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Original article

Checklist and phylogeny of Exxidae (Oligochaeta)

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Abstract

The genus *Exxus* Gates, 1959 was overlooked until its designation as type-genus of the Caribbean earthworm family Exxidae Blakemore, 2000. Four new inclusions are: *Exxus barroi*, *Exxus cubitasensis*, *Exxus righii* (all comb. nov. from *Cubadrilus* Rodriguez and Fragoso, 2002), plus *Exxus taina* (Rodriguez and Fragoso, 1995) comb. nov., that comply with type *Exxus wyensis* Gates, 1959, and with *Neotrigaster complutensis* (Borges and Moreno, 1991) and *N. rufa* (Gates, 1962), the type-species of junior synonym *Neotrigaster* James, 1991. Other tentative *species inquirendae* are *Trigaster minima* Friend, 1911 and *Trigaster setarmata* (?auct.). Phylogenetic placement and distribution of Exxidae relative to Benhami-inae/idae, Diplocardi-inae/idae, Trigastrinae and of these in relation to Acanthodrilidae, Octochaetidae and Megascolecidae are discussed based on key morphological characteristics of the respective type-species of each.

Keywords: Latin American; Earthworm; Biodiversity; Systematics; Taxonomy; Morphology

1. Introduction

The family Exxidae Blakemore, 2000 was initially proposed to accommodate the ''troublesome'' and enigmatic *Exxus wyensis* Gates, 1959[1] (genus ''X'' from location 'Y''), a species with an acanthodriline arrangement of male and prostatic pores that complied with meroic Octochaetidae except for its racemose prostates. Gates believed that tubular prostates were of ectodermal origin and racemose ones mesodermal, but in each case he cited these were for species with acanthodriline and non-acanthodriline male apparatus, respectively, i.e., proven neither for acanthodriline species such as *Ex. wyensis* with non-tubular prostates nor for megascolecine species for genera such as *Pontodrilus* or *Plutellus* with tubular prostates. And, whereas Gates [13] allowed *Ex. wyensis* to introduce an acanthodriline state into his redefinition of the Megascolecidae, other authors allowed it to introduce racemose prostates into definitions of Acanthodrilidae. Both situations were clearly unacceptable, and it became necessary to separate off Exxidae from both Acanthodrilidae and Octochaetidae *sensu* Blakemore, 2000 primarily on its non-tubular prostates, and secondarily on its having multiple (two or three) oesophageal gizzards. Almost simultaneously, Csuzdi [8,9] extracted and restored sub-family Benhamiinae, which also differed from Acanthodrilidae mainly by its acquisition of non-holoic nephridia. The current system of classification [1,3] contrasts with some previous schemes whereby having 'intermediates' between plesiomorphic and apomorphic states—such as tubuloracemose prostates intermediate between tubular and racemose—was thought to negate the value of these characters to earthworm systematics. Some authors went so far as to make the

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[1] Not all taxonomic authorities are cited in the references.

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distinction (if at all), only between racemose and ''non-racemose'' prostates. However, it makes more sense phyolgenetically, tautologically and pragmatically to accept that any derivations from an ancestral plesiomorphic state—such as from tubular to non-tubular prostates or holoic to non-holoic nephridia—are derived apomorphies. Reversion mutations to these basic states are not known, at least in earthworm systematics.

The Exxidae initially comprised the type plus two former *Neotrigaster* James, 1991 species while the third species combined in *Neotrigaster* by James [17], *Trigaster yukiyui* Borges and Moreno, 1991 [5] with tubular prostates, was returned to its original genus that presently resides in Octochaetidae. Csuzdi [8] deliberately excluded genera such as *Trigaster*, the type-genus of Trigastrinae, which lacked extramural calciferous glands when he restored Benhamiinae, retaining them instead in his concept of Octochaetidae [3]. Michaelsen [22] had subsumed the prior Benhamiinae Michaelsen, 1895/7 within his sub-family Trigastrinae Michaelsen, 1900 that disappeared according to Gates [13] when Stephenson [27] and later Michaelsen transferred its genera to the Octochaetidae.

2. Materials and methods

Older and recent publications were trawled for relevant additional taxa that comply with family definition to produce an updated taxonomic species checklist. Phylogeny of super-family Megascolecoidea was evaluated based on weighting of key characteristics of the type-species of the relevant type-genera (Table 1) using PHI-FI [11] to produce a phylogram (Fig. 1). The current revision follows conventions and extends recent classification by Blakemore [1,3] and complies with the International Code [16].

3. Systematics results

3.1. Family Exxidae Blakemore, 2000

3.1.1. Type-genus

Exxus Gates, 1959 with type-species *Exxus wyensis* Gates, 1959, origin unknown but Gates [12] assumed it was ''Australasian'' and perhaps analysis of the gut contents (if any remain) or DNA sample of syntypes may provide evidence for provenance. The other included genus is *Neotrigaster* James, 1991 with type-species *Trigaster rufa* Gates, 1962 [14] that differs mainly in its three rather than two gizzards, and included species come from the following genera originally defined for type-species with tubular prostates: *Zapatadrilus* James, 1991, *Trigaster* Benham, 1886, *Cubadrilus* Rodriguez and Fragoso, 2002 (and, questionably, *Torresiella* Dyne, 1997).

3.1.2. Diagnosis

Acanthodriline male apparatus with non-tubular prostates; lumbricine setae; meroic nephridia; two or more oesophageal gizzards; intestinal modification possible but extramural calciferous glands not recorded. Penial (and copulatory) setae often present.

3.1.3. Distribution

Neotropical: Central America/Caribbean (viz. Puerto Rico, Cuba); no longer considered Australasian [1,4]. Closest relationships are clearly with polygiceriate fauna in the region of Mexico, Cuba, Hispaniola, and the Antilles.

3.2. Species checklist

1. *Exxus barroi* (Rodriguez and Fragoso, 2002: 131). Comb. nov.: *Cubadrilus barroi* Rodriguez and Fragoso, 2002: 131; Fig. 2. From Cuba.

Table 1
Key characters weighted for type-species within the taxonomic family-group of Megascolecoidea each given their prior designation

Type-species	A	B	C	D	E	Total W	(Sub-)Family
Ocnerodrilus occidentalis Eisen, 1878	0	0	0	0	0	0	Ocnerodrilidae
Acanthodrilus ungulatus Perrier, 1872	1	0	0	0	0	1	Acanthodrilidae
Octochaetus multiporus Beddard, 1885	1	0	0	1	0	2	Octochaetidae
Diplocardia communis Garman, 1888	1	0	0	0	0.5	1.5	Diplocardiinae
Benhamia rosea Michaelsen, 1889	1	0	0	1	0.5	2.5	Benhamiinae
Trigaster lankesteri Benham, 1886	1	0	0	1	0.5	2.5	Trigastrinae
Exxus wyensis Gates, 1959	1	0	1	1	0.5	3.5	Exxidae
Pontodrilus litoralis Perrier, 1874	1	1	0	0	0	2	Pontodrilidae
Megascolex caeruleus Templeton, 1844	1	1	1	1	0	4	Megascolecidae

Characters: A, calciferous glands absent or in other than just segment 9; B, non-acanthodriline male pores; C, non-tubular prostates; D, non-holoic nephridia; E, non-polygiceriate; W, weighting (0, ancestral; 1, derived). The appropriate ranks of the family groups are unresolved here.