

Review of Criodrilidae (Annelida: Oligochaeta) including *Biwadrilus* from Japan

R. J. BLAKEMORE¹

Abstract. Palaeartic family Criodrilidae Vejdovsky, 1884 is briefly reviewed and revised to reabsorb Biwadrilidae Brinkhurst & Jamieson, 1971, monotypic for lacustrine/limnic *Biwadrilus bathybates* (Stephenson, 1917) based on examination of new Lake Biwa material from recent earthworm surveys. Comparison is with type species: *Criodrilus lacuum* Hoffmeister, 1845. Synonymy in *Criodrilus* of monotypic genus *Hydrilus* Qiu & Bouché, 1998 from Algeria is accepted but with provisional restoration of its type as *Criodrilus ghaniae* (Qiu & Bouché, 1998) **comb. nov.**, if indeed it belongs in the Criodrilidae. Another recent taxon *Guarani camaqua* Rodríguez & Lima, 2007 from rice fields of Rio Grande do Sul, Brazil is **syn. nov.** of *Criodrilus lacuum* at species and genus level since its characteristics are easily embraced within interspecific variability. Moreover, the prior taxon, *C. lacuum*, was already known from its type-locality. Distribution, ecology and species associations of the criodrilids are briefly summarised including a report of *C. lacuum* maintained in a laboratory culture for >42 years (T. Timm pers. comm.). A key to species is provided.

INTRODUCTION

Michaelsen (1900: 420) had initially assigned the semi-aquatic and Palaeartic subfamily Criodrilinae under Glossoscolecidae, yet Michaelsen (1918) and Stephenson (1930: 888, 904) thought affinities of *Criodrilus* were common descent with Madagascan *Kynotus* from an original *Drilocrius*-form which probably inhabited Ethiopian Africa; they further thought *Criodrilus* was the ancestor of the Lumbricidae. In an alternative view, Stephenson (1930: 889, 904, 910) postulated that *Criodrilus* was a lumbricid modified though having adopted an aquatic life, and that origin of the Lumbricidae needed to be sought elsewhere. For Gates (1972: 50), the closest relationships of Criodrilidae, based on extra-oesophageal trunks of the vascular system lateral to the hearts, were with the Moniligastridae (here thought highly unlikely) or Alluroididae, if not also the Haplotaxidae and the Sparganophilidae (here thought more likely). Differences in the ovaries, he believed, contraindicates close relationships between the Criodrilidae and the Lumbricidae; but Sims (1980: 114), Rota & Omodeo (1992) and Sims & Gerard (1985: 40; 1999: 40), had Criodrilidae with

greater affinities with superfamily Lumbricoidea (at that time comprising of Sparganophilidae, Ailoscolecidae, Hormogastridae, Lumbricidae, and Lutodrilidae), and recent molecular analysis by Pop *et al.* (2004) seems to support similarity to, but separation from, the Lumbricidae.

The following revision of Criodrilidae Vejdovsky, 1884 is augmented from the most recent review by Blakemore (2006) where within it was proposed to return to Criodrilidae the species *Biwadrilus bathybates* (Stephenson, 1917) that was originally in *Criodrilus* and later monotypic for *Biwadrilus* Brinkhurst & Jamieson, 1971 – the erstwhile type genus of their Biwadrilidae – based on newly collected material. This formal publication defines the current taxonomic *status quo* of the family with review of all three of its constituent species including the type *Criodrilus lacuum* Hoffmeister, 1845 which has been, at various times, included in the Lumbricidae.

MATERIALS AND METHODS

The family is reviewed and species are described using format and methodologies of Blakemore (2002; 2006). Taxonomy complies with

¹Dr. Robert J. Blakemore, Yokohama National University, Yokohama, 240-8501, Japan, and Lake Biwa Museum, Oroshimo, Kusatsu, Shiga, 525-0001, Japan. E-mail: robblakemore@bigpond.com

ICZN (1999). The only widely distributed taxon, type-species, *C. lacuum*, is described below and is compared with *C. ghaniae* and a redescription of *Biwadrilus bathybates*. Voucher specimens of *Biwadrilus* and other earthworms are held in the Lake Biwa Museum (LBM) or Yokohama National University (YNU).

TAXONOMIC RESULTS

Family Criodrilidae Vejdovsky, 1884

Biwadrilidae Brinkhurst & Jamieson, 1971: 809, **syn. nov.**
 Criodrilidae Vejdovsky, 1884: 63; Michaelsen, 1921: 141;
 Gates, 1972: 49; Sims, 1980: 107; Blakemore, 2000: 33,
 2002: 243, 2006: 398.
 Criodrilinae: Michaelsen, 1900: 463; Stephenson, 1930: 721.

Type genus: Criodrilus Hoffmeister, 1845 (syns. *Hydrilus* Qiu & Bouché, 1998; *Guarani* Rodríguez & Lima in Lima & Rodríguez, 2007 **syn. nov.**).

Type species: Criodrilus lacuum Hoffmeister, 1845.

A second less well-known and possibly dubious species is *Criodrilus ochridensis* Georgevitch, 1950 (author sometimes miscited as "Gjorgjevic, 1949") from Lake Ochrid, Macedonia. The *Hydrilus* taxon may merit provisional retention as species *Criodrilus ghaniae* (Qiu & Bouché, 1998) **comb. nov.** on such characters as its dorsal pores (?and tubercular pubertatis), but determination of presence or absence of nephridia from the anterior apparently needs further investigation. South American species included in *Criodrilus* by Michaelsen (1900) – e.g., *C. breymanni*, *C. buergeri*, *C. iheringi* – were transferred to *Drilocrius* Michaelsen, 1917 (Family Almididae) by Michaelsen (1918) as they possessed spermathecae rather than spermatophores. The English species from Suffolk *Anagaster fontinalis* Friend, 1921, now in synonymy of *Helodrilus oculatus* Hoffmeister, 1845, was erroneously associated with *Criodrilus* in the past and may account for the only British report. Trans-Aegean *Criodrilus dubiosus* Örley, 1881 was transferred as *Allolobophora dubiosa* by Örley (1885: 24) and now resides in *Aporrectodea* (Lumbricidae). A new inclusion in *Criodrilus lacuum* at both species and genus level is Brazilian *Guarani camaqua* Rodríguez & Lima, 2007 **syn. nov.** for reasons discussed below.

Diagnosis (from Michaelsen 1900; Stephenson 1930; Gates 1972; Sims 1980; Blakemore 2006): Fresh and brackish water worms. Body quadrangular in section (at least in posterior). Prostomium zygotobitic (epilobitic in *Hydrilus*). Nephropores in 6 lines (throughout?). Clitellum multilayered, annular

in (14,15),16-45 or perhaps less extensive (cf. *Biwadrilus*, *Hydrilus*). Tubercula pubertatis typically absent (?cf. *Hydrilus*). Female pores paired on 14. Male pores on 13 (*Biwadrilus*) or 15 (*Criodrilus*) associated with internal bursae or 'prostatic glands'. Spermathecae absent but spermatophores, hornshaped, tubular, or saccular, attached near male pores. Oesophageal and intestinal gizzards, calciferous glands, and caeca absent (but possibly some thickening of oesophagus in 5-7 and intestine in 15-20,21). Intestinal origin around 15-20. Typhlosolate or atyphlosolate. Hearts in (6),7-11. Nephridia holoic (avesiculate?); absent from anterior segments. Ovaries fan-, pear- or paddle-shaped in 13 (but not terminating in a single egg-string). Ova microlecithal (i.e. not yolky). Cerebral ganglia between segments 1 and 2 (as in *Biwadrilus*, cf. Sims, 1980: 114). Lateral lines absent.

Distribution and diversity. Palaearctic: Europe from Mediterranean to Moldavia [e.g. Italy; Hungary (Budapest), Austria (Linz); Germany (Berlin); France; Spain, Portugal, Yugoslavia, Greece [reported by K. Michalis (1993, 2003) as "*Criodrilus lacuum* (Oligochaeta: Criodrilidae) earthworm species new to Greece" – from Internet search, publication unknown], Turkey, Asia Minor, the Maghreb (Tunisia and Algeria) and the Levant (Syria, Lebanon, Israel, Palestine), and from Latvia, Poland, Russia to Amur River region of Siberia on the Pacific coast, and Japan (*Biwadrilus*). Reports are of introduction of *Criodrilus lacuum* to America: plant pots in Baltimore and from rice paddies in Rio Grande do Sul, Brazil (Knäpper & Porto, 1979; Lima and Rodríguez, 2007 for *Guarani*) and, doubtfully, to UK (cf. *Anagaster fontinalis* above). The immature specimens from southern India that Stephenson identified with *Criodrilus lacuum* probably were glyphidriles according to Gates (1972: 50), but Julka (1988: 39) yet claims it from India. Omodeo (1984), Timm (1999) and Martin (2004) provide some additional distribution data for the species.

Biwadrilus bathybates (Stephenson, 1917) (Fig. 1)

Criodrilus bathybates Stephenson, 1917: 96; Stephenson, 1930; Yamaguchi, 1954 (syn. *miyashitai*). Type locality Lake Biwako Shiga-ken, Japan in sediment at a depth of 180 feet (= 60m). Types four immature specimens, sample No. 3 in

the Calcutta Museum.

Criodrilus miyashitai Nagase and Nomura, 1937: 361 figs. 1-43. From catchments of the River Yura, Komorimachi, near Kyoto south central Japan, and from rice paddy irrigation channels at Tsuruoka, Yamagata-ken in coastal NW Japan. Types unknown.

Criodrilus bathybathe: (*laps.*) Nagase and Nomura, 1937: 361. *Biwadrilus bathybates*: Easton, 1981: 40 (syn. *Miyashitai*); Blakemore, 2003, 2005 (syn. *miyashitai*).

Biwadrilus batybates: (*laps.*) Ohtaka and Nishino, 1999: 46.

Taxonomic note. Name sometimes misspelt “*bathybathe*” or “*batybates*”.

Material examined and localities. Current samples consisted of several mature and immature specimens, all collected by RJB 1-2.ii.2007, and 1-5.x.2007 and preserved in 80% EtOH, some deposited in the Lake Biwa Museum (batch accession number LBM Misc. Invert. FY2006-19 – Fig. 1) or Yokohama National University and some sent to Kansas Natural History Museum for DNA analysis. Specific localities are:

1. Fudogawa river in Ojiyama-koen on west shore of south basin, Lake Biwa (upper reaches under old bridge, and abundant beside the creek under exotic *Eucalyptus* trees).

2. On shoreline adjacent to Biwako Museum on west side of Kurasuma Hanto especially in mud around willow roots.

3. Harie (N 35°22'15.3", 136°02'58.5") on west side of north basin in mud under trees on shoreline.

Diagnosis. Unpigmented. Length 150–300 mm. Segments 200–250. Prostomium zyboloid. Body quadrangular and dorsally troughed, most noticeable posteriorly. Setae closely paired, aa=dd. Clitellum in most or all of 16–34. Female pores on 14; male pores on 13; spermathecal pores absent. Gizzards, calciferous glands, typhlosole and caeca absent. Holoic, avesculate, absent from anterior 13 segments. Spermathecae replaced by spermatophores. Prostate-like glands (bursae) exit to male pores.

Distribution. From the Lake Biwa/Kyoto region of southern central Honshu, Japan (as noted in synonymy above), also reported from Tsurugaoka, NW coastal Yamagata-ken and Muko-

gawa of SW coast Hyogo-ken (Yamaguchi, 1953). Known only from Japan.

Habitats. In lake sediments to 60 m in Lake Biwa (Stephenson), or stony shallows of clean flowing streams leading to River Yura, but not found in agriculturally polluted ditches; and in Yamagata from muddy bottoms of rice irrigation channels to a depth of 50 cm to 2 m, or mingling with roots of plants on embankments (Nagase & Nomura and pers. obs.). Also reported by Dr. Machiko Nishino from ca. 10 m depth in the lake on a stony bottom and she also collected it below Amagase Dam on the Uji River and upstream of Seta River that drains Biwa (M.J. Grygier pers. comm.). In current studies found in, and just beside, streams leading to Lake Biwa apparently most abundant in light sandy deposits or submerged organic debris and muddy or stagnant substrates (e.g. in sapropel – the black fetid asphyctic mud). Generally absent from the coarse sandy beaches around the northern basin of Lake Biwa (pers. obs.). The worm has not been reconfirmed from depth >10 m at Lake Biwa despite repeated deep sampling since 1986 (Ohtaka & Nishino, 1999).

Behaviour. Wholly or semi-aquatic and limnic; the worms were observed to be feeding in stagnant or muddy habitats with the furrowed tails protruding 2-3 cm and waving about in the free or flowing water, presumably for respiration and gas exchange (Nagase & Nomura and pers. obs.). On touch and extraction the worms coil tightly, and rapidly succumb to decomposition on exposure, in minutes rather than hours (pers. obs.). Similar behaviour patterns are reported for *Criodrilus lacuum*. Spermatophores frequently observed on bodies of mature specimens, thus is it probable that the muscular male pores facilitate placement and attachment on con-copulant partners.

Length. 150–300 mm.

Width. 3–4 but widest to greater than 5 mm at region of male pores.

Segments and body shape. 200–250; body rapidly tapers at fore and aft, the anterior is concave ventrally, the clitellum is cylindrical, and most of the remainder of the body is quadrangular with the posterior convex ventrally to give a dorsal gutter,

most pronounced in tail segments with setae at edges. (See Fig. 1.)

Colour. In life mostly transparent unpigmented so that blood vessels and ingesta can be seen through body wall except where the pale clitellum obscures, the tail portions are often noticeably vascularized (for gas exchange); on preservation the body becomes opaque, the clitellum more pink and the tail appears yellowy.

Prostomium. Zygotubous with some slight secondary annulation.

First dorsal pore. None.

Setae. (10/ratio of aa:ab:bc:cd:dd): 8 per segment, fairly closely paired (1:7:1:9:6 dd=aa); setae on 13 in immatures small and more closely paired; in matures these are penial in bundles of two to four (or more) small hooked setae. Genital setae are developed on 13 (said to consist of between 2–6 setal bundles by Nagase & Nomura, 1937).

Nephropores. Seen just in front of *a* or *ab* lines, especially obvious on clitellum (none in anterior).

Clitellum. Multilayered, annular in some or all of (14,15),16,17–31,32,(33,34); most pronounced in 18–32 (current specimens).

Male pores. In deep slit on large laterally-extended porophores on 13 that protrude, even in juveniles, and are reported to open and close like pincers (Nagase & Nomura), perhaps for spermatophore molding and placement.

Female pores. In deep clefts on 14 just anterior to ventral setal pairs.

Spermathecal pores. Absent.

Genital markings. None.

Body wall. “Bundles of irregularly or sometimes pinnately arranged longitudinal muscle fibres” (Nagase & Nomura, 1937); = intermediate?

Septa. 5/6–11/12,12/13 slightly thickened, thereafter thin.

Vascularization. Dorsal blood vessel single, along with a ventral vessel and a very weak supra-oesophageal vessel (seen only in 9–11 in current specimens, reported in segments anterior to 9 by Nagase & Nomura). Lateral vessels seen in segments anterior to 14. Sub-neural vessel not found nor reported (?cf. *Criodrilus* – see discussion below).

Hearts. Small commissurals in 5–6, large, paired lateral hearts in 7–11.

Gizzard. Oesophageal and intestinal gizzards absent.

Calciferous glands. Absent.

Intestine origin. Origin difficult to determine but it appears to be in region of 20–21 where alimentary canal widens and thins, cf. indistinguishable from oesophagus (Nagase & Nomura, 1937); intestinal caeca and typhlosole absent.

Nephridia: Holoic from 14, avesculate (cf. *Sparganophilus*, *Pontodrilus*); pharyngeal glands on septa posteriorly in 6 and 7 (and 8 – Nagase & Nomura, 1937).

Male organs. Holandric; iridescent testes and funnels free but invested in coagulum in 10 and 11; saccular seminal vesicles two pairs that fill segments 9 and 12; Stephenson (1917, 1930) said they were in 12 only in his immature specimens, but they are confirmed in 9 too (by Nagase & Nomura and herein).

Ovaries. Fan-shaped in 13 with funnels; ovisacs paired in 14. Ova not yolky.

Prostates. Large cluster of (prostatic?) glands ducting to exit above and below large elongate tubular bursae – what Stephenson called ‘prostate’ glands [also ‘copulation glands’ by Nagase & Nomura (1937) after ‘Copulationstasche’ of Michaelson (1918), sometimes reported as ‘cylindrical setal glands’ or ‘atrial glands’], in 13 that exit to male pore slits (not to setal bundles) and are probably involved in spermatophore production along with the glands and muscles of the male pores. [Note that Nagase & Nomura (fig. 30) show copulatory glands more rounded than in current specimens, perhaps an artefact of development.]

Spermathecae. Spermathecae absent but spermatophores, saccular, and often attached in pairs dorsally or dorso-laterally near, but often dorsally, on segment 13 from exchange with con-copulant(s).

Gut contents. Organic matter and dark material with grits.

Cocoons. Not found in current studies, but reported by Kawamura (1918, from Nagase & Nomura, 1837: 401) to be large, commensurate with the clitellum, and tapering towards both ends, each containing a number of eggs.

Remarks. No obvious internal parasites were found in dissected specimens. No lateral lines were demonstrated; cf. Nagase and Nomura (1937: 368)

who state: “The lateral lines are present on both sides of the body, attached to the circular muscle layer with its distal base, being embedded in the longitudinal muscle layer”. It seems these are simply muscle fibres, not nerves, which Stephenson (1930: 36) noted. As remarked above, these lines may be due to lateral vessels that are particularly obvious in the anterior, as also recorded by Nagase and Nomura (1937: 385).

Ecology. Preliminary Lake Biwa surveys by current author (31st January – 2nd February, and 1st – 5th October, 2007) revealed a total of approximately 15 earthworm species plus several microdriles (e.g. *Branchiura* sp., ?*Tubifex* spp.) and at least one species of freshwater leech around the lake from approximately 25 sample sites. Species more closely associated with *B. bathybates*, especially at the Fudogawa site, were:

1. *Eukerria saltensis* (Beddard, 1895), Ocneorodrilidae (exotic) [reasonably abundant around lake, this only the 3rd record from Japan – see Blakemore *et al.* (2007)].
2. *Amyntas* spp. and *Metaphire* spp., Megascoclecidae (native/exotic), 5–6 spp.
3. *Aporrectodea trapezoides* (Dugès, 1828) Lumbricidae (exotic).
4. *Dendrodrilus rubidus subrubicundus* (Eisen, 1874), Lumbricidae (exotic).
5. *Eisenia japonica* (Michaelsen, 1892), Lumbricidae (?native).
6. Leech (Hirudinea), possibly a predator on these worms as abundant in same habitat (?native).

There was evidence (footprints, spoor and holes in the sand/mud) of long billed bird(s) systematically probing for worms/leeches as food at Fudogawa site, species unknown.

***Criodrilus ghaniae* (Qiu & Bouché, 1998) comb. nov.**

Hydrilus ghaniae Qiu & Bouché, 1998: 17, fig. 1; Omodeo, Rota & Baha, 2003/2004: 463; Omodeo & Rota, 2004: 222

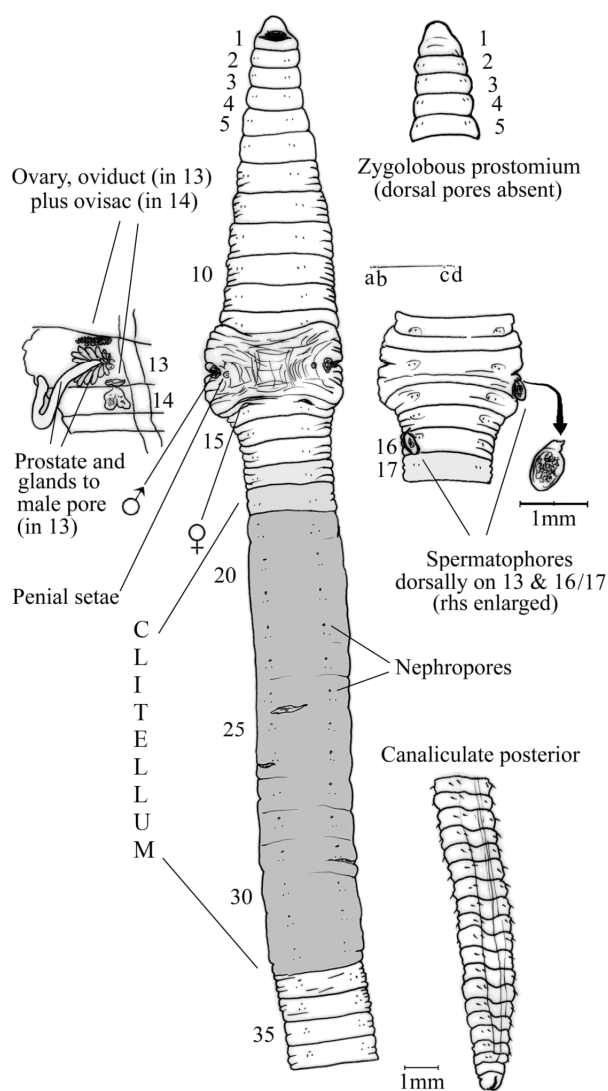


Figure 1. *Bivadrilus bathybates*. Lake Biwa specimen from sample LBM Misc. Invert. FY2006-19, figured and dissected by RJB

(both latter publications proposing synonymy of this monotypic genus and species); Blakemore, 2005, 2006 (accepting its synonymy in *C. lacuum*). From Constantine, Algeria. Types in Montpellier: (H) CO-ECO Authorship 171/2860/5311; (P1-2) 2865/5311. [Note: of the taxon is slightly confused as the Table of Contents (page 1) lists authors as “Oiu Jiang-Ping, G; Ouahrani et Marcel.B. Bouché.” with spelling and punctuation exactly as presented; however, publication (page 17) lists authors only as “Jiang-Ping Qiu et Marcel B. Bouché” (sic) with the taxon name dedicated to “Madame Ghania Ouahrani” for having provided the three specimens].

Diagnosis. Unpigmented. Length 125–150 mm. Segments 295–320. Prostomium epilobic (open). Dorsal pores obvious, present from 11/12. Body quadrangular. Setae closely paired, (ratio 6:1:8:1:8). Setae *ab* on 10–14 on large papillae, 16–22 on smaller papillae. Clitellum extensive on 22,23–34,35,36 (and with slight modification from 17–40). Tubercula pubertatis elongate and ventral to clitellum in mid-*bc* on 30–34,35. Female pores small lateral of *b* on 14; male pores on large porophores between *b–c* on 15; spermathecal pores absent. Longitudinal muscle fasciculated (the ‘primitive’ kind). Septa feeble from 4/5. Hearts 7–11. Gizzards, calciferous glands, intestinal caeca and typhlosole absent. Holoic, avesticulate. Holandric, seminal vesicles in 9–12 (those in 11–12 larger). Male pore has a “sac glandulaire au débouché du pore mâle” (= a roundish prostatic bursa). Spermathecae absent, spermatophores (form?) present in the region of the male pores.

Distribution. Constantine, Algeria.

Habitat. Limicolous, from mud of a refuse discharge channel.

Remarks. The incongruity between the original description and Omodeo & Rota’s synonymy of this taxon indicates some major discrepancy. It should however be noted that, despite the glaringly obvious similarity to *Criodrilus*, the original authors (Qiu & Bouche, 1998), for unknown reasons, made neither connection nor comparison.

***Criodrilus lacuum* Hoffmeister, 1845**
(Figs. 2–4)

Criodrilus lacuum Hoffmeister, 1845: 41, figs. 9a-c (of habitus, anterior and two spindle-shaped cocoons). Type locality Tegel-See, Berlin, Germany. Types Missing.

Criodrilus lacuum: Örley, 1887: 551, Pl. 38, figs. 1-18; Benham, 1887: 561, Pl. 38, figs. 9-19; Michaelsen, 1900: 468; Stephenson, 1930: 904; Gates, 1972: 50; Perel, 1979: 174; Blakemore, 2002, 2006.

Guarani camaqua Rodrigues & Lima in Lima & Rodrigues, 2007: 1, fig. 1. **Syn. nov.** From rice fields in Rio do Sul, Brazil. Types numbered 1-10 initially deposited in “the Ana Cláudia Rodrigues de Lima (ACRL) collection” although this may not be legitimate under the Code (ICZN, 1999).

Non “*Criodrilus lacuum*”: Stephenson, 1914: 256 nec “*Crio-*

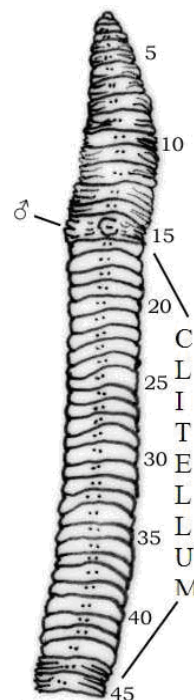


Figure 2. *Criodrilus lacuum* Hoffmeister, 1845. Figure after Perel’ (1979: 175, fig. 40; 1997: 50: fig. 20)

drilus sp. (?*lacuum* Hoffmstr.)” Stephenson, 1925: 903, fig. 13 – both reports of immature specimens from India/Pakistan = *Glyphidrilus* sp. – see Gates (1972: 50).

Diagnosis. In life light- or dark-brown to greenish. Length of adults 120–320 mm. Segments 200–450. Prostomium zybolobic. Dorsal pores absent. Body quadrangular after segment 9 and most noticeable posteriorly. Setae closely paired, *aa*>*dd*. Setae *ab* on 10–14, 17 and 19 often on small papillae. Clitellum extensive, at full development in some or all of

16–47 (i.e. up to ca. 31 segments). Female pores on 14; male pores on 15; spermathecal pores absent. Gizzards absent (or rudimentary in 12–14); calciferous glands and caeca absent. Typhlosole present or absent. Holoic, avesticulate. Spermathecae absent, spermatophores often present.

Materials examined and localities. Not observed in current studies in Australasia/Asia.

Distribution. As for family above excluding Japan, viz. – Tunisia and Algeria (Omodeo & Mar

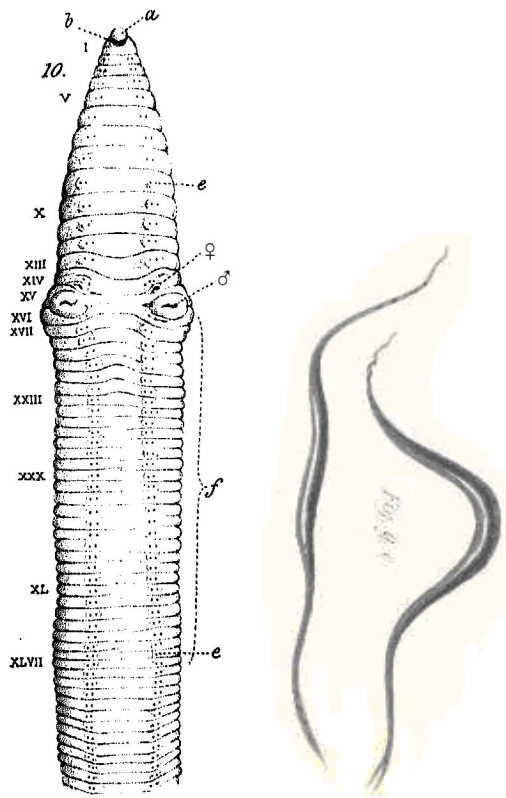


Figure 3. *Criodrilus lacuum*. Left: Modified from Örley, 1887: 551, Pl. 38, fig. 10. Right: Cocoons from Hoffmeister, 1845, fig. 9c (no scale provided but commensurate with clitellum).

tinucci, 1987); Syria; “Palestine” (Israel e.g. by Pavlicek *et al.*, 2003); Lebanon; Turkey [see http://jfas.ege.edu.tr/pdf/29_Yildiz_22_1-2005.pdf]; Southern Russia; Hungary (Budapest); Bulgaria (Srebrana Lake); Greece; Yugoslavia; Italy (Pavia, Treviso, Turin); Austria (Linz); Germany (Berlin); Rivers and tributaries of Danube and Po (e.g. Örley, 1887); France; Spain; Portugal; Latvia; Poland; Moldavia; Amur region of Siberia. Introduced into America [plant pots, Baltimore (Gates) and rice fields Brazil: Rio Grande do Sul (Knäpper & Porto, 1979; Lima & Rodriguez, 2007)]; UK (unconfirmed?); India (unconfirmed cf. Julka, 1988: 39).

Habitats. Mud of fresh and brackish waters (in roots of *Sium latifolium* L. in Europe).

Behaviour. Semi-aquatic; tail often protrudes above substrate (as in *Biwadrilus* for oxygenation?); and regeneration, particularly of ‘tail’ segments,

common (Örley) while Gates (1972) notes anterior ‘head’ regeneration from as far back as 40/41 in *C. lacuum*.

Length. 40–320 mm.

Width. 4–10 mm.

Segments and body shape. 200–450; body quadrangular (after segment 9) and grooved dorsally on and after clitellum (to increase surface area for gas exchange). (See Figs. 2–3.)

Colour. In life light- or dark-brown to greenish; or colourless.

Prostomium. Zygotubous (cf. epilobous in *Hydrilus*).

First dorsal pore. None (cf. 11/12 *Hydrilus*).

Setae. (7/ratio of aa:ab:bc:cd:dd:U) 8 per segment, fairly closely paired (dd>aa).

Nephropores. In *b* lines (none in anterior).

Clitellum. Multilayered, annular in some or all of (14,15),16 – ca. 45; perhaps less detectable in some specimens to give variable (and unreliable) counts (e.g. *Guarani*).

Male pores. On large muscular porophores on 15, approximately in *b* lines (the “vulva” of Hoffmeister) which probably serve for construction of the cocoon.

Female pores. In 14 or towards 14/15 often on small tumescences near *b* lines (reported median to *a* lines in *Guarani*).

Spermathecal pores. Absent (cf. Örley as noted in Remarks below).

Genital markings. Tubercula pubertatis absent (cf. reported on 30–34,35 in *Hydrilus*); some setae in genital tumescences, e.g. some of 9,10-13,14, 17 and 19.

Septa. Feeble.

Vascularization. Single dorsal blood vessel complete, along with ventral subneural and supra-oesophageal vessels.

Hearts. (6?),7–11.

Gizzard. Oesophageal and intestinal gizzards absent [but some thickening of oesophagus in 5–7 and intestine in 15–20,21 (Sims), or slightly muscular in 12–14 (Michaelson)].

Calciferous glands. None.

Intestine origin (typhlosole). Crop in 14–18 and intestinal origin in 19 (Benham), although it is sometimes quoted as 12 (Stephenson) or between 13–18. Typhlosolate according to Benham and others, atyphlosolate by some authors, more often not noted.

Nephridia. Holoic from 13 (sometimes nephridia reported only after 15 or 16), avesciculate (cf. *Sparganophilus*, *Pontodrilus*).

Male organs. Holandric; seminal vesicles four pairs in 9-12 (developed in just 11 & 12 in *Gurani*).

Ovaries. Fan-shaped in 13; ovisacs large in 14. Ova not yolky.

Prostates. Bursae or 'prostatic glands' in 15.

Spermathecae. Spermathecae absent [strangely, Örley (1887: 554) described them ventrally between segments 9/10 and 10/11 and he speculated that they produced the spermatophores, but since no other author found these it is possibly a mistake as suggested by Benham (1887: 569)]; spermatophores (Hoffmeister's "*penis-formige Ktirpehen*"), hornshaped, tubular or saccular, attached externally and usually ventrally although occasionally dorsally near male pores.

Gut contents. Mud?

Cocoons. "*spindle-shaped, parchment like structures with a colour that changes; they are about 5 cm. in length, rapidly diminishing towards each end. One end, drawn out into strongly fibrous threads, serves for attachment to the roots, or more rarely to the leaves and branches of water plants; the other end truncated, with a dentate edge, allows the embryos to escape. As is the form, so also is the color different. The perfectly newly laid cocoons are nearly transparent, horny yellow in color, but after a time they become darker, and towards the time of hatching of the embryos they are blackish in color.*" (Örley, 1887: 556) (Fig. 4).

Remarks. German types were supposedly atyphlosolate like those from Bohemia; while Italian specimens (all?) have a thick typhlosole. Genital setae are reported to have ectal grooving that supposedly demonstrates that *Criodrilus* is closely related to the Lumbricidae.

Criodrilus lacuum is diploid with chromosomes numbering 22 (Omodeo, 1984).

Ecology. Breeding occurs from March to July in Europe (Örley). In Italy *C. lacuum* is often associated with *Eiseniella neapolitana* (Örley, 1885) and *Haplotaxis gordioides* (Omodeo, 1984), and Örley (1887: 560) describes it with his *Apor-*

rectodea dubiosa dubiosa (Örley, 1881) and he also reports that "*amongst the Hirudinea, species of Aulostoma and Nephelis are their greatest enemies; these swallow three or four Criodrili at a time*". Benham (1887) noted presence of common parasitic gregarines near the ovaries in segment 14. Regeneration capacity is high and rapid, perhaps in response to predation relating to its behaviour, as already noted, of protruding its tail above the substrate allowing attack by predators.

DISCUSSION

Family Criodrilidae. Sims & Gerard (1985: 41) suggest the present Palaearctic distribution is relictual of a wider, possibly pre-Pangean range dating to late Palaeozoic times but, despite the return of family Biwadrilidae Brinkhurst & Jamieson, 1971, monotypic for *Criodrilus bathybates* Stephenson, 1917, the Holarctic range is extended only slightly to again include Japan. The diagnosis of Biwadrilidae by Easton (1981: 39) was within the ambit of Criodrilidae. Indeed, Sims (1980: 115; 1982: 285) had suggested that the family be recombined with Criodrilidae as it differs only in details of its vascular system – in particular the presence of a supra-oesophageal vessel and possible lack of a sub-neural vessel, although both these characters are poorly defined in *Criodrilus* (cf. Lima & Rodriguez, 2007). And, further, on the presence of male pores and "prostate glands" in 13 rather than 15. Regarding supposed presence or absence of "paired lateral lines" (as found in fish) – these have not been demonstrated satisfactorily in *Biwadrilus*, despite claims by Nagase & Nomura (1937: 368) as repeated by Sims (1980: 106, 115). The only possible 'lateral lines' are due to blood vessels clearly visible through the body wall in the anterior segments in live specimens (pers. obs.). In fact Stephenson (1917), who described the species, makes no mention and Stephenson (1930: 36) states:

"*In the Limicolae* [small aquatic microdriles, not earthworms *per se*] *there exists on both sides within the body-wall, in the lateral line of the body and extending through the length of the worm, a narrow longitudinal tract of cells, the cells of the lateral line. These are, as has been said, the cell-bodies of*

the circular muscle-layer and of the transverse muscle-bundles which stretch between the inner ends of the dorsal and ventral setal bundles of the same side. They are not, as has often been stated, nerve cells, though, according to a number of authors, ... a nerve from the cerebral ganglion does enter the line.”

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 [within the Lumbricidae] in *Eiseniella*” – thus there is little of significance in position of male pore in 13 or 15, and the species *B. bathybates* is returned to its home family, Criodrilidae.

Recent 18S, 16S rDNA and cytochrome c oxidase sequences molecular studies by Pop *et al.* (2004) show that *Criodrilus lacuum* is relatively primitive compared to lumbricids and is an adelphotaxon (or sister taxon) of either of their two lumbricid species: *Eiseniella tetraedra* (Savigny, 1826) or *Aporrectodea dubiosa* (Örley, 1881), that both share with it an aquatic habitat.

Absence of nephridia from anterior segments and loss of dorsal pores is an adaptation to aquatic life, also found in *Pontodrilus* and *Sparganophilus* and a few aquatic members of other genera; similarly, for the simplification and reduction of the digestive tract (Stephenson, 1930; M. Bouché pers. comm., 2004).

*Key to species of Criodrilidae**

- 1 Male pores on 13.....*Biwadrilus bathybates*
- Male pores on 15.....2
- 2 Dorsal pores and tubercula pubertatis absent
-*Criodrilus lacuum*
- Dorsal pores present (tubercula pubertatis on 30-34,35)
-*Criodrilus ghaniae*

**C. ochridensis* Georgevitch, 1950 from Lake Ochrid, Macedonia is a dubious species.

Genus Biwadrilus. This genus should possibly be maintained on the position of the male pores (as in key above). Gates (1972: 50) found that the

atrial glands associated in 13 with the male pores of Japanese *Criodrilus bathybates* is a condition that characterizes certain parthenogenetic morphs of *Eiseniella tetraedra* and this may be indicative of mutual family origins (cf. Pop *et al.*, 2004 for molecular relationship of Criodrilidae to Lumbricidae).

A new finding is that *Biwadrilus bathybates* (Stephenson, 1917) persists around the shoreline of the southern basin of Lake Biwako, but appears less abundant beside polluted waterways and under cultivation (e.g. paddies around Ogoto on west side) and is absent from coarse sandy or gravelly beaches more prevalent for the northern basin. Sharing the same habitat with *Biwadrilus* are several native/exotic Lumbricidae, a few pheretimoids, and quite often the exotic semi-aquatic *Eukerria saltensis* (Beddard, 1895) that is considered a pest of rice in Australia (Blakemore *et al.*, 2007). The pheretimoids (Megascolecidae, e.g. *Amyntas* or *Metaphire* spp.) are more common and diverse in disturbed agricultural fields (or polluted soils) around the lake. A large Moniligastridae, *Drawida hattamimizu* Hattai, 1930, is also reported (in rice paddy) around the Lake, but it is a restricted species and was not located in current surveys, however a single specimen of the new native *Helodrilus hachiojii* Blakemore, 2007 was found in a paddy at Shitsuhama, Nishiazai-cho to the north of the Lake (collected by R.J.B. on 4.X.2007) and this is now also in the Lake Biwa Museum collection. Thus, biodiversity and distributions of the various species may act as “indicators” to monitor agricultural pollution/health.

An interesting result of the Lake Biwa survey was unexpected activity of both clitellate (breeding) adults and juveniles of several species, including *B. bathybates*, in an unseasonably warm winter, despite deep snow on the final day of survey in February, 2007. This suggests breeding activity is facultative rather than fixed or seasonal.

Genus Criodrilus. Although Omodeo *et al.* (2003, 2004: 463) and Omodeo & Rota (2004: 222) synonymized *Hydrilus ghaniae* under *C. lacuum*, the species possibly merits restoration as *Criodrilus ghaniae* **comb. nov.**, as here, on its characteristics

noted in the key and diagnosis above. Omodeo & Rota (2004: 222) question the presence of tubercula pubertatis claiming prior inspection of specimens from Tunisia and Algeria but they mention neither the dorsal pores nor nephridia and, surprisingly, they failed to inspect types. Superficially it appears to belong to *Criodrilus* despite Qiu & Bouché (1998) failing to note absence (or presence?) of nephridia in anterior segments although they did state that the small nephropores were near *b* lines, the first in segment 4. Even so, it is not clear whether they meant in intersegment 3/4 or 4/5. Nephridia usually commence from segment 2 in Lumbricidae and further back, typically from 14-16, in Criodrilidae. As these are defining characteristics of the families, their exact origin requires confirmation from re-inspection of *C. ghaniae* types. Details of neither the vascular nor nervous systems were provided and the overall impression is of a poorly defined taxon.

Guarani camaqua is combined in *C. lacuum* as its justification relies on seminal vesicles in only 11 and 12, even though these vary at interspecific level and are certainly irrelevant at genus level, also Benham (1887: 567), at least, told us they are “one on each side of each of the somites ix, x, xi, and xii ; they vary in size in these somites, and in different individuals”. As to its blood vessels, the vascular systems of classical taxa, especially those lacking types such as *C. lacuum*, are often poorly defined, however, on this point, Benham (1887: 566) at least reported “The vascular system I have not traced to any extent.... A subneural vessel is present and a typhlosolar vessel, but neither latero-neural nor intestino-tegumentary vessels exist” and it is perhaps rather irrelevant whether subneural vessels are attached or not. A prior report of *C. lacuum* from Rio Grande do Sul, Brazil by Knäpper & Porto (1979) although quoted by Lima & Rodriguez (2007) seem not to have initiated comparison to their rice field specimens, even though such an unnatural habitat suggests an introduced, exotic taxon rather than a new native.

Criodrilus lacuum appears a particularly long-lived culture species – the previous longevity record of 30 years was for *Lumbricus terrestris* L.,

from Sims & Gerard (1985, 1999: 22) – with survival more than 42 years as Dr Tarmo Timm (pers. comm. July, 2007) reports:

“I have maintained aquatic oligochaetes in aquaria (Centre for Limnology, Estonian University of Life Sciences, Estonia) for many decades. Among them, an aquatic “earthworm” *Criodrilus lacuum*. A number of the latter were taken from the Daugava River (Latvia) in 1965, and then held in several small aquaria. Most of them survived but did not reproduce in aquaria. The only individual hatched from a cocoon laid in my aquarium, lived 34 years (1968-2002). Many of the individuals caught in the river as adults, spent in aquaria up to five years, and some single individuals considerably more: 6, 11, 12, 13, 14, 16, 17, 18, 22, >23 (several but dried up), and 38 years; the last individual is yet alive when having survived already 42 years (1965-2007). Published data on the same batch of *Criodrilus lacuum*: Timm, T. (1984)... [there: at least 17 years].”

Acknowledgements – At Lake Biwa Museum I thank Drs Mark J. Grygier, Y. Kusuoka, and Robin J. Smith for facilitating and encouraging this work; while there I also received valuable advice from Prof. Akifumi Ohtaka (Hiroaki University) and Dr Machiko Nishino (Lake Biwa Environmental Research Institute). Some survey support was provided by LBM Comprehensive Project 06-02 under the direction of Dr Grygier. This work was partly compiled initially at Yokohama National University under the COE program. Drs. Eiso Inoue and Tadashi Kobayashi helped Oct, 2007 surveys by providing transport and arranging accommodation around the Lake. I further thank Dr Tarmo Timm for permission to cite his unpublished longevity data. Finally, I appreciate Dr Sam James’ contribution towards this study and eagerly anticipate the results of his DNA analyses.

REFERENCES

(For brevity, not all earlier taxonomic authorities cited)

- BENHAM, W.B. (1887): Memoirs: Studies on Earthworms: No. III. *Criodrilus lacuum*, Hoffmeister *Quarterly Journal of Microscopical Science*, 27: 561-572, Pl. 38, figs. 9-19. [<http://jcs.biologists.org/cgi/reprint/s2-27/108/561>].
- BLAKEMORE, R.J., (2002): *Cosmopolitan Earthworms – an Eco-Taxonomic Guide to the Peregrine*

- Species of the World. *VermEcology, Kippax, Australia*, pp. 426 + 80 figs. [First Edition published September, 2002].
- BLAKEMORE, R.J., (2003): Japanese Earthworms (Annelida: Oligochaeta): a Review and Checklist of Species. *ODE*, 3(3): 241-244. [Published Sept., 2003. <http://www.urbanfischer.de/journals/ode/> Electronic Supplement 2003-11 <http://www.Senckenberg.de/odes/03-11.htm>].
- BLAKEMORE, R.J. (2005): Chapters in: A Series of Searchable Texts on Earthworm Biodiversity, Ecology and Systematics from Various Regions of the World. General editors: M.T. Ito, N. Kaneko. CD-ROM publication. Soil Ecology Research Group, Graduate School of Environment & Information Sciences, *Yokohama National University, Japan*. Online website here: <http://bio-eco.eis.ynu.ac.jp/eng/database/earthworm/> [June, 2005 & July, 2005].
- BLAKEMORE, R.J., (2006): Cosmopolitan Earthworms – an Eco-Taxonomic Guide to the Peregrine Species of the World. (2nd Edition). *VermEcology, Japan*, pp. 630 + 150 figs. [Published August, 2006, with this supplement December, 2006].
- BLAKEMORE, R.J., ITO, M.T. & KANEKO, N (2007): Alien earthworms in the Asia/Pacific region with a checklist of species and the first records of *Eukerria saltensis* (Oligochaeta : Ocnerodrilidae) and *Eiseniella tetraedra* (Lumbricidae) from Japan, and *Pontoscolex corethrurus* (Glossoscolecidae) from Okinawa. In: F. Koike, M.N. Clout, M. Kawamichi, M., De Poorter, and K. Iwatsuki. (eds.), *Assessment and Control of Biological Invasion Risks. IUCN, Gland, Switzerland and Cambridge, UK, and Shoukadoh Book Sellers, Kyoto, Japan*, pp 173-181.
- BRINKHURST, R. O. & B. G. M. JAMIESON. (1971): The Aquatic Oligochaeta of the World. *Oliver and Boyd, Edinburgh, Toronto*, pp 860.
- EASTON, E.G. (1981): Japanese earthworms: a synopsis of the Megadrile species (Oligochaeta). *Bulletin of the British Museum (Natural History) series Zoology*, 40(2): 33-65.
- GATES, G.E. (1972): Burmese Earthworms, an introduction to the systematics and biology of Megadrile oligochaetes with special reference to South-East Asia. *Transactions of the American Philosophical Society* 62(7): 1-326. [Online via subscription: <http://links.jstor.org/journals/00659746.html>].
- HOFFMEISTER, W. (1845): Übersicht aller bis jetzt bekannten Arten aus der Familie der Regenwürmer. *Friedrich Vieweg & Sohn, Braunschweig*, pp. 43. [<http://www.regenwurm.de/pdf/hoffmeister-familie-der-regenwuermer.pdf>].
- ICZN (1999): International Code of Zoological Nomenclature (4th edition). *International Trust for Zoological Nomenclature, c/o Natural History Museum, London*, pp. 306. [<http://www.iczn.org/iczn/index.jsp>].
- JULKA, J.M. (1988): The Fauna of India and the adjacent countries: Megadrile Oligochaeta (Earthworms): Family Octochaetidae. *Zoological Survey of India, Calcutta*, pp. 400.
- KNÄPPER C.F.U. & PORTO, R.P. (1979): Ocorrença de Oligoquetas nos solos do Rio Grande do Sul. *Acta Biologica Leopoldensia*, 1: 137-166.
- LIMA, A.C.R. DE & RODRÍGUEZ, C. (2007): Earthworm diversity from Rio Grande Do Sul, Brazil, with a new native criodrilid genus and species (Oligochaeta: Criodrilidae). *Megadrilologica*, 11(2): 9-18.
- MARTIN, P. (2004): Oligochaeta and Aphanoneura in ancient lakes: a review. *Hydrobiologia*, 334 (1-3): 63-72.
- MICHAELSEN, W. (1900): Das Tierreich. Vol. 10: Oligochaeta. *Friedländer & Sohn, Berlin*, pp. XXIX +575.
- MICHAELSEN, W. (1918): Die Lumbriciden, mit besonderer Berücksichtigung der bisher als Familie Glossoscolecidae zusammengefaßten Unterfamilien. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere, Jena*, 41: 1-398.
- MICHAELSEN, W. (1921): Zur Stammgeschichte und Systematik der Oligochäten, insbesondere der Lumbriculiden. *Archiv für Naturgeschichte, Berlin* 86(8): 130-141.
- NAGASE, I. & NOMURA, E. (1937): On the Japanese aquatic Oligochaeta *Criodrilus miyashitai*, n. sp. *Science Report of Tohoku Imperial University*. 11 (4): 361-402.
- OHTAKA, A. & NISHINO, M. (1999): Studies on the aquatic oligochaete fauna in Lake Biwa, central Japan. II. Records and taxonomic remarks of nine species. *Hydrobiologia*. 406(0): 33-47.
- OMODEO, P. (1984): On aquatic Oligochaeta Lumbricomorpha in Europe. *Hydrobiologia*. 115 (1): 187-190.
- OMODEO, P. & MARTINUCCI, G.B. (1987): Earthworms of the Maghreb. In: A.M. Bonvicini Pagliai and P. Omodeo (eds.): *On Earthworms. Selected Symposia and Monographs. Mucchi, Modena, Italy*, pp 235-250.
- OMODEO, P. & ROTA, E. (2004): Taxonomic remarks on the earthworm inhabiting the Western Alps. In: *Advances in Earthworm Taxonomy*, A. G. Moreno & S. Borges (eds.) *Editorial Complutense, Madrid*, pp 189-259. [Published May, 2004 in Spanish and English].

- OMODEO, P., ROTA, E. & BAHA, M. (2003): The megadrile fauna (Annelida : Oligochaeta) of Maghreb: a biogeographical and ecological characterization. *Pedobiologia*, 47: 463
- OMODEO, P., ROTA, E. & BAHA, M. (2004): The megadrile fauna (Annelida : Oligochaeta) of Maghreb: a biogeographical and ecological characterization. *Pedobiologia*, 47: 458-465.
- ÖRLEY, L. (1881): A magyarországi Oligochaeták faunája. I. Terricolae. *Mathematikai és Természettudományi Közlemények*, 16: 562-611.
- ÖRLEY, L. (1885): A palaearktikus övben élő Terrikoláknek revíziója és elterjedése. *Értekezések a Természettudományok Köréből*, 15: 1-34.
- ÖRLEY, L. (1887): Morphological and biological observations on *Criodrilus lacuum* Hoffmei-ster. *Quarterly Journal of Microscopical Science*, 27: 551-560. [<http://jcs.biologists.org/cgi/reprint/s2-27/-108/551>].
- PAVLICEK, T., CSUZDI, Cs. & NEVO, E. (2003): Species richness and zoogeographic affinities of earthworms in the Levant. *Pedobiologia*, 47: 452-457.
- PEREL', T.S. (1979): Range and regularities in the distribution of earthworms in the USSR fauna. Academy of Sciences of the USSR. *Pub. Nauka, Moscow*, pp. 272. [In Russian with English summary].
- PEREL', T.S. (1997): The earthworms of the fauna of Russia. Cadaster and key. *Nauka, Moscow*, pp. 102. [In Russian with English summary, published with author's name "T.S. Vsevolodova-Perel'"].
- POP A.A., WINK M. & POP V.V. (2004): Use of 18S, 16S rDNA and cytochrome *c* oxidase sequences in earthworm taxonomy (Oligochaeta, Lumbricidae). *Pedobiologia*, 47(5-6): 428-433.
- QIU J-P. & BOUCHÉ, M. (1998): *Hydrilus*, un remarquable nouveau genre de Lumbricidae amphibie (Annelida: Oligochaeta). *Documents pedozoologiques et integrologiques, Dijon*, 4: 1, 17-19, 198. [In French; dated "Décembre 1998"].
- ROTA, E. & OMODEO, P. (1992): Phylogeny of Lumbricina: Re-examination of an authoritative hypothesis. *Soil Biology and Biochemistry*, 24 (12): 1263-1277.
- SIMS, R.W. (1980): A classification and the distribution of earthworms, suborder Lumbricina (Haplotaxida: Oligochaeta). *Bulletin of the British Museum (Natural History) series Zoology*, 39: 103-124.
- SIMS, R.W. (1982): Classification and distribution of the suborder Lumbricina (Haplotaxida: Oligochaeta). *Pedobiologia*, 23: 284-285.
- SIMS, R.W. & GERARD, B.M. (1985): Earthworms. Keys and notes to the identification and study of the species. Synopsis of the British Fauna (New series). *E.J. Brill, Leiden*, No. 31, pp. 171.
- SIMS, R.W. & GERARD, B.M. (1999): Earthworms: Notes for the identification of British species. 4th Edition. *The Linnean Society of London, and The Estuarine and Coastal Sciences Association by Field Studies Council, Montford Bridge, Shrewsbury, UK*, pp. 169.
- STEPHENSON, J. (1917): Zoological results of a tour in the Far East. Aquatic Oligochaeta from Japan and China. *Memoirs of the Asiatic Society, Bengal*. 6: 85-99.
- STEPHENSON, J. (1930): The Oligochaeta. *Oxford University, Clarendon Press*, pp. 978.
- TIMM, T. (1984): Potential age of aquatic Oligochaeta. *Hydrobiologia*, 115: 101-104.
- TIMM, T. (1999): Distribution of freshwater oligochaetes in the west and east coastal regions of the North Pacific Ocean. *Hydrobiologia*, 406: 67-81.
- YAMAGUCHI, H. (1953): Studies on the aquatic Oligochaeta of Japan. VI. A systematic report, with some remarks on the classification and phylogeny of the Oligochaeta. *Journal of the Faculty of Science, Hokkaido University. Series VI (Zoology)*. 11: 277-342.
- VEJDOVSKY, F. (1884): System und Morphologie der Oligochaeten. *Franz Rivnác, Prague*, pp. 1-172.