number of families with their median ratio of *ca.* 130:12:1. If these classifications are neither artefactual nor excessive, this may be due to the habitats of the earthworms imposing uniformity in external characters and their internal morphology differences being subtle. Nevertheless, a precedent is provided for a greater number of family level divisions in the Oligochaeta in order to match the Polychaeta ratio, as indeed suggested by Blakemore (2005). Whilst accepting that families and genera are useful (*i.e.*, pragmatic) taxonomic ‘convenience’ constructs, it is assumed these can be validated nomenclaturally if not phylogenetically.

Under the ICZN (1999) code, “*Each nominal taxon in the family, genus or species groups has actually or potentially a name-bearing type*” that “*provides the objective standard of reference.*” Often yet mistaken by novices as ‘lumbricids = earthworms’, Lumbricidae is just one of the twen-

ty or so megadrile earthworm families (Blakemore 2005: tab. 1, 2008a, c). And, whilst the important Oriental Moniligastridae gets overlooked by most Occidental researchers, a chronic problem with Pangean Megascolecoidea *sensu* Sims (1980) is that types are often ignored, especially by those (e.g. Sims 1980: 115, Csuzdi 1996: 365, 2010a, b, 2012) who follow Gates (1959: 240, 1972) in ascribing taxa with prostates “*racemose in structure of mesoblastic origin*” to a restrictive Megascolecidae whereas those with prostates “*tubular in structure of ectodermal origin*” are placed in an excessive Acanthodrilidae. Yet, as repeatedly shown by Blakemore (2005: 71, 2008a, 2012b), this syllogism is invalid and fatally flawed as the limited cases cited by Gates (*viz.* “*Stephenson & Ram, 1919 and Pickford, 1937*”) referred to samples, none types, of the families Megascolecidae and Acanthodrilidae *sensu* Michaelsen (1900) as restored by Blakemore (2000) that were already differentiated on their male pores!

Stephenson (1930: 716) regarded Michaelsen’s (1900) “*Das Tierreich*” review of the Oligochaeta as “*a triumph of arrangement which brought order into confusion and constituted a remarkable advance in our understanding of the group*”. This stability remained until Gates (1959) proposed a revised scheme. Almost simultaneously, Lee (1959: 17, 32) mostly supported Stephenson’s ‘Classical System’ as did Blakemore (2000) in reverting to an update of Michaelsen’s system, in order to resolve the chronic family level chaos of intervening schemes. Slight refinements by Blakemore (2005, 2008a, 2012b) aimed to reduce residual confusion with family placement as exemplified with some Caribbean taxa described by James (2004: 277) citing “*Acanthodrilidae*” in the title, “*Megascolecidae*” on page 278 yet describing *Dichogaster* species that belong in either Benhamiinae (that had been restored by Csuzdi, 1996) and/or in Octochaetidae.

Recent attempts to redefine some megadrile families based on molecuolcladistics should be tempered within the constraints (and the starting points) of the taxa named under the current conventions of ICZN (1999) code. Seeking taxo-

nomic solution from genetics may not always be appropriate thus the conclusions of a ‘Molecular phylogeny’ of some worms by James & Davidson (2012) must be treated with caution since biased sampling mostly avoided consideration of types and, without good reason, they ‘sunk’ meroic Octochaetidae that is especially dominant in India/New Zealand and is here revived. The weakness in their study was failure to follow ICZN (1999) whereby a family is defined on the basis of the characteristics of a representative type-genus implicit in the name of the family that is itself defined by the characteristics of its type and included species. Such essential samples of the type-genera were absent in their analyses of the major families, even though type-species of many of these are relatively common. Moreover, as already noted by Gates (1959: 241, 1972: 275), Lee (1959) and Sims (1980: 116), polyphyly has been apparent within Acanthodrilidae and Octochaetidae for some time, thus this same conclusion from James & Davidson (2012: 227) does little to actually resolve the ‘problem’ nor break the impasse to assist students properly place a species in the correct genus and correct family. Better if molecular cladists follow a PhyloCode instead of using Linnean taxonomy, as was independently suggested by Timm (2005: 57).

Compliance with a named genus or family is based on definitive characteristics that have traditionally been morphological and behavioural although molecular data are now also gaining ground starting with a study by Siddal *et al.* (2001). But conclusions from chemical/molecular work by non-taxonomist may often be incompatible with those from morphological/ecological studies by biologists depending on what questions we seek to answer and on what levels of division we apply under a particular system of classification. However, in the *ca.* 255 years use of Linnean scientific names it is realized that taxonomy is not necessarily the same as phylogeny: despite this ideal, Nature is not so accommodating. Moreover, classification and ‘cladification’ are not the same processes. Reconciling an evolutionary/systematic Linnean taxonomy scheme with cladistic phylogenies is often impractical, if not impossible, due to different basic assumptions as

noted in the Preface to the latest Code (ICZN, 1999) where it says: “*The conventional Linnaean hierarchy will not be able to survive alone: it will have to coexist with the ideas and terminology of phylogenetic (cladistic) systematics. From a cladistic perspective, our traditional nomenclature is often perceived as too prescriptive and too permissive at the same time. Too prescriptive, in so far as it forces all taxa (and their names) to fit into the arbitrary ranks of the hierarchy; too permissive, in so far as it may be equally applied to paraphyletic as to monophyletic groups.*” [Bolding added for emphasis by the current author].

This argument is succinctly put on Alan Kazlev/Toby White’s *Palaeos* website by Dr R.K. Brummitt (<http://palaeos.com/phylogeny/cladistics/incompatible.html> accessed July, 2005 and October, 2013):

“*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...*” and...

“*The theory of a Linnaean classification without paraphyletic taxa is nonsensical. Hennig’s proposal to eliminate paraphyletic taxa [from Cladistic studies] was based on a failure to see the difference between the Linnaean hierarchy in which all taxa are nested in the next higher taxon, and a phylogenetic hierarchy which is not so nested, the lower levels of the hierarchy being not equivalent to the higher levels. 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.*” [Bolding added for emphasis].

The fundamental incongruity between the approaches of “*Hennigian Cladistics*” vs. “*Darwinian Classification*” is detailed by Mayr (1998),

Grant (2003) and by Mayr & Bock (2002) who, in favouring a combination of morphological and molecular studies using Linnaean systematics (as per Blakemore *et al.* 2010 and as advocated here), said:

“*When the molecular methods were first introduced, some authors thought that these were automatically superior to morphological characters based on subjective evaluations. But different molecular methods also often led to different results, and it was eventually realized that different molecules may have different rates of change (mosaic evolution) and that morphological characters, the product of large numbers of genes, are usually quite reliable.*”

Mayr & Bock’s (2002) distinctions are for Darwinian Classification: – “*A classification based on two criteria – similarity and common descent*”, plus we might add ‘and often proximity’ with “*...almost any method of weighing is preferable to using unweighed characters*”; and for Hennigian Cladification: – “*An ordering system ... arranged with reference to the sequence of the branching points ... based on the principle of holophyly*” with ‘holophyly’ used in its restricted Cladist sense.

Particulars of the current issue are that specimens and species of genera that are acanthodriline but have meroic nephridia derived from the ‘primitive’ holoic state are properly allocated under ICZN priority to the currently defined meroic family Octochaetidae and its sibling or sub-families. In each case the precursor to this development of meroic nephridia may reasonably be accepted as an erstwhile member of Acanthodrilidae, regardless of when or where this development occurred. In addition, the derived taxa will, of necessity, indeed be similar to their precursors in many if not most of their features. This last fact – that taxa at the boundaries of transition we set will be similar – is tautological and even if the process is not often directly observable we can readily deduce this outcome in the specimens of our concern, assuming they are correctly characterized and identified. The similarity of Octochaetidae to Acanthodrilidae species was recog-

nized by Lee (1959: 32) although additional information has somewhat eroded his argument for their combination. Thus the current and relatively stable working model for earthworm systematics has yet to be conclusively and definitively refuted, and, even when weaknesses were identified, few workable alternatives were suggested. This issue is treated further in the Results and Revision section below.

Here it is necessary to again restate and refine taxonomic families with the realization that not all the components of an ordered earthworm phylogeny may be available due to extinction and lack of funding support for soil eco-taxonomy such that terrestrial surveys are far from complete and that some taxa remain misdescribed pending revision, ideally based on primary types or neotype specimens (see Blakemore 2008a, Blakemore *et al.* 2010). Earlier, Blakemore (2000, 2005, 2006b) had discussed the key issues and problems of previous family level classification and noted that Michaelsen (1900) disassociated his Megascolecidae subfamilies Acanthodrilinae (on page 122) and Diplocardiinae (on page 324) using a key to megascolecoidea from Michaelsen (1900: 121), similar to the following that is still applicable today:

1. Calciferous gland or oesophageal pouches in 9, 10 (last hearts in 11)..... **Ocnerodrilinae**
 – Calciferous glands/pouches absent or not in 9, 10 (last hearts after 11) **2**
2. (Acanthodrilinae male pores and) two or three gizzards in front of first testes **3**
 – Not such an arrangement of (male pores and) gizzards... **4**
3. Holoic nephridia (two per segment) **Diplocardiinae**
 – Meroic nephridia (more than two)
 **Trigastriinae** (*cf.* Benhamiinae and Exxidae)
4. Spermathecal pores behind 8/9 often fused with female pore **Eudrilinae**
 – Spermathecal pores on or before 8/9, or absent..... **5**
5. Vasa deferentia combined with prostatic pores exit on 18 **Megascolecinae**
 – Vasa deferentia not so combined with prostatic pores on 18 **6**
6. Holoic **Acanthodrilinae**
 – Meroic..... **Octochaetinae**

Michaelsen’s divisions seem remarkably insightful and phylogenetically valid based on contemporary knowledge, except that Eudrilidae is now separated off and most other sub-families merit elevation to family level plus addition of Exxidae – perhaps a local derivation of Trigastriinae Michaelsen, 1900 (*cf.* Benhamiinae Michaelsen 1895) as discussed herein. An ‘ideal’ phylogenetic arrangement for these megascolecoidea taxa based on weighted morphology of their primary types is shown in Fig. 1.

Any family review without consideration of types is meaningless; however, if monophyly is strictly employed then each type deserves its own unique family or else all families may telescope into the earlier taxon. Clearly a rational moderation is required.

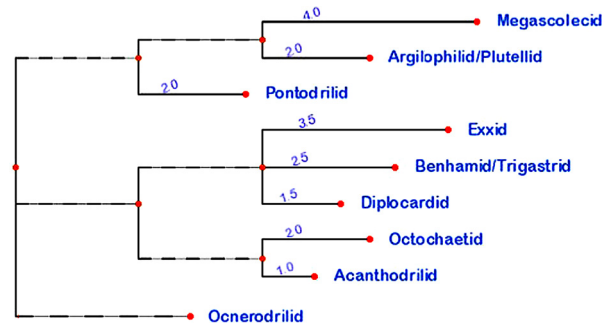


Figure 1. Phylogeny of the Megascolecoid taxa constructed on weighted morphology of their types after Blakemore (2008: fig. 3 corresponding to an actual molecular phylogram presented in Blakemore 2005: fig. 2, 2008: fig. 1).

TAXONOMIC RESULTS AND REVIEW

Annelida Lamarck, 1802: Oligochaeta Grube, 1850 suborder Lumbricina De Blainville, 1828, was classed as Terricolae Örsted, 1843 (part.) or, most appropriately, as Megadrili Benham, 1890, now constructed as Superorder Megadrilacea when used by Gates (1972, 1982), Sims (1978, 1980), Easton (1981: 33) and Righi (1984) to described Stephenson’s (1930) megadriles, *i.e.*, mainly ‘true’ terrestrial earthworm as opposed to smaller, aquatic microdriles that lack capillaries on their nephridia (Beddard 1895: 157) and other features noted by Gates (1972: 28). Megadrilines

comprise the Moniligastrida (for Moniligastridae Claus, 1880) + Lumbricina or Haplotaxida from Easton (1981: 35) “*After Sims, in press*”. Megadrilacea seems to have priority to later non-inclusive names and includes the very important Oriental terrestrial family Moniligastridae and some lesser families. Although theoretical or ‘higher’ taxa are unregulated by ICZN code, henceforth the Megadrilacea is composed of what some authors insist on calling ‘Crassiclitellata’ (= Lumbricina or Haplotaxida) plus the Exquisiclitellata that is newly defined for those non-crassiclitellate members of the Megadrilacea, (viz. families Moniligastridae and Alluroididae Michaelsen, 1900 along with monotypic Syngenodrilidae Smith & Green, 1919) characterized by their delicate or thin (single-cell) clitella and concomitant large ova. Aside from phylogenetic merit, this term avoids the inexactitude of what James & Davidson (2012: 213) call in part “*the non-crassiclitellate ‘earthworms’*” and what Pop *et al.* (2005: 143) tag as “*Alluroidina and Moniligastrida*” that they properly include under megadrile oligochaetes in their molecular studies.

Review and revision of Onerodrilidae, Acanthodrilidae and Octochaetidae

Classically seen as closest to the root-genus in the phylogenic ‘tree’ of all megascolecoïd worms (Stephenson 1930), the tropical Afro-American Onerodrilidae Beddard, 1891 currently includes Indian sub-family Malabariinae Gates, 1966 the members of which, however, lack ‘onerodriline diverticula’ and thus may have different origins, possibly meriting elevation to separate family status. As Gates (1942: 66, 1979: 162) initially suggested, the Onerodrilidae are considered a more primitive sibling group of the Megascolecoidea, closest to ancestral forms, an idea that has gained support from preliminary molecular data (Blakemore, 2005: figs. 1–2, 2008; Pop *et al.*, 2005; Christoffersen, 2008: 97).

For Acanthodrilinae Claus, 1880, Michaelsen (1910: 53), in a paper seemingly often overlooked, subdivided the family into several ‘sectio’ or tribes that should be reconsidered: viz. Acantho-

drilacea that presently includes his Diplotremacea (syn. Eodrilacea Michaelsen, 1910), Neodrilacea (syn. Maoridrilacea Michaelsen, 1928), Chilotaacea [type Chilean *Chilota* Michaelsen, 1899 (non Aubertin, 1930 Diptera), type *Mandane littoralis* Kinberg, 1867: 100 (et *littoralis* = *Mandane patagonica* Kinberg, 1867)], and Maheinacea [types *Maheina* Michaelsen, 1899 for monotypic *Acanthodrilus braueri* Michaelsen, 1897 from Mahé, Seychelles that Cs. Csuzdi (pers. comm. 13th May, 2008) says is probably an Onerodrilidae], plus meroic Howascolacea belonging in, or allied with Octochaetidae. This latter, perhaps the most primitive of the octochaetids, is now monotypic for Malagasy *Howascolex madagascariensis* Michaelsen, 1901 as remarked on by Stephenson (1930: 819, 843) with removal of similar species garnered in the genus from China (now in *Ramiella* Stephenson, 1921), India (now in *Konkadrilus* Julka, 1988 or *Wahoscolex* Julka, 1988) and America (now in *Ramiellona* Michaelsen, 1935 and *Graceevelynia* Graff 1957).

Following Pickford’s (1937) extensive revision, Lee (1959) maintained two tribes of his concept of Acanthodrilinae, one equivalent to Neodrilacea Michaelsen, 1910 having regular alternation of holoic nephropores much like in strictly megascolecoïd Plutellinae members with type-genus *Plutellus* Perrier, 1873 presently restricted to a few species from central coastal New South Wales (see Blakemore 1994b).

Csuzdi (1996: 350-351) redefined Acanthodrilidae to accept either the holoic (Acanthodrilinae s. Csuzdi) or meroic (Octochaetinae Michaelsen, 1900) states, but this was soon confounded by a rather contrived tribe Neogastrini Csuzdi, 1996: 363 that allowed either state and was unacceptably heterogeneous, consequently its genera were re-allocated by Blakemore (2005: 72): holoic genera to Acanthodrilidae and meroic genera to Octochaetidae. Furthermore, it was noted that Csuzdi’s (1996: 365) definition of Megascolecoidea with only racemose prostates separated from Acanthodrilidae s. Csuzdi with tubular prostates (and holoic or meroic nephridia) is super-

ceded by the redefinitions by Blakemore (2000, 2005, 2008a) as repeated herein. Revisions by Csuzdi (1995, 1996, 1997, 2010a, b) had re-established “Benhamiinae Michaelsen, 1897” for meroic species with 2–3 pairs of extramural calciferous glands beginning in or after segment 14 but its relationships to other sub-families were unclear. Blakemore (2005, 2008a) accepted a reduced Benhamiinae and considered revision and restoration of Diplocardiinae Michaelsen, 1900 (but with meroic components removed to Octochaetidae as per Michaelsen 1933) and of Trigastriinae, which seems to be gaining support. Moreover, Benhamiinae may be elevated having an independent lineage possibly with no relation to Indian/NZ octochaetids (Blakemore 2005: tab. 2, fig. 2; Csuzdi pers comm. Aug. 2013) nor to the other two American taxa.

Monotypic West African genus *Monogaster* Michaelsen, 1915 (type-species *M. bidjumentensis* Michaelsen, 1915 from Cameroon) according to Csuzdi (1996: 358) belongs in (Acanthodrilidae: Benhamiinae) tribe Benhamiini as defined by Csuzdi (1996: 351) with two large gizzards before segment 10, three extramural calciferous glands in 14–17 and meroic nephridia with meganephridia caudally. This genus *Monogaster* is unusual in having a single, combined gizzard in 5–6, calciferous glands in 15–17 and saccular meroic nephridia, thus it should possibly be separated off

into a new sub-family (as Monogastrinae) leaving a restricted definition of Benhamiini.

The other tribe, Neogastrini, was newly defined by Csuzdi (1996: 363) with a single gizzard in 5 (sometimes rudimentary), calciferous glands in 14–15 and holoic or meroic nephridia. Csuzdi (2010b: 105) retained this diagnosis (but with gizzard in 6 sometimes vestigial or absent), yet having holoic taxa in this group is still problematic.

Csuzdi (1996: 365, 2010b) included holoic West African genera *Wegeneriella* Michaelsen, 1933 and *Pickfordia* Omodeo, 1958 in subfamily Benhamiinae that was originally as Sippe (German = clan or tribe) Benhamiacea Michaelsen, 1895: 23 and later as Benhamini (Michaelsen, 1897: 3, 7, 25) then Benhaminae (Eisen, 1900: 208) – as reported in Michaelsen (1900: 330) where it was included in synonymy of his subsequent Trigastriinae Michaelsen, 1900: 330 perhaps because Benham (1890: 231) had made *Benhamia* Michaelsen, 1889 a junior synonym of his prior *Trigaster* Benham, 1886, but this genus was later restored, as Benham (1890: 281) indeed proposed; see also Stephenson (1923: 469; 1930), Gates (1959: 256). Thus it seems the correct date and orthography is Benhaminae Michaelsen, 1895 rather than “Benhamiinae Michaelsen, 1897”. Nevertheless, these holoic taxa belonging in Acanthodrilidae as redefined by Blakemore (2000, 2005, 2008a) are here revisited (Table 1).

Table 1. Characters distinguishing ‘Neogastrini’ genera after Csuzdi (2010b: tab. 1)

Genus	Distribution	Nephridia	Gizzard	Ca glands	Spermathecae
<i>Wegeneriella</i> Mich., 1933	W. Africa	Holoic	Present	Common duct	Unpaired
* <i>Neogaster</i> Čern., 1934	S. America	Meroic*	Present	Common duct	Paired
* <i>Wegeneriona</i> Čern., 1939	S. America	Meroic*	Present	Common duct	Unpaired
<i>Pickfordia</i> Omod, 1958	W. Africa	Holoic	Absent	Separate duct	Paired (and diverticulate)
<i>Omodeoscolex</i> Csuzdi, 1993	S. America	Holoic	Absent	Separate duct	Paired (adiverticulate)
<i>Afrogaster</i> Csuzdi, 2010	W. Africa	Holoic	Absent	Common duct	Paired (adiverticulate)
<i>Pickfordiella</i> Csuzdi, 2010	W. Africa	Holoic	Present	Common duct	Paired (and diverticulate)

*The two meroic genera comply with Octochaetidae/Benhamiinae/Neogastrini; all other holoic genera returned or newly transferred to Acanthodrilidae and now Wegeneriellinae (details in body of text).

Table 1 reproduces information provided by Csuzdi (2010b: tab. 1) of characteristics of the Neogastrini sorted chronologically. Retention of genera separated only on their unpaired male and/or spermathecal pores is tenuous as several other genera (e.g. *Amyntas* Kinberg, 1867) include both paired and unpaired states, although some other genera, e.g. megascolecid *Fletcherodrillus* Michaelsen, 1891 and eudrilids such as *Libyodrillus* Beddard, 1891, are primarily defined by the unpaired state. Thus *Pickfordiella* Csuzdi, 2010 may be derived from *Wegeneriella* Michaelsen, 1933, and *Wegeneriona* Černosvitov, 1939 from *Neogaster* Černosvitov, 1934. These latter two meroic genera comply with Neogastrini Csuzdi, 1996 *s. strict* (types *Neogaster* Černosvitov, 1934 and *Neogaster americanus* Černosvitov, 1934) and both are from South America.

However, the other holoic genera in the table do not comply and should be returned to Acanthodrilidae and possibly to a restored Diplocardiinae but, since they lack the required duplication of gizzards, they qualify for a new sub-family as here proposed:

Family Acanthodrilidae Claus, 1880

Sub-family Wegeneriellinae sub-fam. nov.

Diagnosis. Acanthodriline male pores, holoic nephridia, presence of a single gizzard in 5 or 6 sometimes vestigial or absent, calciferous glands in segments 14–15 and with lumbricine setae.

Types. *Wegeneriella* Michaelsen, 1933 and *Notiodrilus valdiviae* Michaelsen, 1903.

Distribution. Africa and South America as show in Csuzdi (2010b: fig. 1 although this differs somewhat to Csuzdi, 1996: fig. 7 especially for *Pickfordia* and *Wegeneriella*) for genera *Wegeneriella*, *Pickfordia*, *Omodeoscolex*, *Afrogaster* and *Pickfordiella* but excluding the two remaining Neogastrini *s. stricto* genera (*Neogaster* and *Wegeneriona*).

Remarks. Wegeneriellinae currently complies with Acanthodrilidae. It is possible that different phylogenetic origins apply to African and American taxa (e.g. Diplocardiidae, Benhamiidae and Exxidae) compared to the Australasian taxa (Acanthodrilidae, Octochaetidae, Megascolecidae) as keyed from Michaelsen (1900) in the Introduction above (see Fig. 1). Moreover, the retention of some previous sub-families and proposal of new ones may be appropriate (see later sections).

Benhaminae and related groups are shown by Csuzdi (1996, 2010a) to occur in the tropics, in Africa and South America. The mystery remains of why Octochaetinae is more prevalent in India whereas Acanthodrilidae, that occurs mostly in southern lands, is absent from both India and Asia [with possible extinctions from Gondwanan India except for a single dubious species, *Diplocardia* (?) *indica* Stephenson, 1924]. This may have been partly explained >60 years ago by Bahl (1947) when he talks of certain anatomical novelties (e.g. enteronephry) for moisture conservation in monsoonal regions. Thus we may speculate that adaptation of meronephry as a means of water conservation has favoured meroic Octochaetidae in these regions subjected to seasonal but regular floods.

In contrast, the native holoic Acanthodrilidae in Australia (e.g. *Diplorema* spp.) endure periodic and sometimes extended drought, surviving by diapause as discovered by Blakemore (1994a) e.g. for *Diplorema narayensis* Blakemore, 1997; whereas only a few native ‘missing link’ Octochaetidae species are currently known from there, although the massive Northern Territory is currently unsurveyed. Compared to random droughts, seasonal monsoons are more regular and probably survivable for earthworms, with such a climate more conducive to meroic adaptation rather than conservation of an ancestral holoic state. For these meroic octochaetids abundant in India, their most advanced genera are those with development of multiple male pores for which a new Octochaetidae division is here proposed.

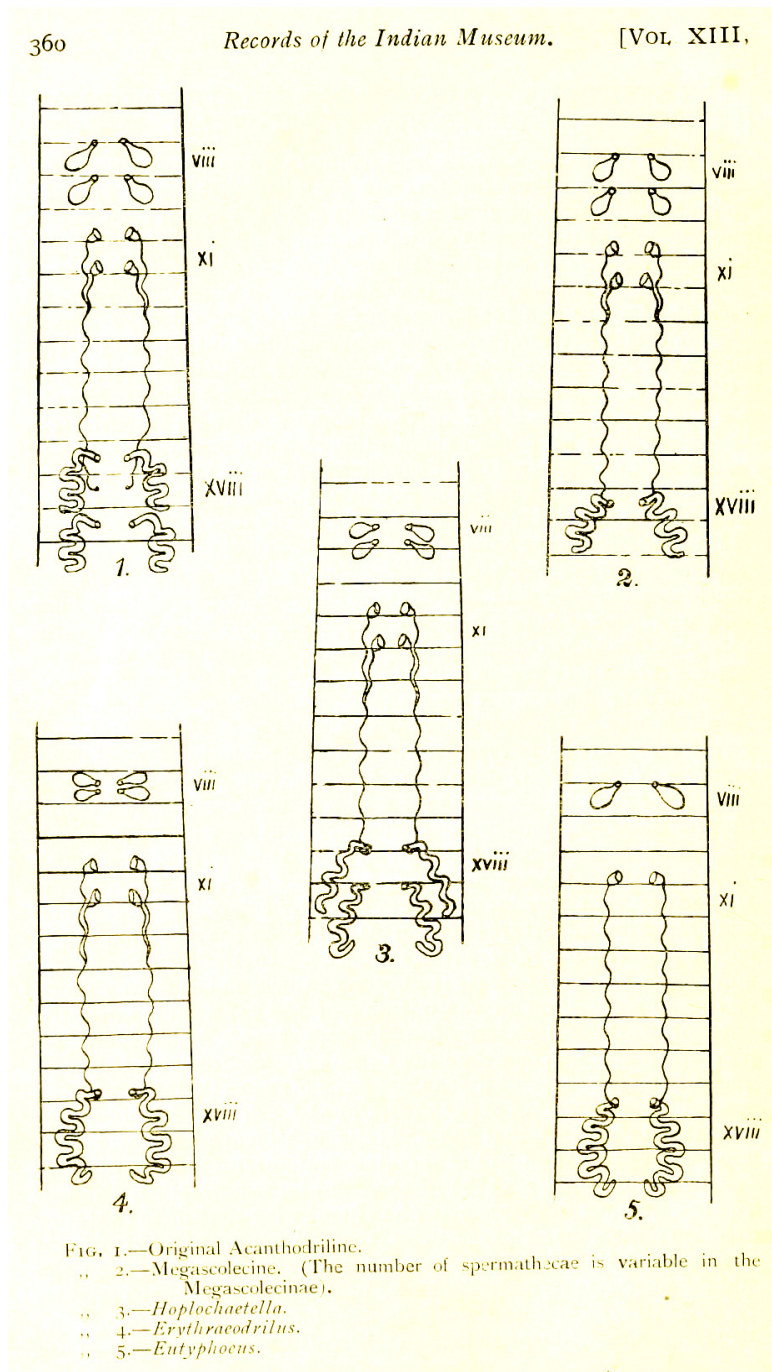


Figure 2. Schema of male fields and of hoplochaetellid earthworms from Stephenson (1917).

Family Octochaetidae Michaelsen, 1900

Sub-family Hoplochaetellinae sub-fam. nov.

Diagnosis. Octochaetidae with perichaetine setae. Male field similar to the acanthodrilinae with

prostatic pores on both 17 and 19 with male pores closely aligned with those either on 17 or with both 17 and 19, a condition termed 'hoplochaetelline' after Gates (1972: 329). Single oesophageal gizzard before testes. Nephridia meroic.

Types. *Hoplochaetella* Michaelsen, 1900: 321 and *Perichaeta stuarti* Bourne, 1886: 667 (?syn. *Erythraeodrilus* Stephenson, 1915 with type *E. kinneari* Stephenson, 1915). See Fig. 2.

Distribution. East India (that now involves Sri Lanka and Myanmar) with type plus eighteen species listed by Csuzdi (2012).

Remarks. *Hoplochaetella* type and Stephenson's (1917) species have male pores co-incident near those of the anterior pair of prostates on 17 whereas other species, such as *H. anomala* Stephenson, 1920 have two pairs of male pores near both sets of prostates in 17 and 19. Stephenson (1920: 226) remarked that a similar situation pertained to lumbricine *Eutyphoeus* Michaelsen, 1900: 322 (Octochaetinae) species but that the male pore combined only with the single pair of prostates on 17 (i.e., no prostates on segment 19, similar to the microscolecine reduction with male and prostatic pores closely converged). Gates (1959: 247) notes that these pores are not co-incident in *Eutyphoeus* contrary to earlier assertions

Questions now raised are whether the type of *Hoplochaetella* is representative of all other included members, or should *Erythraeodrilus* be restored and established as the type of a sub-family similar to the one proposed here. Another question concerns the closeness of relationship of perichaetine *Hoplochaetella* to lumbricine *Eutyphoeus*. As only the setae separate them, is it more appropriate to re-establish the existing sub-family Typhaeinae Benham, 1890: 220? Whatever the final outcome, this latter sub-family is corrected to Typhoeinae for type *Typhoeus orientalis* Beddard, 1883 for the following reasons.

Regarding ICZN priority of *Typhoeus* Beddard, 1883: 219, it was given a replacement name *Eutyphoeus* Michaelsen, 1900: 322 (n. n. pro *Typhoeus* Beddard, 1883) seemingly invalidly since the preoccupying Coleoptera genus having type *Scarabaeus typhoeus* Linnaeus, 1785 [itself later un-necessarily renamed *Typhoeus* Boucomont, 1911 (n. n. pro *Typhaeus* Leach, 1815)] was

Typhaeus Leach, 1815 (with an "a" rather than an "o"). "*Typhaeus* Beddard, 1888: 111" is also listed for *Typhaeus gammii* Beddard, 1888: 111 (<http://jcs.biologists.org/content/s2-29/114/101.full.pdf>) although it is a *lapsus* for *Typhoeus* Beddard, 1883. This information is from Michaelsen (1900), Beddard (1901: 195), and from Airey-Neave's Nomenclator Zoologicus (<http://uio.mbl.edu/NomenclatorZoologicus/> accessed 30th Sept. 2013). Thus it seems the name *Typhoeus* Beddard, 1883 should strictly be restored with junior synonym *Eutyphoeus* Michaelsen, 1900; under current ICZN (1999: art. 23.9.1.1) prevailing usage should be set aside since Beddard (1901) vehemently re-establishes the name. This name restoration affects the ca. 50 *Eutyphoeus* taxa accumulated in the last 140 years as provided in the database of Csuzdi (2012).

Typhoeinae (and/or 'Erythraeodrilinae') may in time legitimately replace proposed Hoplochaetellinae; alternatively, all three may be maintained as sub-families of Octochaetidae (at the same time with elevation of Benhamiinae to separate family level?).

As Stephenson (1920: 184) keenly observed: "*The new Hoplochaetella raises some interesting points of morphology and phylogeny, and helps to show, – what is illustrated by other parts of the paper also, and indeed, I suppose, by the experience of systematists in general, – that the smaller our material, the more precise and satisfactory is our systematic work. Here as elsewhere increase of knowledge brings sorrow and trouble, and where before we walked confidently as in the daylight, we hesitate and feel befogged.*"

Revival of Trigastrinae Michaelsen, 1900 and retention of Exxidae Blakemore, 2000

Genus *Exxus* Gates, 1959 was defined on its non-tubular prostates, and Blakemore (2000, 2006a, 2007a) had argued for merger of *Neotrigaster* James, 1991 from Puerto Rico, as the type-species *Neotrigaster rufa* (Gates, 1962), initially poorly characterized but re-described on new material by several authors with 'racemose'

prostates in 17 and 19, differs substantially from *Exxus* only by having three gizzards [in 5–7 (James, 1991: 348) or 6–8 (Borges & Moreno, 1992)]. Of the other two species included in *Neotrigaster* by James (1991) only *N. complutensis* (Borges & Moreno, 1991) belongs in this family. The third species, *Trigaster yukiuyi* Borges & Moreno, 1991, with tubular prostates required returning to its original genus in the family Octochaetidae.

However, since the meric genus *Trigaster* was formerly representative of sub-family Trigastriinae Michaelsen, 1900, this taxon is provisionally restored for consideration as origin of (and/or alternative to) Benhamiinae and/or Octochaetidae Michaelsen, 1900 in the Neotropical region of Central America and the Caribbean. Michaelsen (1900: 330) defined his Trigastriinae either with calciferous glands after ovarial segment 13 (*Dichogaster*) or without these (*Trigaster*); the former condition is characteristic of the prior Benhamiinae leaving the boundaries of a restored Trigastriinae *s. stricto* as redefined below.

(Family Octochaetidae Michaelsen, 1900)?

Sub-family Trigastriinae Michaelsen, 1900 (part.)

Diagnosis. Acanthodrilic male pores with tubular prostates and meric nephridia (as in Octochaetidae); lumbricine setae; two or three oesophageal gizzards; calciferous glands absent.

Types. *Trigaster* Benham, 1886 and *Trigaster lankesteri* Benham, 1886.

Distribution. Mexico and the Caribbean (mostly).

Remarks. Michaelsen (1900: 332) included eight taxa, but those three from India that had calciferous glands (before segment 14) were since reallocated to Indian *Eudichogaster* Michaelsen, 1903 having calciferous glands uniquely in the region of 10–13; and whereas Csuzdi (2012) lists ten *Trigaster* taxa inadvertently included are *Benhamia lankesteri* Michaelsen, 1889 and *Trigaster rufa* Gates, 1962 that was moved to *Neotrigaster* and then to *Exxus* in family Exxidae.

The database also omits *T. yukiuyi* noted above. Thus just ten or so species belong in this sub-family, including *Trigaster minima* Friend, 1911 and *T. setarmata* (?auct.) *species inquirendae*, both of which appear to have been overlooked and for which further work is required (see also Stephenson 1923: 362, 469; 1930; Gates, 1959: 256).

Family Exxidae Blakemore, 2000

The family Exxidae Blakemore, 2000 was revised by Blakemore (2006a, 2007a) to have the following characteristics.

Diagnosis. Acanthodrilic male pores and meric nephridia (as in Octochaetidae) but with non-tubular prostates; lumbricine setae; two or more oesophageal gizzards; intestinal modification possible but calciferous glands not recorded.

Types. *Exxus* Gates, 1959 and *Exxus wyensis* Gates, 1959 (?syn. *Neotrigaster* James, 1991 with type *Trigaster rufa* Gates, 1962 differing mainly in its three gizzards, although either two or three gizzards are permissible in some other genera, such as *Digaster* Perrier, 1872).

Distribution. Neotropical, Central America/Caribbean (viz. Puerto Rico, Cuba); no longer considered ‘Australasian’ (despite two doubtful Australian records). Eight or nine confirmed species transferred from three or four genera. Closest relationships are clearly with fauna in the region of Mexico, Cuba, Hispaniola, and Antilles. Other included species – but not types – come from these genera: *Zapatadrilus* James, 1991, *Trigaster* Benham, 1886, *Cubadrilus* Rodriguez & Fragoso, 2002 (and, doubtfully, *Torresiella* Dyne, 1997).

Remarks. The family as augmented by Blakemore (2007a) includes *Exxus barroii*, *E. cubitensis*, *E. righii* (all comb. novs. from *Cubadrilus* Rodriguez and Fragoso, 2002), plus *E. taina* (Rodriguez and Fragoso, 1995) that comply with *Exxus* type, with *Neotrigaster complutensis* (Borges and Moreno, 1991) and with *N. rufa* (Gates, 1962), the latter type-species of synonymic, heterogeneous genus *Neotrigaster* James, 1991.

Further refinement of subfamilies of Megascolecidae

The diversity within the large family Megascolecidae Rosa, 1891 *s. stricto* is such that a case is put forward for resurrection of some, and proposal of several new, sub-families under ICZN (1999: art. 26) as summarized in Table 2.

Re-analysis again shows the Megascolecidae diagnosed only by its derived megascolecine male field (male and prostatic pores combined on segment 18 or its homeotic equivalent) as opposed to an acanthodriline male field, irrespective of any other character (Tab. 2; Fig. 2). Moreover, it is newly resolved into sub-families mostly from the numerous Australasian taxa comprising ca. 715 species from Australia (Blakemore & Paoletti, 2006, Blakemore, 2008b) and 228 from NZ (Blakemore, 2012a).

Megascolecid species with tubular prostates (and holoic nephridia) are placeable in Vejdov-

sky's (1884: 63) resurrected families Plutellinae (with objective junior synonym Plutellini Eisen 1894: 55) and Pontodrilinae [types Indo-australasian *Pontodrilus marionis* Perrier, 1874 (= *litoralis* Grube, 1855) – see Blakemore (2007c) and Australian *Plutellus heteroporus* Perrier, 1873 – see Blakemore (1994b), respectively]. Note that the name Plutellinae is a senior homonym of a large lepidopteran family of *Plutella* Schrank 1802 (diamondback moths) that requires replacement. Whether Nearctic sub-family Argilophilinae Fender & McKey-Fender, 1990 (type American *Argilophilus marmoratus ornatus* Eisen, 1893: 253) should be merged or separated from Plutellinae, as was suggested by Blakemore (2008), remains to be resolved. Heterogeneously meroic *Driloleirus* Fender & McKey-Fender, 1990 should be excluded from both Plutellinae and Argilophilini (and possibly it too merits a new tribal or sub-family status as Driloleirinae?) – but see Megascolidesinae below.

Table 2. Contingency table of Megascolecidae *s. stricto* sub-families and type of representative type-genus (loosely based on “Bestimmungstabelle der Megascolecinen-Gattungen” (Identification Table of the Megascolecid genera) from Michaelsen (1907: 160) and Blakemore's (2000: 47) table of Tasmanian genera.

Prostates	Nephridia	Setae	Sub-family	Genus
Tubular	Holoic (absent from anterior)	8	Pontodrilinae Vejdovsky, 1884	<i>Pontodrilus marionis</i> Perrier, 1874
Tubular	Holoic	8	Plutellinae Vejdovsky, 1884	<i>Plutellus heteroporus</i> Perrier, 1873
Tubular	Holoic	8	Argilophilinae Fender & McKey-Fender, 1990 (for USA)	<i>Argilophilus marmoratus ornatus</i> Eisen, 1893
Tubular	Holoic	>8	Diporochaetinae*	<i>Perichaeta intermedia</i> Beddard, 1889: 380
Tubular	Meroic	8	Megascolidesinae*	<i>Megascolides australis</i> McCoy, 1878
Tubular	Meroic	>8	Celeriellinae*	<i>Spenceriella duodecimalis</i> Michaelsen, 1907
Non-tubular	Holoic	8	Woodwardiellinae*	<i>Woodwardia callichaeta</i> Michaelsen, 1907
Non-tubular	Holoic	>8	Perionycinae Benham, 1890: 221	<i>Perionyx excavatus</i> Perrier, 1872
Non-tubular	Meroic	8	Cryptodrilinae Beddard, 1890: 236 / 1891: 256	<i>Cryptodrilus rusticus</i> Fletcher, 1886
Non-tubular	Meroic	>8	Megascolecinae Rosa, 1891	<i>Megascolex caeruleus</i> Templeton, 1844

* Sub-family nov.

Megascolecidae Rosa, 1891

Sub-family Diporochaetinae sub-fam. nov.

Diagnosis. Megascolecidae with tubular prostates, holoic nephridia and non-lumbricine setae.

Types. *Diporochaeta* Beddard, 1890 and *Perichaeta intermedia* Beddard, 1889 syn. *Perichaeta novae-zelandiae* Beddard, 1888: 434 (nomen nudum) – see Blakemore (2012a: 130).

Remarks. Included genera are those such as *Diporochaeta* and *Provescus* Blakemore, 2000 that comply with the diagnosis above. Note that Reynolds & Cook (1993: 4) cited family “*Diporochaetidae*” (actually a lapsus for Lumbricidae (sub-)family Diporodrilidae Bouché, 1970) – see Blakemore (2008c).

Sub-family Megascolidesinae sub-fam. nov.

Diagnosis. Megascolecidae with tubular prostates, non-holoic nephridia and lumbricine setae.

Types. *Megascolides* M’Coy, 1878 and *Megascolides australis* M’Coy, 1878.

Remarks. Included are Indian species of *Megascolides* that were transferred to *Scolioscolides*, *Barogaster* and *Travoscolides* by Gates (1940) leaving the original genus confined to Australian and New Zealand (North Island). North American species of *Megascolides* transferred to *Driloleirus* by Fender & McKey-Fender (1990) may possibly be included or should be retained separately as noted above. Based on contemporary knowledge Benham (1890: 220) had included *Megascolides* in his family Typhoeidae Benham, 1890 (corr. of Typhaeidae) that was (in part) in synonymy of Michaelsen’s Octochaetinae its type-genus being *Typhoeus* Beddard, 1883 that, however, had already been (invalidly) renamed *Eutyphoeus* Michaelsen, 1900 as discussed above under the proposed Hoplochaetellinae sub-fam. nov.

Sub-family Celeriellinae sub-fam. nov.

Diagnosis. Megascolecidae with tubular prostates, non-holoic nephridia and non-lumbricine setae.

Types. *Celeriella* Gates, 1959 and *Spenceriella duodecimalis* Michaelsen, 1907

Remarks. The new sub-family is proposed to accept the residue of perichaetine, meroic taxa with tubular prostates, since *Spenceriella* Michaelsen, 1907 type was synonymized following supposed discovery of non-tubular prostates in the type species, *Diporochaeta notabilis* Spencer, 1900 that made it comply with prior *Anisochaeta* Beddard, 1890, (see Blakemore, 2000: 455; 2008b) in sub-family Megascolecinae. However, this requires re-evaluation on better preserved material as the prostates of this species may in fact be tubular in which case *Spenceriella* and ‘Spenceriellinae’ could be restored as priority replacements for Celeriellinae. Transfer of Australian species (and the four New Zealand species with tubular prostates that were formerly placed in *Spenceriella* in Lee, 1959) to the primarily Indian genus *Celeriella* was thought a probable temporary taxonomic ‘convenience’, pending further review of constituent species, by Blakemore (2000).

Sub-family Woodwardiellinae sub-fam. nov.

Diagnosis. Megascolecidae with non-tubular prostates, holoic nephridia and lumbricine setae.

Types. *Woodwardiella* Stephenson, 1925 and *Woodwardia callichaeta* Michaelsen, 1907.

Remarks. Diagnosed as in the table (Tab. 2) and redescription by Blakemore (2000: 283) with component taxa in Australia and New Zealand, including *Zacharius* Blakemore, 1997, as per Blakemore (2008b, 2011, 2012a). Note that Sri Lankan and Indian taxa formerly in *Woodwardiella* such as *W. uzeli* Michaelsen, 1903 and *W. kayankulamensis* Aiyer, 1929 were removed by Gates (1960: 240) to meroic *Notoscolex* Fletcher, 1886 and/or to *Lenoscolex* Gates, 1960 and thus belong in other sub-families.

Table 2 shows Cryptodrilinae Beddard, 1890 and Perionycidae Benham, 1890 provisionally restored for megascolecids with non-tubular prostates, meroic nephridia and setae that are lumb-

ricine or perichaetine, respectively, as originally comprised but with compliant genera updated and provided in Blakemore (2000: 46, 2008b, 2012b). The residue of megascolecoid species are most derived with their non-tubular prostates, meroic (i.e. non holoic) nephridia and perichaetine (i.e., non lumbricine) setae in sub-family Megascolecinae Rosa, 1891 *s. stricto*; examples of member genera are such as Indian *Megascolex* and Australasian *Anisochaeta* Beddard, 1890 plus Oriental pheretimoids – the *Pheretima* auct. of Sims & Easton (1972).

Michaelsen (1900: 161) included prior Pleurochaetidae Vejdovsky, 1888 in synonymy of Megascolecinae since its type-genus, *Pleurochaeta* Beddard, 1883 was found a synonym of *Megascolex*. Another claimed synonym (Michaelsen, 1900: 120) was Perichaetidae Claus, 1880 for *Perichaeta leucocycla* Schmarda, 1861 that, although probably still an available name, should be avoided for nomenclatural stability. Homonymy of *Perichaeta* Schmarda 1861 with *Pericheta* Rondani, 1859 (Diptera) was due to confusion of an extra “a”. cf. Airey-Neave (<http://www.ubio.org/NZ/>) and Sabrosky (1999 http://www.sel.barc.usda.gov/Diptera/people/FCT_pdf/FGNAMES.pdf) for Dipteran homonyms in which it is stated:

“*Pericheta Rondani 1859: 152 (unjustified new name for Policheta Rondani). Type, Tachina unicolor Fallen 1820 (aut.) = Policheta unicolor (Fallén). Tachinidae. Senior synonym (not the basis of a family-group name): Policheta Rondani 1856: 67. Type, Tachina unicolor Fallén 1820 (orig. des.) = Policheta unicolor (Fallén). Tachinidae.*”

Perichaeta (error) Brauer & Bergensta 1889: 99 (31). Perichaetidae Brauer & Bergensta 1889: 82, 99 (14, 31). Note. Herting (1984: 23) adopted Perichaeta on the ground that Policheta was the “misspelled homonym of Polychaeta Macquart 1851.” The “homonym” was repeated in Herting & Dely-Draskovits (1993: 153). However, Policheta and Polychaeta are distinct names (Code, Art. 56b), not homonymous.”

Although there may be rare citations after 1899, Michaelsen (1900: 212) reported the last species named was *Perichaeta schmardaie macrochaeta* Michaelsen, 1899 (= *Duplodicrodrilus schmardaie*) from Japan and China. Since “*Perichaeta paeta* Gates, 1935: 13” is a mistake for *Pheretima paeta* (= *Metaphire paeta*) from China, thus, the requirements for ICZN (1999: Art. 23.9) reversal of precedence are met and as Sims & Easton (1972: 176) explain: “*Michaelsen made Perichaeta Schmarda, 1861 a junior syn. of Megascolex which it has remained ever since and perhaps should continue to do so for reasons of nomenclatural stability, although non-occupied and still available*”.

Eudrilidae revision and division to sub-families

African Eudrilidae Claus, 1880 is perhaps the most developed family with special euprostates receiving the sperm ducts and with ovaries closely connected to modified spermathecal openings that allow possibility of direct, internal fertilization of eggs (e.g. Sims 1969). Current sub-families are Eudrilinae Claus, 1880 with calciferous glands and testes enclosed in sperm reservoirs or Pareudrilinae Beddard, 1894 that has calciferous glands absent or modified from the usual and free testes. Taxa that have lapsed or been overlooked are Tribe Teleudrilini Michaelsen, 1891: 57 (type *Teleudrilus ragazzii* Rosa, 1888) plus monospecific Hippoperidae Taylor, 1949 that was erected for *Hippopera nigeriae* Taylor, 1949, supposedly distinguished by a second pair of male pores and mostly ignored since (cf. Gates 1959). Here a new sub-family is advanced.

Eudrilidae Claus, 1880

Sub-family Polytoeurtinae sub-fam. nov.

Diagnosis. Eudrilidae with lumbricine setae, holoic nephridia, oesophageal gizzard and calciferous glands present. Male pores with euprostates opening midventrally in or near segment 17. Spermathecal pores also midventral, typically behind the male pores.

Types. *Polytoreutus* Michaelsen, 1890 and *Polytoreutus coeruleus* Michaelsen, 1890: 24 (genus misspelled 'Polytoreutes' by Benham, 1890). See Fig. 3.

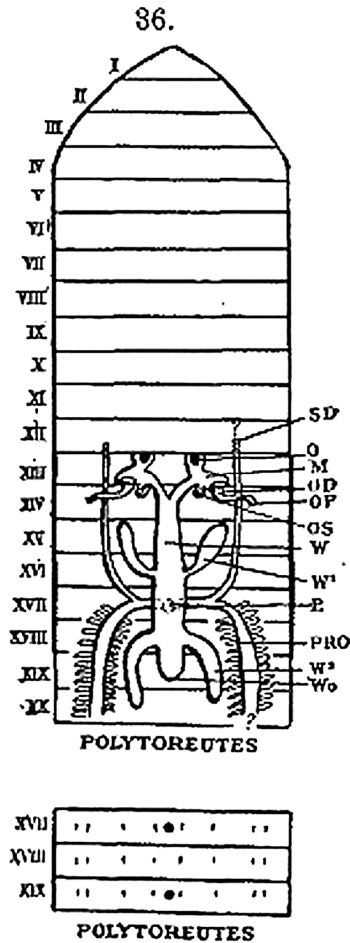


Figure 3. *Polytoreutus* diagram (misspelt POLYTOREUTES) from Benham (1890: fig. 36)

Distribution. East and Central Africa. Csuzdi (2012) databases ca. 40 species of *Polytoreutus*. Compliance of similar genera will be considered on their particulars.

Remarks. This sub-family belongs to the section of the family characterized by unpaired, mid-ventral male (and spermathecal pores) grouped under the name "Teleudrilinen" by Michaelsen (1891: 41) that he defined (according to Beddard: 265 as tribe Teleudrilini) thus: "Die Teleudrilinen sind meganephridische, mit 4 Borsten-paar Rei-

hen ausgestattete Terricolen, die eine einzige ventral-mediane männliche Geschlechtsöffnung auf oder am 17 Segment und eine einzige ventral-mediane Samentaschenöffnung hinter der Intersegmentalfurche 10/11 besitzen". Although he included *Polytoreutus* in his list of genera (Michaelsen, 1891: 55), he later abandoned the group and, moreover, the type-genus definitions of *Teleudrilus* (from Michaelsen, 1900: 411) has male pore in 19 preceded by spermathecal pore in 13/14.

Especially unique in Polytoeutinae and *Polytoreutus* is having the spermathecal pore behind the male pores, possibly as the most advanced development from the usual paired situation and with the spermathecal pores in front of the male pores. Whether all other eudrilids having mid-ventral reproductive pores should be included at this time is uncertain as, for example, in *Buettneriodrilus* Michaelsen, 1897 like in *Teleudrilus* these typically precede the male pores. Other similar genera are reviewed by Owa (1998).

A similar genus is *Hyperiodrilus* Beddard, 1890: 563 that has intestinal as well as or instead of the usual oesophageal gizzard; it has about a dozen species (plus other species of synonyms *Heliiodrilus* Beddard, 1890: 627; *Alvania* Beddard, 1893 and *Iridodrilus* Beddard, 1897) with erst-while synonym *Segunia* Sims, 1985. Inclusion of these latter two genera, plus those of Segun (1980) [viz. *Parapolytoreutus* and *Digitodrilus* (= *Tubiscolex* Michaelsen, 1935) see also Owa (1998)] is also uncertain at present despite them sharing midventral male and spermathecal pores as indeed do the Pareudrilin *Eudriloides* Michaelsen, 1890 and *Libyodrilus* Beddard, 1891, etc., to mention just a few genera. Genus *Keffia* Clausen, 1963 sometimes has spermathecal pores behind male pores but this location may be independently acquired and, since these are paired, it is thus non compliant.

The question of restoration of the prior Teleudrilinae in place of Polytoeutinae remains uncertain and further family refinement is obviously required, although some support for this new sub-

family is provided by preliminary molecular studies. Pop *et al.* (2005: fig. 3) showed some separation of *Polytoreutus* spp. from *Polytoreutus montsikenya* Beddard, 1902 and James & Davidson's (2012: fig. 4 cf. Fig. 3) Eudrilidae groupings had one composed of *Polytoreutus finni* Beddard, 1893 plus an "*Hyperiodrilus* sp." separate from an "*Eudriloides* sp.", although the other *Hyperiodrilus* specimen (*H. africanus*) appeared unresolved, possibly due to misidentification of specimens. Unfortunately, the types were not tested for Eudrilidae [type: *Eudrilus decipiens* Kinberg, 1867 a junior synonym of the common 'African Night Crawler' *Eudrilus eugeniae* Kinberg, 1867 that is readily available globally as a vermicomposting species, e.g. Blakemore (1994a) provides its first Australian records, and full characterization and distribution are in Blakemore, 2012b] nor for *Polytoreutus coeruleus* type of Polytoerutinae. James & Davidson (2012: 225) incorrectly state suboesophageal sacs are always unpaired in Eudrilidae (cf. Segun, 1980).

Evaluation of James & Davidson's (2012) molecular phylogeny

Whilst acknowledging the research supported in part by US National Science Foundation Awards (DEB- 0516439 and 0516520) funded collection trips "*in the USA, France, Spain, Andorra, Romania, Hungary, Gabon, Kenya, South Africa, Madagascar, Thailand, the Philippines, Brazil, Fiji, the Antilles, Japan, and Australia*", despite this travel, a major difficulty with the study by James & Davidson (2012) is a general lack of representative material and the non-identification of many of the specimens providing the samples: these merely being categorized to a genus or to a presumably *a priori* family allocation (e.g. "*Ocnerodrilidae* sp.", "*Acanthodrilidae* sp.", "*Almidae* sp."). Giving the impression of progressing revision of the major families they yet failed to test the key type-genera, admitting (James & Davidson, 2012: page 226) that "*we did not have material from the diverse 'Octochaetidae' of the Indian subcontinent*", and "*we did not have them represented in the taxon*

sample" [referring to holoic genera excluded from Banhamiinae *vide infra* but they mistakenly include meroic *Wegeneriona* as an holoic taxon], and "*leave the status of the Exxidae until such a time as someone actually finds a specimen of Exxus...*", and (on page 227) a "*lack of material from South Asia, where there are many Megascolecidae, including the type genus Megascolex*". For Acanthodrilidae (page 226) they accept their "*lack of data*" and only give two examples for their analysis. However, neither of these two samples may be reliable as one is identified only as "*0828 Acanthodrilidae sp. Madagascar*" and the other as "*0904 Diplotrema sp. Australia*". Whilst Malagasy Acanthodrilidae are not particularly well represented and are far from the New Caledonian type-locality, some of those few species known there are reported in Razafindrakoto *et al.* (2010) and Blakemore (2012b). But by being unidentified, not even to genus, this specimen must be suspect since all other specimens in their study labelled "*Acanthodrilidae*" actually belong to Octochaetidae/Banhamiinae or to Exxidae. As for their "*Diplotrema* sp.", this is an Australian/New Zealand genus frequently misidentified in the past from America and/or Africa (often as its junior synonym *Eodrilus* Michaelsen, 1907) – it is again unfortunate that the specimen was not identified to species at least, since some supposed Australian members were actually octochaetids.

For example, several native *Diplotrema* spp. described from Queensland were subsequently found to belong to *Octochaetus*, e.g. *Octochaetus ambrosensis* (Blakemore 1997) and those formerly in *Neodiplotrema* Dyne, 1997 (nom. preocc. Yamaguchi, 1938 = *Adroitplema* Blakemore, 2006 nom. nov.) are all now in synonymy of *Octochaetus* Beddard, 1893. The preoccupied genus *Neodiplotrema* had been used in molecular phylogeny (quoted for instance by Csuzdi, 2010a), as evidence that Acanthodrilidae was separate from Octochaetidae although this genus was recognized (by Blakemore, 2000: 46; 2004: 175; 2008b, 2009, 2012a: 129) as a junior synonym of *Octochaetus* – the type-genus of the family – and may be more properly used in such limited phylograms to defend retaining the Octochaetidae.

James & Davidson (2012: 227) also misinform on Australasian taxonomy when they mention New Zealand *Megascolides* and *Spenceriella* having “*tongue-shaped prostates*” because, firstly, *Spenceriella* Michaelsen, 1907 was determined by Blakemore (2000) to be a junior synonym of *Anisochaeta* Beddard, 1890 and, secondly, *Megascolides* M’Coy, 1878 members just have tubular prostates. Those taxa from New Zealand described with “*tongue-shaped*” prostates properly belong in a restored genus *Tokea* Benham, 1904, which was recently resolved by Blakemore (2012a: 120). They also recited “*Terriswalkerius* sp.” (sic - misspelling) that actually belongs in either of prior *Diporochoeta* Beddard, 1890 or *Perionychella* Michaelsen, 1907 or in *Reflechto-drilus* Blakemore, 2005 as demonstrated by Blakemore (2000, 2008b, 2011, 2012a). Many similar problems in the previous molecular phylogeny by Buckley *et al.* (2011) – oft cited by James & Davidson (2012) for support – were already addressed in Blakemore (2011: 25, 42–43) where it was noted “*Thus, rather than clarity we get further confusion and, as with several previous molecular phylogenetic works, the only errors in their otherwise informative study are the names.*”

Species of polygicierate Exxidae Blakemore, 2000 that share the type’s meric nephridia plus ‘non-tubular’ prostates (rather than “*racemose*” as misrepresented by James & Davidson, 2012: 215, 226) are here restored as noted above even though they left this problem for “*someone*” else to fix. Their sample, identified with *Neotrigaster rufa* (= *Exxus*?), was found to be most closely related molecularly to a *Diplocardia* sp. (*D. conoyeri* Murchie, 1961). This in no way detracts from the inclusion of the former taxon in the family Exxidae since its acquisition of non-tubular prostates and meronephy is probably via precursors that would be attributable to a restored Diplocardi-inae/-idae as Blakemore (2005, 2008a) indeed proposed that gains some support from the study by Pop *et al.* (2005). James & Davidson (2012: 215, 222) prelabel and conclude these two taxa (i.e., non-type representatives of Diplocardiinae and of Exxidae) as “*ACANTHODRILIDAE*”.

Surprisingly for an authority who claims familiarity with the debate, James (1991) seemed to have missed the essential similarity of *Trigaster rufa* Gates, 1962 (mislabelled as “*T. rufa* Gates, 1954” www.jstor.org/stable/3226771), the type-species of his *Neotrigaster* James, 1991, that was placed by Blakemore (2005) as a probable junior synonym to the genus *Exxus* Gates 1959 – the establishment of which was the reason for Gates’s (1959) revision of Megascrolecoidea families that of itself caused so much unnecessary confusion since. James & Davidson (2012), as with James (1991), fail to even cite Gates (1959).

Their only novel contribution was erection of Pontoscolecidae James & Davidson, 2012: 227 that, unfortunately, is an objective junior synonym with same type as Urochaetidae Beddard, 1891 – long since combined, along with Geoscolecidae Rosa, 1888 and Rhinodrilidae Benham, 1890, under Glossoscolecidae Michaelsen, 1900: 420.

It is of note that Beddard’s papers were “*Read 19th February and 19th March 1890*” and if he had distributed separates (‘preprints’) at that time it would take precedence under ICZN (1999: art. 21.8.1), and although date for Rhinodrilidae Benham, 1890 is not obvious, on page 280 Benham adds a postscript dated “*April 30th*”. Furthermore, Geoscolecidae Rosa, 1888 (corr. Geoscolicidae Beddard, 1895: 622) has overall priority over Glossoscolecidae Michaelsen, 1900 although *Geoscolex* Leuckart, 1841 is now held a junior synonym of *Glossoscolex* Leuckart, 1835. Unless the breaking up of the classical Glossoscolecidae Michaelsen, 1900 is not warranted, there may then be an argument for restoration of reconstituted (sub-)families: Urochaetidae, Geoscolicidae and Rhinodrilidae as by Benham (1890: 221) and Beddard (1891, 1895: 626). Possibly another sub-family is merited for perichaetine *Periscolex* Cognetti, 1905 (as ‘Periscolicinae’). Shuffling of these groups has been unnecessary in the century following Michaelsen’s (1900) excellent review that admirably provided an ideal for ICZN aims of “*Standards, sense and stability for animal names*”. Work is yet required to fully resettle this important family group from the Neotropics.

Despite their conclusion of separation of *Biwadrilus bathybates* (Stephenson, 1917) from Criodrilidae, only partial sequence data (James & Davidson, 2012: 225) was presented for the widespread and common type-species of the family, *Criodrilus lacuum* Hoffmeister, 1845, and no morphological differentiation was provided at all. Blakemore (2007b) dismissed the distinguishing characteristic of Biwadrilidae of a supposed ‘lateral line’ as found in a fish, leaving only its distinctive male pores in 13. The lateral line was a figment and having male pores varying from segment 13 to 15 is entirely permissible in genus Lumbricidae. As Blakemore (2007b) stated: “Justification for separation off of Biwadrilidae (or Biwadrilus) on this character now seems invalid (cf. Sims, 1980). Moreover, Stephenson (1930: 911) remarking on his *Criodrilus bathybates* under *Criodrilinae* further says: “the forward shifting of the male pores is paralleled in *Eiseniella*.”” DNA barcode data (COI gene) from topotypes of *Biwadrilus bathybates* are provided in the Appendix to help confirm identity of this species and thus the resolution of the family.

Regarding Benhaminae revision as noted above, James & Davidson (2012: 226) further say: “Blakemore (2005) considers this inclusion [of merioic genera in an holoic Acanthodrilidae] by *Csuzdi* ‘unacceptable’ but gives no reasons for preferring the condition of the nephridia over the condition of the calciferous glands as indicators of phylogeny.” To clarify, the rather obvious reason is that when we follow the ICZN code it is the condition found in the representative type of the type-genus that defines the family and it is a fundamental flaw to consider or report otherwise. Thus only holoic species strictly belong in holoic genera and only holoic genera belong in Acanthodrilidae; merioic genera belong elsewhere (in present or proposed families) albeit nephridia are secondary to the condition of the reproductive organization as is consistently shown by Michaelson (1900, 1907) and by Blakemore (2000, 2005) (and intuitively in Plisko, 2013: tab. 2). Also, the presence or absence of gizzards and calciferous glands has long been recognized as of lesser importance since they may be more adaptive due to

the “well known dependence of the conformation of the alimentary tract on food and environment” accorded by Stephenson (1930: 720).

As further justification, a recent new African family Tritogeniidae Plisko, 2013 is separated from Microchaetidae Beddard, 1895 by virtue of its merioic nephridia, although she defines it (Plisko, 2013: 79) as “merioic; two or more small nephridia per segment” meaning probably ‘merioic: two or more pairs of small nephridia per segment’. Having non-holoic nephridia is the same reason why (Indo-Australasian?) Octochaetidae is separated from Acanthodrilidae, again giving support to the reasonable separation of the latter two families with the proviso, as proposed by Blakemore (2005, 2008a) that polygiceriate Diplocardiinae/idea be restored for North American acanthodrilids as per Michaelson (1900). If this were the case, then relationship and origin of the American octochaetids (cf. Trigastriinae) is likely with this group as, in its turn, would be the Caribbean Exxidae Blakemore, 2000.

James & Davidson (2012: 226) conclude “The problematic Acanthodrilidae, Megascolecidae and Octochaetidae” with the speculation that: “It seems simpler to afford racemose prostates less weight, in recognition that evolution of complex prostates from simple ones [which they, like Gates and Sims before, misconstrue as “non-racemose”] has taken place several times in the history of megascolecoid earthworms.” Albeit this particular argument relates more to Exxidae (see Blakemore, 2005, Introduction and Fig. 1 above), James & Davidson (2012: 227) did finally agree with Blakemore’s (2000) classification of the Acanthodrilidae and Megascolecidae. Consistently, Blakemore (2000, 2005, 2008a) had explained that the morphological division is not between tubular and racemose prostates, rather it is between tubular and non-tubular, i.e., any derivation from the ancestral (plesiomorphic) tubular prostate form. Thus, Blakemore’s (2000) revision was well founded since it endorsed the views of Johann Wilhelm Michaelson (1860–1937) and John Stephenson (1871–1933), the two pillars of Classical earthworm studies, when

Michaelsen (1907a: 160) divided his Megascolecinae *s. stricto* primarily on the basis firstly of either tubular or non-tubular prostates, and secondly on holoic or meroic nephridia, and Stephenson (1923: 7, 316) when he 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*”.

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Appendix.

DNA COI barcode of *Biwadrilus bathybates* (Stephenson, 1917)

Data courtesy of S. Prosser, N. Ivanova and P. Hebert of Guelph University, Canada with donor specimens now in Tokyo Museum under curatorial care of Dr T. Kuramochi.

BLAST analysis is from <http://www.ncbi.nlm.nih.gov/genbank/>.

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>JET096|Tokyo specimen An-414.1|Criodrilus_bathybates|COI-5P
AACACTATATTTTATTCTTGGCGTATGAGCGGGAATAATTGGGGCTGGAATAAGCCTTCTAATTTCGAATTGAGCTAAG
ACAGCCTGGTGCCTTTTTAGGAAGAGACCAACTTTACAATACCATTGTCACAGCCCATGCTTTCATTATAATTTTCTTT
TTAGTGATAACCAGTATTATCGGGGGATTGGAAATTGATTACTACCTTTAATACTGGGGGCACCTGACATAGCTTTCC
CACGATTAACAATATAAGATTTTGGCTACTACCCCATCCCTAATTCTTTTAGTATCTTCAGCTGCAGTTGAGAAGGG
GGCTGGGACTGGATGAACTGTATATCCTCCACTTGCCAGAACTTAGCCACGGAGGGCCCTCCGTGGATTTAGCAA
TTTTTCACTTCACTTGGCTGGAGCCTCCTCCATTTTAGGGGCTATCAATTTTATTACAATTAATATACGATGA
AACGGCTACGCCTAGAGCGAATCCCATTTTGTGGAGCCGTAACCATTACAGTTGTTCTGCTACTTCTATCCCTTC
CTGTTCTAGCTGGAGCCATTACTATGCTATTAACAGACCGAAATCTAAATACATCATTTTTTGACCCTGCTGGCGCG
GTGACCCTGTTCTATACCAACACCTATTT
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megaBLAST Max Id. 82% GU014166 Glossoscolecidae sp. [sic] from Brazil (DPEW86596 voucher EW-SJ-867).

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>JET098|Tokyo specimen An-414.3|Criodrilus_bathybates|COI-5P
AACACTATATTTTATTCTTGGCGTATGAGCAGGAATAATTGGGGCTGGAATAAGCCTTCTAATTTCGAATTGAGCTAAG
ACAACCTGGTGCCTTTTTAGGAAGAGACCAACTTTACAATACCATTGTCACAGCCCATGCTTTCATCATAATTTTCTTT
TTAGTGATAACCAGTGTATCGGGGGATTGGAAATTGATTACTACCTTTAATACTGGGGGCACCTGACATAGCTTTCC
CACGATTAACAATATAAGATTTTGGCTACTGCCCCATCCCTAATTCTTTTAGTATCTTCAGCTGCAGTTGAGAAGGG
GGCTGGGACTGGGTGAACTGTATATCCTCCACTTGCCAGAACTTAGCCACGGAGGCCCTCCGTGGATTTAGCAA
TTTTTCACTTCACTTAGCTGGAGCCTCCTCCATTTTAGGGGCTATCAATTTTATTACAATGTAATTAATATACGATGA
AACGGGCTACGCCTAGAGCGAATCCCATTTTGTGGAGCCGTAACCATTACGTTGTTCTGCTACTTCTATCCCTTC
CTGTTCTAGCTGGAGCCATTACTATGCTATTAACAGACCGAAATCTAAATACATCATTCTTTGACCCGGCTGGTGCG
GTGACCCTGTTCTATACCAACACCTATTT
```

BLASTn comparison JET096 vs. JET098 Id. 646/658 (98%), i.e., slight difference from two samples of topotypic Lake Biwako specimens collected and identified by RJB.

Note. Genbank voucher samples HQ728920 HQ728949 and JF267906 of *B. bathybates* were reported in James & Davidson (2012) for 16S, 18S and 28S genes possibly based on samples sent by the author to Dr S. James in 2006 (see Blakemore, 2007b: 20) although I cannot find their particulars online via GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>).