

Revised checklist of the Family Exxidae Blakemore, 2000

by R.J. Blakemore,

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COE Fellow, Soil Ecology Group, Yokohama National University, Japan.

Summary

The Caribbean earthworm family Exxidae, now containing eight or nine species, was initially proposed to accommodate the “troublesome” *Exxus wyensis* Gates, 1959, a meroic species with an acanthodriline arrangement of male and prostatic pores that complied with the Octochaetidae except for its racemose prostates. Gates (1959: 258) had allowed *Ex. wyensis* to introduce an acanthodriline state into his redefinition of the Megascolecidae, whereas other authors later allowed it to introduce racemose prostates into the Acanthodrilidae. Neither of these schemes was acceptable, and now this family is separated from Octochaetidae *sensu* Blakemore, 2000 primarily by its non-tubular prostates, and secondarily by having two or three oesophageal gizzards. Both Octochaetidae and Exxidae differ from Acanthodrilidae *sensu* Blakemore, 2000 by their non-holoic nephridia (cf. Benhami-inae/-idea *sensu* Csuzdi, 1996; Blakemore, 2005a; b). This system of classification contrasts with some previous schemes where having 'intermediates' between plesiomorphic (i.e., ancestral) and apomorphic (i.e., derived) states - such as tubuloracemose prostates intermediate between tubular and racemose, was thought to negate the value of these characters in earthworm systematics. Some authors went so far as to make the distinction (if at all), only between racemose and "non-racemose" prostates. Whereas it makes more sense phylogenetically, tautologically, and pragmatically to accept that any derivation from a plesiomorphic state is an apomorphy. Reversion mutations back to these basic states are not known.

Thus, with this reasoning, a sustained increase in setae above 8 per segment in any part of the body is an apomorphy (from lumbricine to anisochaetine or perichaetine states); similarly any combination greater than one pair of nephridia per segment is a valid derivation (from holoic to meroic or to a 'non-holoic' state), and prostates are either tubular or 'non-tubular'.

In general, when regarding tubular prostates, the question is whether they resemble the form found in the undisputedly more primitive families (e.g. Ocnerodrilidae; Acanthodrilidae), and in the primitive genera of Megascolecidae *sensu* Blakemore, 2000 (e.g., *Pontodrilus*, *Argilophilus*, *Plutellus*, *Sebbius*). Some specimens, particularly those that attain large size by surviving for several seasons, appear to have particularly thick tubular glands as the columnar gland-cells regenerate from the periphery, and these may be easily confused with tubuloracemose prostates. We can also find gradations in non-tubular glands, with tubuloracemose glands perhaps

becoming more racemose as the specimen ages. The method of preservation or degree of maceration of specimens may also distort superficial determination of prostate form. For example, the "tubular and highly warty" prostates of the octochaetid specimen described in detail by Chen (1935, 113, fig. 2) as *Howascolex sinicus* Chen, 1935 [= *Ramiella bishambari* (Stephenson, 1914)] probably still qualify as 'tubular'.

It is interesting that no Acanthodrilidae are known to occur naturally in India where Octochaetidae is dominant. Moreover, the Octochaetidae *sensu lato* is probably polyphyletic (as stated by Gates, 1972) with a disjunct distribution in New Zealand, Australia, India, Africa, and Central America, although separation off of Benhami-nae/-idea genera from the latter two locations may resolve this (see Blakemore, 2005c, 2005d). The long anticipated 'missing-link' of native Octochaetidae in Australia was newly determined by Blakemore (2000), e.g., *Octochaetus ambrosensis* (Blakemore, 1997) and several other subsequently described taxa.

Of the names combined in *Neotrigaster* by James (1991), only two belong in Exxidae, the third species, *Trigaster yukiyui* Borges & Moreno, 1991 with tubular prostates, probably requires returning to its original genus in the family Octochaetidae or Benhami-inae/idae. Newly added here are species from the genus *Zapatadrilus* that were recently transferred to *Cubadrilus* as well as other species from this latter genus that have "racemose" prostates (not the type); these appear to merit new combination in *Exxus*. An unauthored taxon, *Trigaster setarmatus* (sic), is also tentatively added to Exxidae, and several similar species are reported to be in preparation from Cuba that possibly would also belong Rodriguez & Fragoso (2002). *Trigaster minima* Friend, 1911, found in soil imported to Kew (from the Caribbean?), seems to have been overlooked in revisions by subsequent authors (eg. Fragoso, James & Borges, 1995; James, 1991; Rodrigues & Fragoso, 2002), thus its status is uncertain.

Two poorly-characterized Queensland taxa, possibly with non-tubular prostates, are *Diplorema? scheltingai* Jamieson, 1997 that, as discussed by Blakemore (2000: 40; 2005a; b), was described with "tubuloracemose prostates" that "appear racemose" but, from the evidence provided, they appear merely thickly tubular (moreover, the probably holoic nephridia were inadequately described), and also the meroic *Torresiella singularis* Dyne, 1997 for which the form of the balantine prostates was not described nor sketched. Both are unlikely to belong in Exxidae as the family is typically for species with multiple gizzards and non-tubular prostates (see Blakemore, 2005).

Precursors to the family would be sought in Acanthodrilidae that secondarily developed meroic nephridia (as in Octochaetidae) and non-tubular prostates (eg. with branching of a central prostatic canal as reported by Michaelsen, 1900, Stephenson,

1930: 370 and Gates, 1959: 258 for *Diplocardia michaelsoni* Eisen, 1899 and *D. udei* Eisen, 1899 this latter miscited by James, 1995: 34 as by "Gates, 1955"). The Benhami-inae/-idae, as recently restored, has multiple gizzards and could be expected to provide direct precursors. If resurrection of the Diplocardi-inae/-idae is warranted, as suggested by recent molecular studies (Blakemore, in press), then this would be a theoretical basal group for both Benhamiinae and Exxidae.

Systematics results

Family **Exxidae** Blakemore, 2000: 33

Type-genus: *Exxus* Gates, 1959. Possible syn. *Neotrigaster* James, 1991: 346 with type *Trigaster rufa* Gates, 1962 that differs mainly in its 3 gizzards [in 5-7 (James, 1991: 348) or 6-8 (Borges & Moreno, 1992)]. Other included species— not types, come from these genera: *Zapatadrilus* James, 1991, *Trigaster* Benham, 1886, *Cubadrilus* Rodriguez & Fragoso, 2002 (and, doubtfully, *Torresiella* Dyne, 1997).

Distribution: Neotropical. Central America/Caribbean (viz. Puerto Rico, Cuba); no longer considered 'Australasian' (despite 2 doubtful Australian records). Eight or nine confirmed species in 3 or 4 genera. Closest relationships are clearly with fauna in the region of Mexico, Cuba, Hispaniola, and Antilles.

Diagnosis: Octochaetidae (i.e. acanthodrilid male pores; meric nephridia) with non-tubular prostates; lumbricine setae; two or more oesophageal gizzards; intestinal modification possible but calciferous glands not recorded. The diagnosis is here emended to allow two or more gizzards.

Gates' (1959: 234) definition of his new genus EXXUS was entirely as follows:

“*Definition.* Quadriprostatic, prostates racemose and of pheretima sort but with ducts opening externally at equators of xvii and xix. Male pores (in seminal grooves that extend from eq/xvii to eq/xix) at eq xviii (?). Setae, eight per segment and paired (throughout?). Gizzards in v-vi. (Intestinal origin in xv?). Calciferous glands (typhlosole, intestinal caeca and supra-intestinal glands?) lacking. Vascular system with complete (single) dorsal trunk, with extra-oesophageal trunks median to hearts, with a supra-oesophageal trunk in ix-xiii but without a subneural (?), (lateroparietal trunks?), and with latero-oesophageal hearts in x-xiii. Excretory system meronephric, nephridia astomate and exonephric (throughout or enteronephric in iii-iv?), massed on parietes in iii-iv, but posteriorly – on each side of each segment – in a transverse row, extending from A nearly to mD just in front of the septum.”

For his species *Exxus wyensis* Gates, 1959 has: size range with macerated posteriors as 450-500 mm by 7-8 mm (estimated to be 150-250 by 9-10 when living).

Spermathecal pores slightly in front of segmental equators in 8-9. Genital markings (with small glands internally) ventral, unpaired presetally in 20, 21 and often one or more similar markings in some of 15-16, 22. Ventral copulatory and penial setae present in 8 and 9, and 17 and 19, respectively. Pigmentation, red(?). Gut filled with humus. "Characterization of excretory organs behind xxx [segment 30] is impossible". Origin: "unknown" but Gates (1959: 253) assumed it Australasian.

Species Checklist:

1. *Exxus barroii* (Rodriguez & Fragoso, 2002: 131). **Comb. nov.**
Cubadrilus barroii Rodriguez & Fragoso, 2002: 131, fig. 2. From Cuba.
2. *Exxus cubitasensis* (Rodriguez & Fragoso, 2002: 133). **Comb. nov.** Ex
Cubadrilus cubitasensis Rodriguez & Fragoso, 2002: 133, fig. 3. From Cuba.
3. *Exxus righii* (Rodriguez & Fragoso, 2002: 134). **Comb. nov.**
Cubadrilus righii Rodriguez & Fragoso, 2002: 134, fig. 4. From Cuba.
4. *Exuus taina* (Rodriguez & Fragoso, 1995: 23). **Comb. nov.**
Zapatadrilus taina Rodriguez & Fragoso, 1995: 23. From Cuba [originally as *Zapatadrilus taina* with etymology: "Se refiere a uno de los grupos aborigenes de Cuba" these peoples also known as "Taino" or "La Taina", thus the noun does not require declension to match the genus and the name remains the same].
5. *Exxus wyensis* Gates, 1959: 234. Origin unknown; syntypes in Harvard MCZ catalogue (erroneously?) listed as coming from Singapore.
6. *Neotrigaster complutensis* (Borges & Moreno, 1991: 40).
Trigaster complutensis Borges & Moreno, 1991: 40. From Puerto Rico.
Neotrigaster complutensis : James, 1991: 348.
7. *Neotrigaster rufa* (Gates, 1962: 3).
Trigaster sp. Gates, 1954: 244. From Puerto Rico.
Trigaster rufa Gates, 1962: 3 [made type]; Borges & Moreno, 1992.
Neotrigaster rufa : James, 1991: 248.
[This taxon not listed in Reynolds & Cook (1979); sometimes miscited as "Gates, 1954" eg. by James (1991: 346, 348, 349), cf. Borges & Moreno (1992)].
- ?8. *Trigaster setarmata* [authorship unknown, cited as *Trigaster setarmatus* (sic – although ICZN, 1999: Art. 30 says genera ending in *-gaster* are feminine) in Rodriguez & Fragoso (2002: 128) having non-tubular (= racemose?) prostates and with 3 gizzards]. **Species incertae sedis.** From Cuba.
- ?9. [*Diplostrema ? scheltingai* Jamieson, 1997: 241. From Queensland (poorly described)]?

- ?10. [*Torresiella singularis* Dyne, 1997: 153. From Torres Straits (merozoic i.e. Octochaetidae, but form of prostates unspecified)]?

Discussion of phylogenetic analyses of Exxidae

A phylogram presented by Rodrigues & Fragoso (2002: fig. 5) appears to show their computed species, now included in *Exxus s. lato* (and therefore in Exxidae), are paraphyletic as their taxa group only loosely. However, these authors also recognize (page 136) that in their analysis *Zapatadrilus* forms a paraphyletic group, so extra work is required for adequate resolution. Possibly if apomorphic character states such as non-tubular prostates had been weighted in the computations, or if the prostate form had been characterized for the chosen outgroup [two of Csuzdi's (1994) *Eutrigaster* species: *E.(E.) pobozsnyae* and *E. (Graffia) rodriguezii* that had prostates either small, or large but "ebenfalls zusammengerollten" (mutually interlinking) and so probably tubular], then the result would be more phylogenetically informative. When James (1991) considered "ancestral" states, the resulting phylogram he presented has the two *Neotrigaster* members of Exxidae separating out on synapomorphies of "racemose" prostates (and tanylobic prostomia). No other evidence has been located to deduce phylogeny of Exxidae although the excluded species in the two phylograms mentioned above were not considered in Csuzdi's (1996, 2000) catalogues of Benhamiinae species, thus by default the precursors remain in Octochaetidae. Further refinement of family definitions is in progress.

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