Zootaxa 5529 (3): 401–435
https://www.mapress.com/zt/
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Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5529.3.1
http://zoobank.org/urn:lsid:zoobank.org:pub:C0662CC3-C5B1-4230-BF8D-EE6336A85242

A monograph of the Oligochaete family Alluroididae

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This monograph is dedicated to Ralph Brinkhurst.

Abstract

The Alluroididae is a small oligochaete family with 8 genera and 13 known species occurring in freshwaters and in riverine soils in Africa, the Caribbean and Central and South America. It is here argued that their anatomy shows a transition from that of microdriles to that of megadriles (Metagynophora). A detailed description of comparative anatomy is given, followed by the systematics and some aspects of the ecology of all known genera, species and subspecies.

Key words: Oligochaetes. Africa, Caribbean and Central and South America. Microdrile-megadrile transition

Introduction: The microdrile–megadrile transition

Schmelz *et al*. (2021) recognized the Order Alluroidida of Timm & Martin (2015) and gave this the same rank as the Order Moniligastrida of Brinkhurst & Jamieson (1971). We accept this name, irrespective of its rank, in place of the Alluroidina of Jamieson (1978) which was a suborder of a very large Order Haplotaxida. Hennigan relationships of all opisthopore families were examined for 50 species and 51 characters, with nearest–neigbour clustering (Fig 1A). Subsequently (Jamieson 1988), a morphological parsimony analysis was performed (Fig. 1B). Differences in the relationships between the two phylograms signal the need for molecular analyses.

James & Davidson (2012) provided a profound molecular analysis of the Crassiclitellata (earthworms with multilayered clitella) of the greatest importance, but that analysis did not include the Alluroidida. No published molecular phylogenetics of Oligochaeta have included Alluroidida (see for example the recent papers of Anderson *et al*. 2017 and Erséus *et al*. 2020). A phylogenetic classification of the oligochaetes (Jamieson 2006) (Fig 2) extensively utilized molecular data though the Allurodida had yet to be subjected to molecular analysis. From a morphological point of view, the Alluroidida, containing the family Alluroididae with the subfamilies Alluroidinae and Syngenodrilinae, is the sister group of the Crassiclitellata (oligochaetes with a multilayered clitellum in contrast with the single cell thick clitellum of the Alluroididae). The Alluroidida and Crassiclitellata comprise the Opisthopora which in turn is the sister group of the Moniligastrida. The Alluroidida are thus transitional between 'microdriles' and 'megadriles' (Metagynophora *sensu* Jamieson 2006). In collecting *Alluroides pordagei* Beddard (1894), on the banks of the Athi River, Kenya, one of us was struck by their appearance as small reddish earthworms which were at first rejected as juveniles, only later to be identified as alluroidids. Omodeo (1996) was aware of the transitional status of alluroidids, specifically *Kathrynella*. He considered that the body thinness and the large blood vessels were typical of microdriles living in anoxic mud; the long egg sacs and sperm sacs, as well as the absence of capillaries, resembled those of some Haplotaxidae. However, penial setae and the complex structure of vasa deferentia were, he considered, similar to those of the alluroidids *Brinkhurstia* and *Standeria,* questionably likened to megadriles, as was the anatomy of the nephridia. Long before, Beddard (1894), in naming *Alluroides,* recognized that it made division into the Limicolae and Terricolae (equivalent to microdriles and megadriles) untenable.

Accepted by M. Bartz: 13 Aug. 2024; published: 29 Oct. 2024

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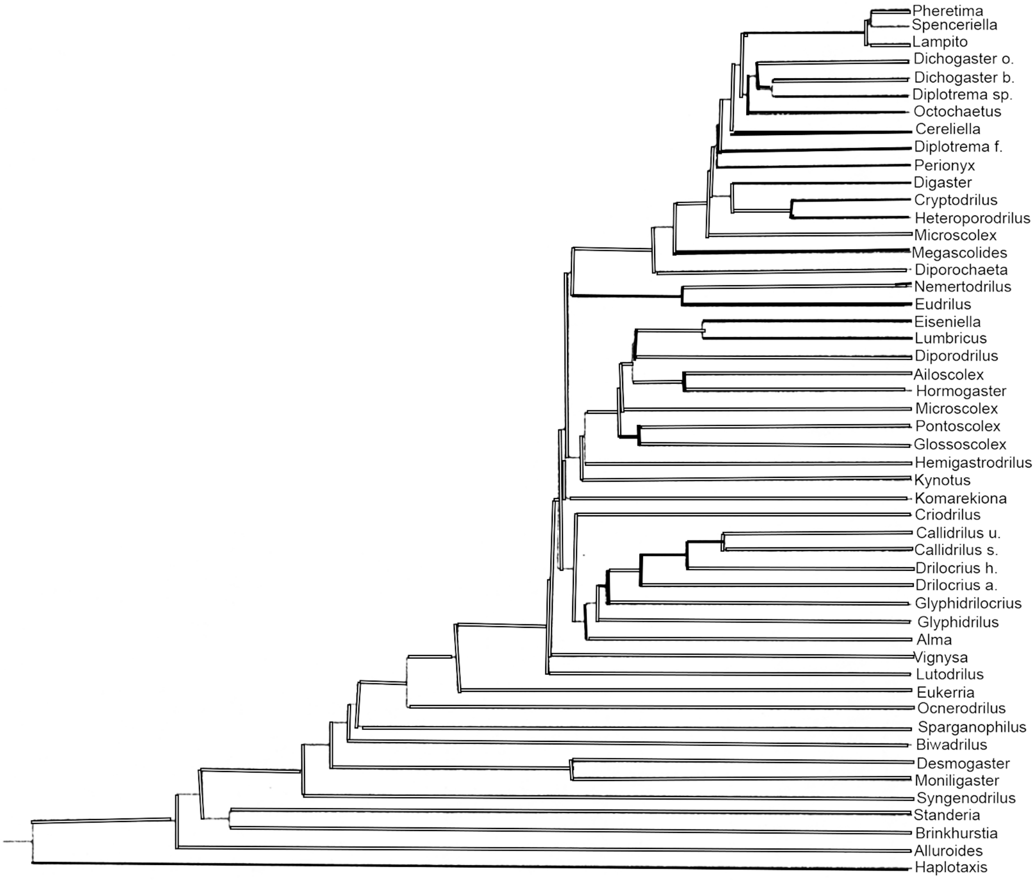


FIGURE 1A. Hennigram (morphological phylogram) for all families of the opisthoporous oligochaetes constructed by nearest-neighbour clustering. For details see Jamieson (1978). Redrawn.

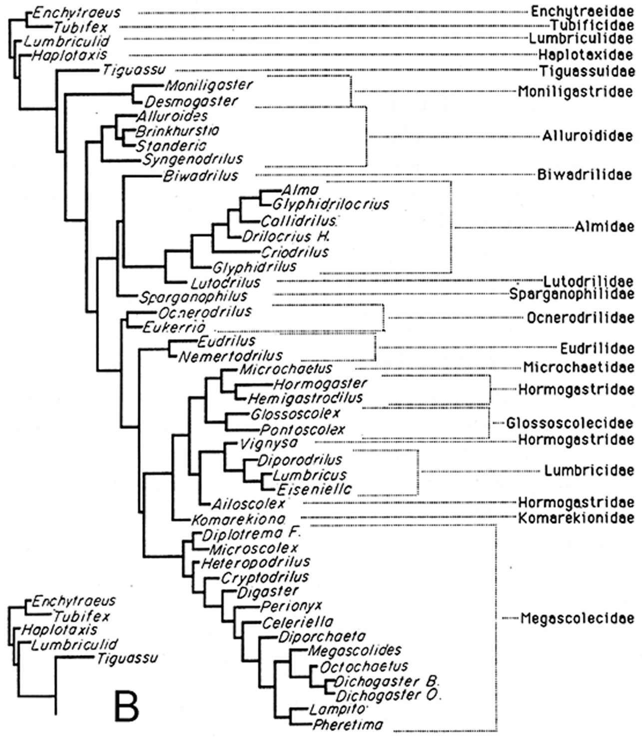
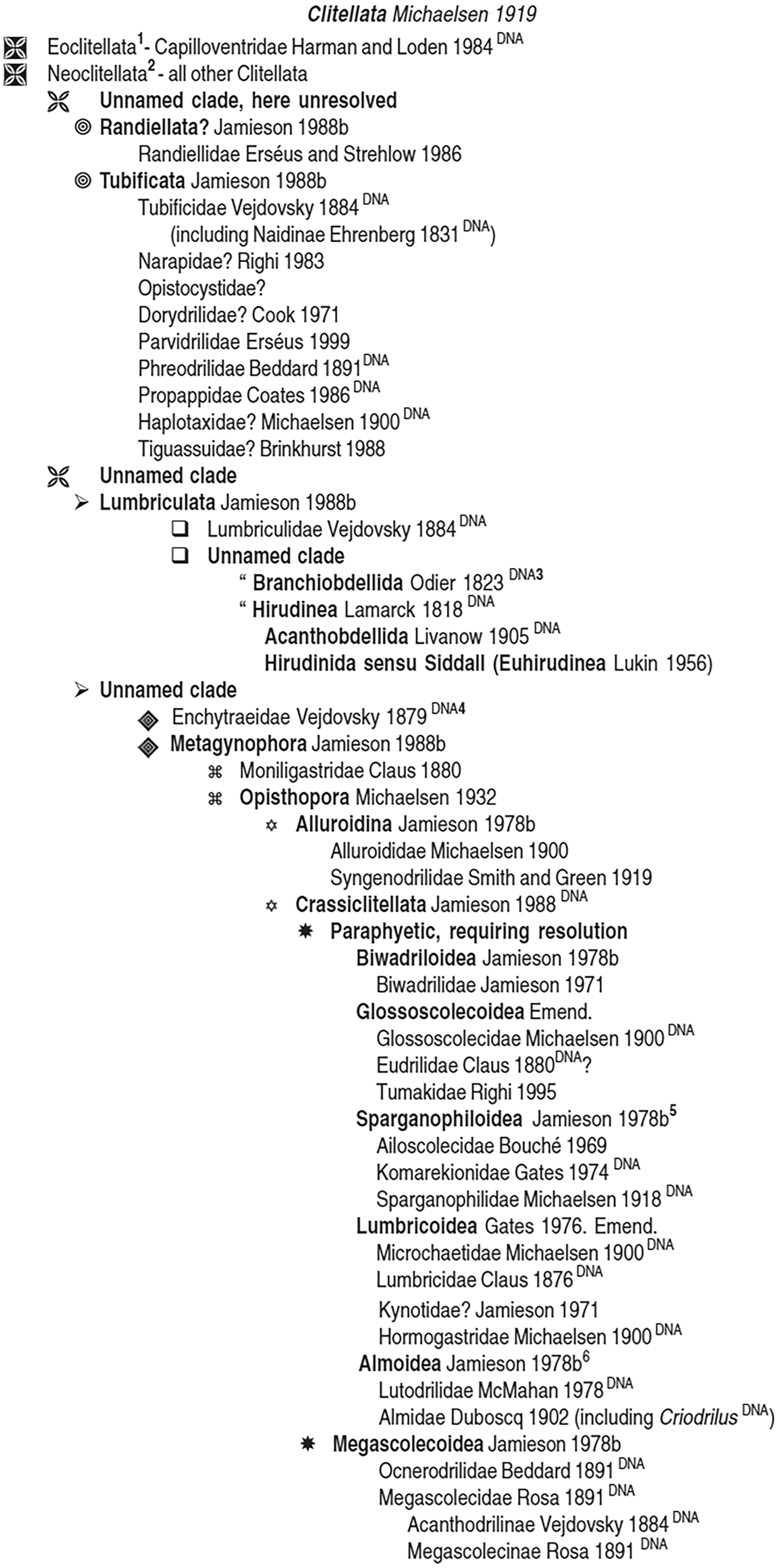


FIGURE 1B. Two most parsimonious cladograms obtained with the PAUP program for 49 oligochaete taxa and 68 characters. Moniligastridae are shown to be more basal than Alluroididae. Sparganophilidae appear more distant from Alluroididae. (From Jamieson (1988).



***Clitellata** Michaelsen 1919*

- ⌘ Eoclitellata[1]- Capilloventridae Harman and Loden 1984 $^{\text{DNA}}$
- ⌘ Neoclitellata[2]- all other Clitellata
  - ✻ **Unnamed clade, here unresolved**
    - ◎ **Randiellata?** Jamieson 1988b
      - Randiellidae Erséus and Strehlow 1986
    - ◎ **Tubificata** Jamieson 1988b
      - Tubificidae Vejdovsky 1884 $^{\text{DNA}}$
        - (including Naidinae Ehrenberg 1831 $^{\text{DNA}}$)
      - Narapidae? Righi 1983
      - Opistocystidae?
      - Dorydrilidae? Cook 1971
      - Parvidrilidae Erséus 1999
      - Phreodrilidae Beddard 1891 $^{\text{DNA}}$
      - Propappidae Coates 1986 $^{\text{DNA}}$
      - Haplotaxidae? Michaelsen 1900 $^{\text{DNA}}$
      - Tiguassuidae? Brinkhurst 1988
  - ✻ **Unnamed clade**
    - ➢ **Lumbriculata** Jamieson 1988b
      - ❑ Lumbriculidae Vejdovsky 1884 $^{\text{DNA}}$
      - ❑ **Unnamed clade**
        - “ **Branchiobdellida** Odier 1823 $^{\text{DNA3}}$
        - “ **Hirudinea** Lamarck 1818 $^{\text{DNA}}$
          - **Acanthobdellida** Livanow 1905 $^{\text{DNA}}$
          - **Hirudinida sensu Siddall (Euhirudinea** Lukin 1956)
    - ➢ **Unnamed clade**
      - ◈ Enchytraeidae Vejdovsky 1879 $^{\text{DNA4}}$
      - ◈ **Metagynophora** Jamieson 1988b
        - ⌘ Moniligastridae Claus 1880
        - ⌘ **Opisthopora** Michaelsen 1932
          - ✡ **Alluroidina** Jamieson 1978b
            - Alluroididae Michaelsen 1900
            - Syngenodrilidae Smith and Green 1919
          - ✡ **Crassiclitellata** Jamieson 1988 $^{\text{DNA}}$
            - ✸ **Paraphyletic, requiring resolution**
              - **Biwadriloidea** Jamieson 1978b
                - Biwadrilidae Jamieson 1971
              - **Glossoscolecoidea** Emend.
                - Glossoscolecidae Michaelsen 1900 $^{\text{DNA}}$
                - Eudrilidae Claus 1880 $^{\text{DNA}}$?
                - Tumakidae Righi 1995
              - **Sparganophiloidea** Jamieson 1978b[5]
                - Ailoscolecidae Bouché 1969
                - Komarekionidae Gates 1974 $^{\text{DNA}}$
                - Sparganophilidae Michaelsen 1918 $^{\text{DNA}}$
              - **Lumbricoidea** Gates 1976. Emend.
                - Microchaetidae Michaelsen 1900 $^{\text{DNA}}$
                - Lumbricidae Claus 1876 $^{\text{DNA}}$
                - Kynotidae? Jamieson 1971
                - Hormogastridae Michaelsen 1900 $^{\text{DNA}}$
              - **Almoidea** Jamieson 1978b[6]
                - Lutodrilidae McMahan 1978 $^{\text{DNA}}$
                - Almidae Duboscq 1902 (including *Criodrilus* $^{\text{DNA}}$)
            - ✸ **Megascolecoidea** Jamieson 1978b
              - Ocnerodrilidae Beddard 1891 $^{\text{DNA}}$
              - Megascolecidae Rosa 1891 $^{\text{DNA}}$
                - Acanthodrilinae Vejdovsky 1884 $^{\text{DNA}}$
                - Megascolecinae Rosa 1891 $^{\text{DNA}}$

FIGURE 2. A phylogenetic classification of the Clitellata. (From Jamieson 2006).

Turning to microdrile v. megadrile features, the deposited cocoon of the microdrile *Tubifex hattai* is oval in shape and is composed of a cocoon membrane, terminal plugs and an internal cocoon fluid in which are the large, fertilized eggs 300 x500 µm in size. In 'megadriles', such as Lumbricidae, the cocoon fluid, more nutritive than that of microdriles, contains many small oocytes, reaching a maximum diameter of only 100–120 µm (references in Jamieson 1980). In this regard, alluroidids have retained the microdrile thin clitellum and large eggs.

Another microdrile feature is the occurrence in some alluroidids of one or more mid–dorsal spermathecal pores. This is seen in *Alluroides*, *Brinkhurstia* and *Righiella* whereas the pores are paired and lateral in *Standeria*, *Kathrynella*, *Barriejamiesonia* and *Lacandodrilus*. We are not aware of the mid–dorsal position in any megadriles but it is known sporadically in microdriles (see Male Genital Field).

A megadrile feature which alluroidids share with the Crassiclitellata, is location of the male pores in XIII. The most posterior location of the male pores in microdriles is XII, in the Enchytraeidae. In megadriles location in XIII, as in alluroidids, is seen in the Biwadrilidae, Moniligastridae (both Brinkhurst & Jamieson 1971), and *Eiseniella tetraedra* (Savigny 1826). In other megadriles the male pores are more posterior. They are located in XV in *Criodrilus* and most lumbricids, XV or XVI in the Kynotidae, XVII in ocnerodriles, XVII or XVIII in Acanthodrilinae, XVII in the Megascolecinae, 18/19 or XIX in Sparganophilidae, and the vicinity of XVII to XIX to as far posteriorly as XXIX in Almini (Brinkhurst & Jamieson 1971).

Accordingly, alluroidids qualify well to be considered members of the Metagynophora, comprising the megadriles. Loss of the anterior ovaries of a hypothetical octogonadial set, with retention of ovaries in XIII so that a segment lacking gonads intervenes between the posterior testes and the ovaries, or two segments in proandric taxa such as the majority of alluroidids, diagnoses all oligochaetes above the tubificid-enchytraeid assemblage and the Lumbriculidae, i.e. from the Moniligastridae through the Megascolecidae, loosely termed 'megadriles'. This synapomorphy characterizes the Metagynophora of Jamieson (1988b), equivalent to the Lumbricida of Brinkhurst (1982). Although two of the most plesiomorphic representatives, Alluroidinae and Syngenodrilinae, have not been sequenced for DNA, monophyly of the Metagynophora seems to be real as it has been observed when Moniligastridae was included in several molecular analysis (James & Davidson 2012, Erséus *et al.* 2020). An implication of placing the Alluroidida in the Metagynophora is that an ancestor may have had ovaries in XII in addition to the present XIII. Two pairs of ovaries are very rarely seen in metagynophoran worms (known only, to our knowledge, in *Enantiodrilus borellii* Cognetti (1902), *Diplocardia sandersi* Gates (1955) and *Glyphidrilus kukenthali,* Michaelsen (1896), see Jamieson (1978)).

A further characteristic of metagynophorans is replacement of the very variable setae of many microdriles with four pairs of simple setae. With the earthworm-like appearance and habitation, in some cases in terrestrial soil, these are 'megadrile' features.

One might question whether the first metagynophoran family derived from a microdrile precursor is still extant. The Moniligastridae compute as the most basal family in the molecular phylogenies of James & Davidson (2012) and show a transitional state in being the only metagynophorans to conserve the single–layered clitellum and large-yolked eggs. The Sparganophilidae are also near the base of the trees, are more truly aquatic, and keep the lateral lines but are crassiclitellate and in the molecular analysis and the phylogenetic classification of Jamieson (1978) are further from the alluroidids. Moniligastrids thus show in what ways steps in the transition from microdriles may have occurred but have undergone their own major apomorphic changes (Jamieson 1977, 2006). Neither family is geographically close to the Alluroididae. Omodeo (1996) found a noteworthy resemblance of the 'atria' of *Kathrynella* to the typical 'euprostates' of the Eudrilidae, an African family 'of unknown kinship' but these have evolved far beyond any microdrile context. What may be considered a euprostate is also clearly depicted by Brinkhurst (1964) for *Alluroides ruwenzoriensis* (Fig.9).

Comparative anatomy of the Alluroididae

The following account updates that of Jamieson (1968). For additional references to taxa, and details of the subfamily Syngenodrilinae, see Systematics below.

Dimensions. Maximum length of Alluroidinae varies from 25 mm (*Standeria*), 30 mm (*Brinkhurstia americanus* Brinkhurst 1964); 32 mm (*Brinkhurstia donaldi* Omodeo & Coates, 2001), 35 mm (*Righiella*), 45 mm (*Alluroides brinkhursti brinkhursti* Jamieson 1968), 48 mm (*Alluroides pordagei* Beddard 1894), 58 mm (*Barriejamiesonia; Lacandodrilus*), 60 mm (*Alluroides lauzannei* Ljungström 1971), 89 mm (*Kathrynella*) to 100 mm (*Alluroides* *ruwenzoriensis* Brinkhurst 1964; *Alluroides pordagei congicus* Michaelsen 1936); maximum width from 0.6 mm (*Kathrynella*), 0.64 mm (*Lacandodrilus*), 0.75 mm (*B. americanus*), 0.9 mm (*B. donaldi*), 1 mm (*A. pordagei*), 1.4 mm (*Standeria*), 1.5 mm (*A. brinkhursti brinkhursti*, *Alluroides tanganyikae* Beddard 1906), to 1.6 mm (*Alluroides brinkhursti abyssinicus*); and number of segments varies from 60 (*A. tanganyikae* Beddard 1906), 82 (*Standeria*), 105 (*Righiella*), 130 (*B. americanus*), 142 (*B. aberratus*), 144 (*A. brinkhursti, brinkhursti*), 150 (*B. donaldi*; *A. ruwenzoriensis*, *A. lauzannei*), 202 (*A. pordagei*), 210 (*A. p. congicus*), 248 (*Lacandodrilus*) to 259 (*Kathrynella*). *Syngenodrilus* falls within these size ranges, with a length of 52 mm, 137 segments though with a greater width of 4 mm.

Pigmentation. Body wall pigmentation is absent, but the clitellum is pigmented, greyish brown, in A. *brinkhursti abyssinicus*. The reddish colouration of *pordagei* (*vide A. tanganyikae* Michaelsen 1913) was presumably due to the vascular system and may be general in the genus.

Prostomium. In some members of the Alluroidiinae, the prostomium is unlike that of terrestrial families and is reminiscent of that of Tubificidae (Naididae sensu Erséus *et al*., 2008) having the form of a triangle with the broad base attached to the peristomium to approximately midway between the setal couples of each side (*A. brinkhursti abyssinicus*; *Standeria*, Fig 17). In *A. tanganyikae* Beddard, it is long and pointed, transversely bisected by a constriction, but zygolobous. In *B. americanus* it is short and rounded (Brinkhurst 1964). In *A. lauzannei* the prostomium is conical, divided into two parts and said to be ciliated (Lauzanne 1968). In *Barriejamiesonia* and *Lacandodrilus* it is prolobous. In *Kathrynella* it is zygolobous and conical on a short peristomium. It is epilobous 1/2 although lacking a separate dorsal tongue in *Standeria*.

Lateromuscular groove. Transection of the body reveals an interruption of the longitudinal body wall musculature between the setal couples of each side which is the sole break in the muscular sheath with the exception of those made by the setal follicles (Jamieson 1968). This hiatus corresponds with an external longitudinal groove which runs the length of the body, commencing at the junction of the lower edges of the prostomium with the first segment (*A. b. brinkhursti* and *A. b. abyssinicus* (Fig 6); *B. americanus*; and *Standeria*). A similar groove occurs in the Tubificidae (Jamieson 1968), that in *Tubifex* and *Limnodrilus* being termed the "Seitenlinie" by Pointner (1911) after Hesse. It is possibly homologous with the lateral organs which occupy a similar position in many sedentary polychaetes. It is said not to have been observed in *Kathrynella* but is clearly shown in Fig 1A of Omodeo (1996) (Fig 13A). They have been reported as 'lateral bands' in aclitellate individuals of *Lacandodrilus*. They are present in IV–XIV in *Righiella*. Lateral lines have been reported in the Haplotaxidae and Biwadrilidae (see Jamieson 1978). The groove has not been observed in the Syngenodrilinae.

Setae. Basically, there are eight closely paired setae in each segment except for the peristomium (all species). A seta is sigmoid, single-pointed with small nodulus, and is unornamented (*A. b. brinkhursti*; *A. b. abyssinicus*; *B. americanus* and S*tanderia*), caudal setae, only, are ornamented in *Kathrynella*. At maturity the ventral setal couples of XIII are absent (*A. tanganyikae* Beddard 1906; *A. b. brinkhursti*, *A. b. abyssinicus*, *A. ruwenzoriensis* and *Righiella*) or are replaced by a single penial seta on each side in *Brinkhurstia*. Penial setae also occur in *Kathrynella*, in XIV, where it is inferred that the grooved penial setae are introduced into the spermathecae for sperm transfer (Omodeo 1996). Ventral, but not lateral, pairs are questionably illustrated by Beddard (1894) for segment XIII in *A. pordagei*. In *Standeria* each ventral couple of XIV and XV is replaced by as many as six genital setae, which are about twice as long as the normal setae but are otherwise unmodified and unornamented. The dorsal median intersetal distance is often unusually small (for earthworms) relative to the circumference of the body, so that the lateral couples are situated on the dorsal surface. It is noteworthy that the lateral bundles in aquatic microdriles, *e.g.* the Naididae (including Tubificidae) are also dorsally situated. The setal ratio *dd:u* is ca 0.2 in *A. b. abyssinicus*, *B. americanus*, *B. donaldi* and *Standeria* but this is not constant for the subfamily. In the illustration of the holotype of A. *pordagei* the male pores, which are said to be laterally situated, are shown to lie in line with the lateral setae, in which case *dd:u* would approximate to 0.5 but the dubious accuracy of this illustration is noted. However, in *Barriejamiesonia* the dorsal median intersetal distance (*DD*) is 0.44 of the circumference (C or U) (Ljungström 1971). In *Kathrynella*, also, the dorsal median interval is large (Omodeo 1996); in *Lacandodrilus dd:u* is 0.32 but it calculates as 0.15 in *Righiella*. Genital and penial setae are absent in the Syngenodrilinae.

Clitellum. The clitellum appears distinctly saddle–shaped in *Standeria,* although accompanied by ventral tumescence, and *Barriejamiesonia*; or is annular in *A. brinkhursti brinkhursti*, *A. b. abyssinicus*, *A. pordagei*, *B. americanus, B. donaldi, Kathrynella, Lacandodrilus* and *Righiella* (Fig 15). It includes segment XIII which bears the male pores (the intraclitellar condition). It is poorly developed in IX–XIII, in *A. lauzannei*. The maximum recorded extent is 1/2XII–1/2XVII (= 5 segments) in a specimen of *S. transvaalensis* (Fig 17). As is characteristic of aquatic oligochaetes, the clitellum is only one cell thick (*A. pordagei* Beddard 1894, *A. b. brinkhursti* (Fig 5), *Standeria* and the Syngenodriliinae). A suggestion of a multi–layered condition in *A. b. abyssinicus* is possibly an artifact of sectioning.

Male genital field. The single pair of male pores is situated on XIII in all known species, including the Syngenodriliinae, with the exception of *Kathrynella* in which they are in XIV (Fig 13). Their location is precisely lateral (*A. pordagei* Beddard 1894, *A. brinkhursti abyssinicus*) or ventrolateral just above setal lines *b* (*A. b. brinkhursti* confirmation of Brinkhurst, 1964; *À. pordagei vide* Michaelsen 1913), or at the sites of the absent ventral setae (*A. tanganyikae* Beddard 1906; *Standeria*, Fig 16) or closely associated with the penial setae (*B. americanus*). There is no coincidence longitudinally of the male pores with the position of the spermathecal pores, these varying from lateral (but not when the male pores are lateral) to mid–dorsal in location. Penes are present in *A. pordagei*, *A. ruwenzoriensis*; *A. brinkhursti brinkhursti; A. lauzannei* and *Righiella,* suggesting that the male and spermathecal pores are apposed in copulation. It is evident therefore that, if simultaneous mutual interchange of sperm occurs, the two concopulants must coil around one another (Jamieson 1978), as earlier argued for the naidid (tubificid) *Aktedrilus monospermathecus* by Knöllner (1935), so that each has its male pores opposite the spermathecal pore(s) of the partner. It is very likely that the unpaired mid–dorsal spermatheca evolved to facilitate copulation, the coiling giving a more stable contact (Erséus, Ph.D. thesis 1980). Mid–dorsal unpaired spermatheca are also found in the naidid (*sensu* Erséus *et al.* 2008) *Inanidrilus* (Erséus 1979); here the length of ribbon–like penial setae (which are paired) roughly corresponds to the length of the spermathecal duct; one such seta probably assists in transferring the sperm "securely" into the spermathecal ampulla of the recipient partner, as suspected for some alluroidids. Further examples of a mid–dorsal spermathecal pore are the naidid [tubificid] *Limnodriloides* (Erséus 1990, page 280) and the enchytraeid *Grania* (see *G. monospermatheca*, Erséus & Lasserre 1976).

There is clearly no well–developed protogyny or protandry as sperm are found in the spermathecae and atria simultaneously with ripe oocytes in the same individual (e.g. *A. pordagei* and S. *transvaalensis*).

Female pores. The female pores lie in XIV at or near its anterior border (*A. pordagei* Beddard 1894, Michaelsen 1913; *A. tanganyikae* Beddard 1906; *A. b. brinkhursti*; *A. b. abyssinicus*; *Brinkhurstia*; *Standeria*; *Lacandodrilus; Righiella*). Each forms a black spot in *A*, in *Barriejamiesonia*. They lie in line with the male pores except in *A. b. abyssinicus*, in which they are slightly more ventral and in *Brinkhurstia donaldi* they are slightly ventral of *a* lines. They are unusual in *Kathrynella* in lying near the ventral midline. They are anterior to setae *b* of XIV in the Syngenodrilinae.

Spermathecal pores. These are paired (*A. pordagei* Beddard 1894, and Jamieson 1968,1971); *Standeria transvaalensis*) or unpaired, median and dorsal (*A. pordagei*; Michaelsen 1913; *A. tanganyikae* Beddard 1906). Their precisely lateral location in *Standeria* is exceptional and when paired in *A. pordagei* they lie near the middorsal line. In all but one known species the pores lie at or near the anterior borders of their segments. They lie in segments VII (*Kathrynella*, in furrow 6/7 on setal line *a*); in VI, VII and VIII (exceptional *A. ruwenzoriensis*), VII and VIII only (*A ruwenzoriensis*, commoner location, Brinkhurst 1964); VIII only (*A. pordagei* Beddard 1894; Michaelsen 1913, 1914b, *A. b. abyssinicus; Barriejamiesonia,* at the extreme posterior margin of VIII in 1/2 *BC*; *Brinkhurstia donaldi*, a mid–dorsal cleft in furrow 7/8; *Righiella jamiesoni*, at 7/8 but ampulla in XII); or in IX only (*A. tanganyikae* Beddard 1906; *A. b. brinkhursti*; *Brinkhurstia americanus*; *S. transvaalensis*; paired at 9/10(?) in *Lacandodrilus*). In *A. ruwenzoriensis*, in which the spermathecae are normally unpaired, Brinkhurst (1964) observed an individual with two spermathecal ampullae attached to a single duct. This perhaps indicates former, possibly recent, pairing of the spermathecae in *A. ruwenzoriensis* and justifies inclusion of the unithecal material described by Michaelsen (1913) as *A. tanganyikae* in *A. pordagei*, as Michaelsen himself (1936) later suggested. In *A. lauzannei* the single spermathecal pore opens dorsally in VIII very near to intersegment 7/8. There are two pairs, posteriorly in VIII and IX, in the Syngenodrilinae.

Dorsal pores. Unknown in both subfamilies.

Nephropores. Rarely externally visible but minute in straight lines in 1/2 *BC*, situated in intersegmental furrows in *Barriejamiesonia*.

Septa. In all species of *Alluroides* s. strict, investigated for septal thickening, thickened septa extend posteriad as far as 12/13; septum 3/4 is delicate and imperfect or is not apparent and no septa are developed more anteriorly (*A. pordagei*, *A. brinkhursti,* both subspecies; Jamieson (1968)). In *Brinkhurstia* 3/4 is delicate, thickening extends to 14/15, and 10/11 is neither attenuated nor backwardly deflected. *Standeria* resembles *Alluroides* in having septal thickening which extends posteriorly as far as 12/13 but 10/11 has a tier of muscle fibres and, although relatively attenuated, is not backwardly deflected; 3/4 is absent. In *A. brinkhursti brinkhursti* the septa are very muscular from 4/5–9/10 inclusive; 3/4 not apparent; 10/11 dorsally partially thickened, mostly evaginated posteriad as a very thin–walled seminal vesicle; 11/12 and 12/13 only slightly thickened; 13/14 posteriad are not appreciably thickened. In *A. brinkhursti abyssinicus* septa 4/5–12/13 are fairly strong, with the exception of 10/11 which is very thin and is evaginated posteriad. In *Brinkhurstia donaldi* septum 3/4 is incomplete, septa 4/5–12/13 are fairly thick. In *Kathrynella* septa 5/6–10/11 are thickened and funnel–shaped. In *Lacandodrilus* the septa all thin and membranous. In *Righiella* septa 4/5–11/12 are fairly thick. Some septa are very strong in the Syngenodrilinae.

Septal glands. These are attached dorsally to the posterior, or sometimes the anterior wall of anterior segments. Brinkhurst (1964) drew attention to their similarity to those of the Enchytraeidae. In *Barriejamiesonia* they lie in V–VII depending from the anterior face of 5/6–8/9; all of same size, small or large, covering the dorsal surface of the gut. In *Lacandodrilus* they lie in V, VI, VII, VIII and IX (in X incipient) as paired glands present on the dorsolateral walls, attached to the corresponding posterior septum, mixed with lateral vascular commissures. In *Righiella* they are moderately developed, in V–VIII. In *Standeria* they are attached dorsally to the anterior faces of septa as far as 9/10 and also 11/12, 12/13? In *A. brinkhursti brinkhursti* there are chromophil septal glands in V–VIII, attached to the posterior septum and in *B. b. abyssinicus* chromophil glands extending to the posterior wall of VII.

Alimentary canal. In several alluroidine species, the roof of the pharynx forms a pad of elongated cells (Brinkhurst 1964, Jamieson 1968). The canal is simple, lacking gizzards, calciferous glands or other appendages. The segment of origin of the intestine, of suprageneric significance in some 'megadriles', here appears to vary intragenerically or even intraspecifically, but there is some possibility that the apparent diversity is due to identifying it in terms of dilatation of the canal rather than histological structure, partly owing to the inadequate condition of the available preparations. In most species the origin has been determined in only a single specimen. Dilatation occurs in the following segments in species investigated: XIII in *A, pordagei* (*v*. Beddard 1894); XIII–XV in *A. brinkhursti abyssinicus*; XIV in *A. lauzannei* and *Righiella*; XV in *S. transvaalensis; Barriejamiesonia and Standeria*; XVI in A. *b. brinkhursti* and *B. americanus* and XIX in *A. tanganyikae* (Sims *in litt*., confirmation of Beddard 1906). No transition is apparent in *Kathrynella* and *Lacandodrilus*. Curiously. Chagné & Giani (1998) do not mention gizzards for their Syngenodrilid but the presence of two gizzards is a major difference of *Syngenodrilus* from Alluroidines.

Blood vascular system. The vascular system is characterized by the existence of single dorsal and ventral vessels, the presence of meandering lateral loops (dorso-ventral commissurals) in anterior segments as far posteriad as XI (*Righiella*, Fig 15) or XII (*S. transvaalensis*) and the absence of a subneural vessel (*A. pordagei*, *Righiella, Standeria*). In *Alluroides pordagei* the dorsal blood vessel is large and adherent to the gut in XIII posteriorly; slender and freer anteriorly to this; hearts very tortuous extending posteriorly into XI(XII?). In *A. lauzannei*, the circulatory system consists of a large contractile dorsal vessel and a smaller ventral vessel. In the midregion the commissures are short and not ramifying and attached to the intestine. In the anterior region (II–XII) the commissures are long, powerful, contractile, and coiled. The posterior region is richly vascularized; the commissures ramify into numerous vessels; this region possibly functioning as gills. In *Barriejamiesonia* hearts lie in X (not seen in XI) or in XI (not seen in X**).** In *Brinkhurstia donaldi* dorsal and ventral vessels have large diameters; commissural vessels in V–XI are tortuous with thin walls, diameter *ca* 17 µm; their dorsal loops in V–VIII embedded in the septal glands; commissurals in X and XI are compressed and hidden by large gregarine gamonts; numerous capillaries beneath and among the epidermal cells, especially in the clitellar region, and among the glandular cells covering the prostates; diameter *ca* 3.5 µm. In *Kathrynella* the circulatory apparatus is strongly developed (Fig 13), showing in the anterior segments long lateral commissures between dorsal and ventral vessels rolled into a ball. In *Lacandodrilus*, the dorsal vessel is single; sometimes increasing from XIV posteriad; vascular commissures are long and contorted vessels in segments V?, VI–XI; embedded in septal glands; the ventral vessels single. No subneural vessel. A pair of commissural loops winding far laterally is present in XII anteriad. In *Righiella* the perienteric sinus begins in XIV (Fig. 15A); commissural vessels are sinuous, moderately large (diameter 18 µm) in V–XI, as elegantly depicted by Omodeo and Coates (2001). In *Standeria* dorsal and ventral blood vessels are single; there is no subneural vessel; a pair of commissural loops winding far laterally is present in XII anteriad.

Nephridia. The nephridia are stomate, exonephric holonephridia. The funnel, which is preseptal, has approximately six marginal cells in the upper lip and a well–developed lower lip (*A. pordagei*). The small number of cells in the upper lip represents an intermediate condition between the mesonephridiostomal condition of the Lumbriculidae, order Lumbriculata, and the meganephridiostomal condition of the members of the order Opisthopora to which

Alluroides belongs. This relative simplicity of the nephrostome is not necessarily of phylogenetic significance as it is probably a function of the small size of the alluroidines. The nephridia, unlike those of the Syngenodrilinae, are avesiculate. The terminal region of the duct has been observed in *S. transvaalensis*. It is straight and shows a slight trumpet–shaped enlargement in the outermost region of the longitudinal muscle.

Stephenson (1930) reported, on the basis of existing accounts, that nephridia were absent from the anterior portion of the body; there was no record of their occurrence in front of IX in which the first pair is located in *Brinkhurstia donaldi,* and somewhat questionably in *B. americanus*, until they were observed in VII in *Barriejamiesonia* and in VIII in *A. lauzannei*. The first visible pair in *S. transvaalensis* lies in XI. They commence in XII–XVI in *A. pordagei* and XV in *Lacandodrilus*; in XV and XVI in the two subspecies of *A. brinkhursti* and XVII in *Righiella*. Nephropores are rarely visible but are minute in straight lines in 1/2 *BC*, situated in intersegmental furrows in *Barriejamiesonia*. Nephridia are vesiculate in *Syngenodrilus*.

Anterior male organs. The Alluroidinae are mostly proandric, having testes in segment X only; however, *Kathrynella* is metandric, with testes located in the anterior part of XI facing the large seminiferous funnels. *Righiella* is also metandric with sperm funnels in the posterior part of XI but testes regressed, apparently in the same segment. The developing sperm masses lie in the unexpanded segment X (*B. americanus*, *S. transvaalensis*) or septum 10/11 and the enclosed sperm masses project posteriad so as almost to occlude XI (*Alluroides*). In *A. pordagei* the whole septum is backwardly deflected to touch septum 11/12 but in both subspecies of *A. brinkhursti* distinct seminal vesicles are formed. Where spermatogenic masses project into XI, the sperm funnels are directed dorsally to serve both the masses within X and those protuberant into XI. *Lacandodrilus* is holandric, with male funnels in X and XI. Syngenodrilines are also holandric.

Male terminalia and atria. In *Alluroides ruwenzoriensis* each vas deferens enters the median aspect of an erect tubular atrium near the middle of its length (Fig 9). Each of the two atria narrows distally and terminates in a well–defined penis visible externally on a raised papilla (Brinkhurst 1964). The vas deferens is seen in *A. pordagei* to run within the glandular covering of each coiled tubular atrium posteriorly as far as XVI and presumably enters the lumen of the atrium entally (Jamieson 1968). In *Brinkhurstia americanus*, however, the excessively attenuated tubular atrium enters an ectal terminal chamber, in common with but quite separately from the opening of the corresponding male duct into the chamber (Fig. 3). The three *Sparganophilus*–like pairs of prostates, separate from the male pores, are distinctive from the alluroidines, excepting *Lacandodrilus*.

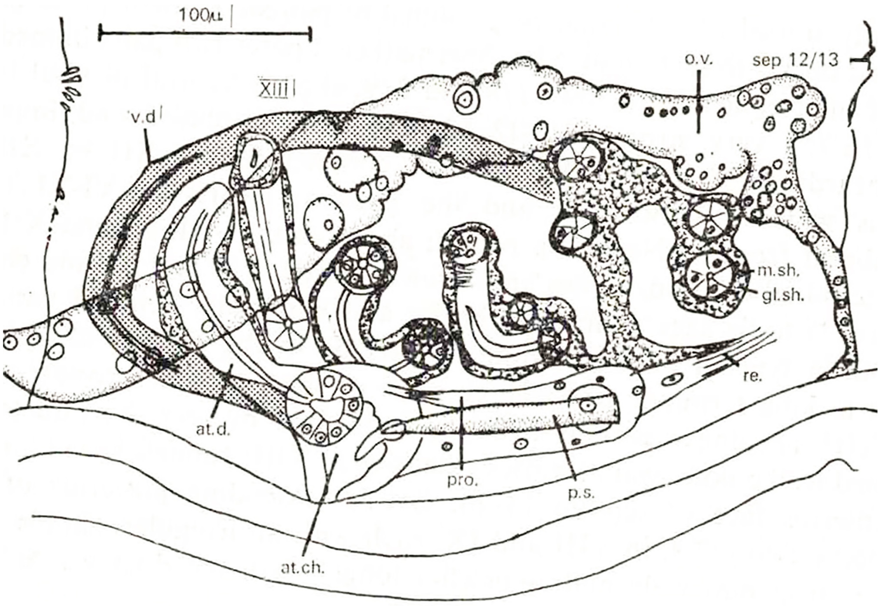


FIGURE 3. ***Brinkhurstia americanus*** (Brinkhurst 1964). Longitudinal section through the male terminalia. at.ch, terminal chamber of atrium; at.d, atrial duct; gl.sh, glandular sheath; m.sh, muscular sheath; o.v, ovary; pro, protractor muscle; p.s, penial seta; re, retractor muscle; sep, septum; v.d, vas deferens. From Jamieson (1968).

A similar condition appears to exist with respect to the more robust atria of *Standeria transvaalensis* (Jamieson 1968) (Fig 16). While the atria in *Alluroides* are terminal continuations of the vasa deferentia, the atria of *Brinkhurstia*

(Fig 3) and *Standeria* (Fig 16) are distinct sperm–filled diverticula of the terminal chambers or copulatory pouches as the latter might be called, but in the two subspecies of A. *brinkhursti* they are bulbous and in *A. b. brinkhursti* are almost as wide as long (Fig 4). Their form in *A. tanganyikae* Beddard 1906, is questionable as Beddard (1906), in a definition of the genus including *pordagei* and *tanganyikae*, stated that the atria are long and coiled, a condition which Michaelsen (1913, 1914a, 1914b, 1915, 1935) found in the material which he ascribed to *A. tanganyikae*. In 1936, when Michaelsen united *tanganyikae* with *pordagei*, he recognized three subspecies but mentioned no diversity in the form of the atria. Brinkhurst (1964) found Beddard's holotype of *A. tanganyikae* to have "massive globular atria" apparently similar to those of the Elgon material which has been made the type series of *A. brinkhursti* by Jamieson (1968).

In the specific description of *A. tanganyikae*, Beddard described the atria as being directed posteriorly from the male pores and ending in oval expansions. Uncertainty as to the precise form of the atria and the existence of other peculiarities has necessitated taxonomic separation of Beddard's material from that subsequently described as *A. tanganyikae*.

In *Alluroides s. strict*., and in *B. americanus*, the histological structure of the atria resembles that of some moniligastrids in the presence of an external and an internal glandular layer with an intervening muscular layer (*A. pordagei*, Fig 8D). In *A. b. brinkhursti* the external gland cells have been shown to communicate with the lumen of the atrium by many small ducts which traverse the thick muscular walls (*A. tanganyikae*; Brinkhurst 1964). This was confirmed by Jamieson (1968) and was demonstrated in addition for *A. pordagei*, *A. brinkhursti abyssinicus* and *A. lauzannei* (Fig 7). The external unicellular glandular cells send small ductules through the muscular sheath which in some cases appear to enter swollen cells. In *Barriejamiesonia* prostates are one pair originating in XIII. The prostatic duct swells up into a muscular bursa at the parietes. The bursa is somewhat spindle–shaped; from the bursa the duct gradually attenuates towards the gland from which it is not sharply demarcated. The prostate glands reached to 19/20 on the right and to 20/21 on left side in one worm of this species (Ljungström 1971).

In *Lacandodrilus paludosus* (Fig. 14)*,* two pairs of lobulate, rosette–shaped glands lie internally on the ventral body wall of XIII and XIV, the anterior the larger; composed of several short lobules almost fixed to the ventral wall and deduced to be prostatic glands. No tubular, atrium-like glands are present (Fragoso & Rojas, 2023). In *Kathrynella* the atria possess thick muscular walls (Fig 13B) and appear as shining, bent, spindles which open in the middle of XIV, behind the penial setae; the atria (which Omodeo considers to correspond to the 'euprostates' of Eudrilidae) have a thin external coating of non–glandular cells.

Female organs. The ovaries depend from the anterior wall of segment XIII, the typical location in Metagynophora. Oocytes extend posteriorly through several segments (in *B. americanus* forming a continuous chain) maximally to segment XXI (*A. pordagei*, Jamieson 1968). Brinkhurst (1964) was the first to recognize ovisacs (in *B. americanus*). They are seen in both subspecies of *A. brinkhursti* and in *S. transvaalensis*. The mature oocytes are very large, filling much of the width of a segment, and are packed with yolk granules, characteristics of the eggs of 'plesiopores', e.g. Tubificidae. In *Brinkhurstia donaldi* two ovisacs extend from XIII to XVI; at maturity they disappear, leaving large eggs free in the coelom of XV and XVI. In *Kathrynella*, two long cylindrical egg sacs, apparently beginning in XVII, extend as far back as XXXV; they possess thick glandular walls and contain up to a dozen large ripe eggs (*ca* 530 µm wide) between XXV–XXXV. The largest oocyte nucleus was measured in each of several species and a remarkably small range in diameter was found. Nuclear diameters in *pordagei*, both forms of *A. brinkhursti*, *B. americanus* and *Standeria* were respectively 40, 42, 55, 33 and 31 µm (Jamieson 1968). Ovaries are also located in XIII in the Syngenodrilinae and long ovisacs are present in *Syngenodrilus*.

Spermathecae. The spermathecal diameter in *A. pordagei*, both forms of *A. brinkhursti*, *B. americanus* and *Standeria* varied within remarkably narrow limits being respectively 161, 138, 136, 87 and 107 µm (Jamieson 1968). Only in *B. americanus*, did the spermathecae lack sperm. The highest number of spermathecal segments is three (dorsomedian), in one individual of *A. ruwenzoriensis* (see Brinkhurst 1964). Three segments possibly represent a basic condition in the Alluroidinae, restriction to two segments in other individuals of this species and to one segment in other species may be due to reduction. Intra–specific variation (from segment VIII to IX) may occur as in *A. brinkhursti*. Spermathecae are paired and ventrolateral in *Barriejamiesonia*, *Kathrynella* (Fig. 13G), *Standeria* (Fig 17) and *Lacandodrilus* and vary from paired to single (dorsal and anterior in VIII) in *A. pordagei* (Fig. 8A). The single spermathecal pore is mid–dorsal in *A. ruwenzoriensis*, *Brinkhurstia* (Fig 10) and *Righiella* (Fig 15). Pairing of the spermathecae may also be a basic condition from which the unpaired condition in the other species of Alluroidinae has been derived by fusion. In the Alluroidinae, the male pores are always lateral to ventral, (in XIII, excepting XIV in *Kathrynella*) Movement of the spermathecal pores from the lateral to the dorsal position precludes copulation simply by apposition of the ventral surfaces of the worms and promotes stability.

Evidence that transition from the paired to the single condition has been by fusion of analogues rather than by loss of one of the pair is perhaps seen in the duplication of the ampulla on a single duct in a specimen of *A. ruwenzoriensis* reported by Brinkhurst (1964). In agreement, Michaelsen (1936) had already considered that the wide spermathecal duct and certain histological features of the spermathecae of *A. tanganyikae* Beddard 1906, and *sensu* Michaelsen 1913, were evidence of union of two spermathecae and represented an intermediate condition between the two spermathecae of *A. pordagei* Beddard 1894 and the single spermatheca with a narrow pore in his Congo material. In *A. pordagei* the spermatheca is invested by a tall peritoneum and lined internally by a columnar epithelium. Between the layers is a band of muscle, mainly circular with an external sheath of longitudinal fibres, which is approximately as thick as the internal epithelium but ectally is greatly thickened as a sphincter. The lining epithelium has distinct oval nuclei in a regular row. Its inner boundaries are indistinct and have the appearance of being drawn out into filaments (cilia?) which merge with the sperm rope which fills the lumen. The spermathecae of material described by Michaelsen (*tanganyikae* 1914b; *congicus* 1936) had distinct ducts but in other Alluroidinae then known the spermathecae were simple pouches or (*Standeria*), showed only slight differentiation of a duct. In contrast, the single spermatheca of *Righiella* has a very long duct, so that the spheroidal ampulla lies in segment XIII, connecting to the median dorsal pore anterior in VIII, as elegantly illustrated by Omodeo & Coates (2001) (Fig. 15). In *Brinkhurstia donaldi* the duct is shown traversing two segments and is highly unusual in having a diverticulum (Figs 11 and 12); this and the duct contain spermatozoa, but the ampulla contains sponge spicules. Conversely a short, vertical duct is in *B. americanus* (Fig. 10). In *Kathrynella* (Fig.13B) two large, convoluted spermathecae occur in VII and consist of a short, partly ciliated duct and elongate ampulla; the ectal section of the latter contains the bulk of the spermatozoa, whereas the ental section is filled with a hyaline secretion (Omodeo 1996). In *Lacandodrilus* the pair of spermathecae opens lateroventrally at 9/10. In *A. lauzannei*, the muscular duct of the voluminous single spermatheca opens mid–dorsally in VIII. In *A. brinkhursti abyssinicus* the unpaired spermatheca is a simple, narrow, blind tube, 0.14 mm wide, recurving at the ental third, widening ectally before opening, via a narrower section at its pore dorsally in VIII. Two pairs of spermathecae occur in *Syngenodrilus* and one pair in the other species.

Systematics

FAMILY ALLUROIDIDAE Michaelsen 1900, emend. Jamieson 1968

Type genus: *Alluroides* Beddard 1894

Setae single–pointed, sigmoid, 4 pairs per segment commencing on II; genital or penial setae sometimes present. Lateral line (lateromuscular groove) present or absent. Clitellum one cell thick, commencing on XI, XII or XIII and occupying 2–6 segments. Male pores one pair, intraclitellar, either at the anterior border of XIII, or in its setal arc, or in XIV. Female pores one pair, at the anterior border, or more posterior in XIV. Spermathecal pores on one to three of segments VI–IX, at or near their anterior margins, lateral to dorsal, paired or single. Dorsal pores absent. Alimentary canal with or without oesophageal gizzards; lacking diverticula or other appendages. Nephridia holonephridia. Testes in X or in X and XI or in XI only (proandric, holandric or metandric). Seminal vesicles, when present, projecting into XI only or extending posteriorly through several segments as in microdriles. Prostate glands (euprostates or atria) either discharging separately from the male pores or through the latter, in some cases receiving the vasa deferentia entally. Ovaries anterior in XIII. Mature oocytes large and yolky, in ovisacs which extend posteriorly through several segments. Spermathecae without diverticula, sometimes (*Brinkhurstia donaldi*) with a single diverticulum.

Distribution. Alluroidinae, Colombia; Brazil; Saint Lucia; Mexico; Tanzania; Uganda; Zimbabwe; South Africa; Ethiopia; Argentina; Guyana; Chad; Paraguay; Kenya; Democratic Republic of the Congo; Panama. Syngenodrilinae: Kenya; Tanzania; Martinique?.

The family Alluroididae was established by Michaelsen (1900) for *Alluroides pordagei* Beddard (1894). Subsequent additions were *A. tanganyikae* Beddard (1906), and two species erected by Brinkhurst (1964) in a revision of the family, namely *A. ruwenzoriensis* and *A. americanus*. The latter species, referred to a new genus

Brinkhurstia by Jamieson (1968), was the only American record for an otherwise African group until descriptions from Guyana of *Kathrynella guyanae* by Omodeo (1996) and *Righiella jamiesoni* by Omodeo & Coates (2001) with redescription of *Brinkhurstia americanus* and addition of *B. donaldi. Barriejamiesonia aberratus* from South Africa and *Alluroides lauzannei* (described as *A. tanganyikae* from Lakes Chad, Léré and Fianga by Lauzanne 1968) were added by Ljungström (1971). Recently *Lacandodrilus paludosus* was added by Fragoso & Rojas (2023) from southern Mexico.

A number of forms have been described (Michaelsen 1913, 1914 a, 1914 b, 1915, 1935, 1936) which are of uncertain status but are referred to *A. pordagei* (as did Michaelsen 1936). In a taxonometric investigation, Jamieson (1968) tentatively included, in the Alluroididae, the sub–family Syngenodrilinae, a monotypic group containing only *Syngenodrilus lamuensis* Smith & Green 1919, which those authors had placed in the Moniligastridae. In the same work (Jamieson 1968) the type of a new monotypic alluroidine genus, *Standeria transvaalensis* (from Lake Chrissie in the former Transvaal, now the Province of Mpumalanga) was described, *Alluroides americanus* was made the type of the new, monotypic genus, *Brinkhurstia*; *A. tanganyikae s*. Brinkhurst 1964, (Mt. Elgon) was removed from *A. tanganyikae* Beddard and made the type of a new species, *A. brinkhursti* of which a new sub–species, *A. brinkhursti abyssinicus* was described from Ethiopia. *Barriejamiesonia*, *Alluroides*, *Brinkhurstia, Kathrynella, Righiella*, *Lacandodrilus* and *Standeria* constitute the sub–family Alluroidinae while the Syngenodrilinae, as Gates (1945) had suggested it should, forms the other sub–family of the Alluroidinae. The two sub–families may be distinguished as follows:

1. Outer setal couples dorsal or lateral. Gizzards absent. Prostates (atria) 1 pair; pores combined with the male pores, or (*Lacandodrilus*) absent. Alluroidinae.

2. Outer setal couples lateral, not dorsal. Gizzards present. Prostates (atria) 3 pairs, pores separate from the male pores. Syngenodrilinae.

SUBFAMILY ALLUROIDINAE

Type genus: *Alluroides* Beddard 1894

Key to the genera of the Alluroidinae

1	Spermathecal pore(s) mid–dorsal	2
	Spermathecal pores paired lateral	4
2	Testes in X	3
	Testes in XI	*Righiella*
3	Penial setae present	*Brinkhurstia*
	Penial setae absent	*Alluroides*
4	Testes in X and XI	*Lacandodrilus*
	Testes in X or XI	5
5	Testes in X	6
	Testes in XI	*Kathrynella*
6	Genital setae absent	
	Seminal vesicles present	*Barriejamiesonia*
	Genital setae present	
	Seminal vesicles absent	*Standeria*

TABLE 1. The most significant characters distinguishing the genera of the Alluroidinae (modified and expanded from Omodeo and Coates, 2001).

	Alluroides Beddard, 1894	*Standeria* Jamieson, 1968	*Brinkhurstia* Jamieson, 1968	*Righiella* Omdeo & Coates, 2001	*Kathrynella* Omodeo, 1996	*Barriejamiesonia* Ljungström, 1971	*Lacandodrilus* Fragoso & Rojas, 2023
Male pores	XIII	XIII	XIII	XIII	XIV	XIII	XIII
Spermathecal pores	Mid-dorsal, some or all of VI-VIII	Lateral 8/9	Mid-dorsal 7/8, IX	Mid-dorsal 7/8	Lateral 6/7	Lateral 8/9	Lateral 9/10
Testes in	X	X	X	XI	XI	X	X and XI
Male ducts insertion	In ectal terminal chamber	In ectal terminal chamber	In ectal terminal chamber	On the ental tip of prostates	On the ental tip of prostates	In ectal terminal chamber	Not seen
Penial setae	no	no	yes	no	yes	no	no
Secondary annulation	no	yes	no	no	yes	VIII	yes
Genital papillae	no	no	no	no	yes	yes	no
Geographical Distribution	Central Africa	Central Africa	South America	Guyana	Guyana	Central Africa	Mexico

A longitudinal lateral line (latero–muscular groove) present on each side between the ventral and dorsal setal couples, or absent. Dorsal median intersetal distance (*dd*:u), *ca* 0.2 to 0.5 of the circumference of the body; genital setae or penial setae present or absent. Clitellum commencing in XII or XIII, maximally extending for five segments. Male pores ventral to lateral in XIII or exceptionally XIV. Female pores at or near the anterior border of XIV in line with the male pores or nearly so or exceptionally near the ventral midline. Spermathecal pores lateral to dorsal but never in line with the male pores, paired or dorsal median and single in VI–IX, maximally in three of these segments. Dorsal pores absent. Subneural blood vessel absent. Nephridia avesiculate. Prostates (atria) tubular, lobulate or bulbous, receiving the male ducts, or discharging with the latter but separately from them into a terminal chamber; internal epithelium surrounded by a muscular sheath outside which prostatic cells are usually present. Gizzards absent. Proandric, testes in X only; or less commonly holandric, testes in X and XI, or metandric, testes in X, Seminal vesicles projecting into XI, or more elongate, or absent. Ovisacs extending posteriorly through several segments; eggs large and yolky.

Distribution. Colombia; Brazil; Saint Lucia (Caribbean); Mexico; Tanzania; Uganda; Zimbabwe; South Africa; Ethiopia; Argentina; Guyana; Chad; Paraguay; Kenya; Democratic Republic of the Congo; Panama.

GENUS *Alluroides* Beddard 1894, emend. Jamieson 1968

Type species: *Alluroides pordagei* Beddard 1894

Alluroidinae in which the atria are wide, coiled tubes or are bulbous; prostate cells surround the muscular sheath of the atrium, and the vas deferens enters each atrium near the midlength of the latter or entally. Male pores lateral; ventral setae of XIII present or absent; genital and penial setae absent. Spermathecal pores paired or single, dorsal in VI, VII and VIII, or in VII and VIII only, or in either VIII or IX. First septum 3/4; septum 10/11 attenuated. First nephridia in VIII or XV or XVI. Intestine commencing in XIII–XIX. Testes in X. With or without distinct seminal vesicles but with spermatogenic masses partly occluding XI.

Distribution. Tanzania; Uganda; Zimbabwe; South Africa; Ethiopia; Chad; Kenya; Democratic Republic of the Congo.

Remarks. Collectively the features listed above adequately diagnose *Alluroides* from the remainder of the sub–family. An individual character of particular note which is not shared with *Brinkhurstia* and *Standeria* is the termination of the vasa deferens entally on each atrium, clearly demonstrated by Brinkhurst (1964, Fig. 9) for *A. ruwenzoriensis* and observed by Jamieson (1968) in *A. pordagei*. The vasa deferentia of *A. brinkhursti* and *A. tanganyikae* have not been observed but the overall phenetic resemblance of these to the other two species points to the existence of such a connection. In the other genera entry of two ducts into each terminal male chamber is readily seen while A. *tanganyikae* and *brinkhursti* show no semblance of dual terminalia. At the specific level the systematics of *Alluroides* cannot be considered settled. Much larger series, from more localities, together with ecological and molecular data, are needed before the validity of the present division into A. *pordagei*, *lauzannei*, *tanganyikae*, *ruwenzoriensis* and *brinkhursti* can be conclusively determined.

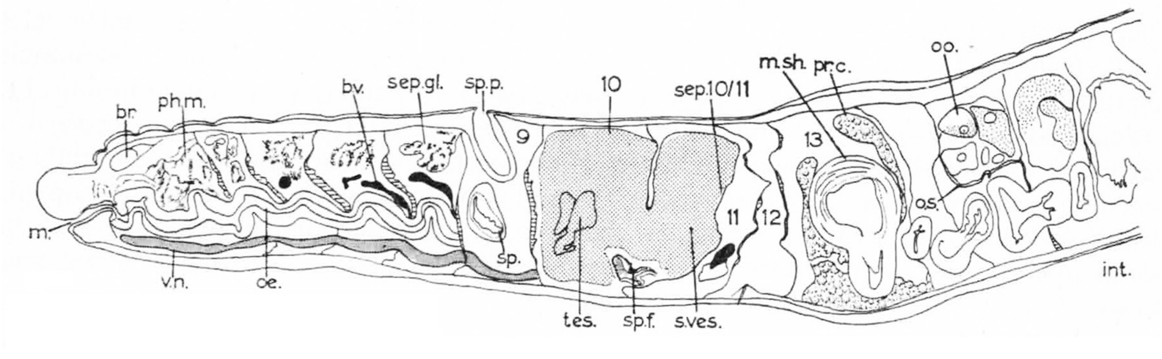


FIGURE 4. ***Alluroides brinkhursti brinkhursti*** Jamieson (1968). Longitudinal section of the holotype. Abbreviations: br, brain; bv, blood vessel; m, mouth; msh, muscular sheath of atrium; oe, oesophagus; oo, oocyte: os, ovisac; ph m, pharyngeal musculature; pr c, prostatic cells; sep, septum; sep gl, septal gland; sp p, spermathecal pore; s. ves, seminal vesicle; sp, spermatheca; sp f, sperm funnel; tes, testis; vd, vas deferens; v n, ventral nerve cord. Adapted from Jamieson (1968).

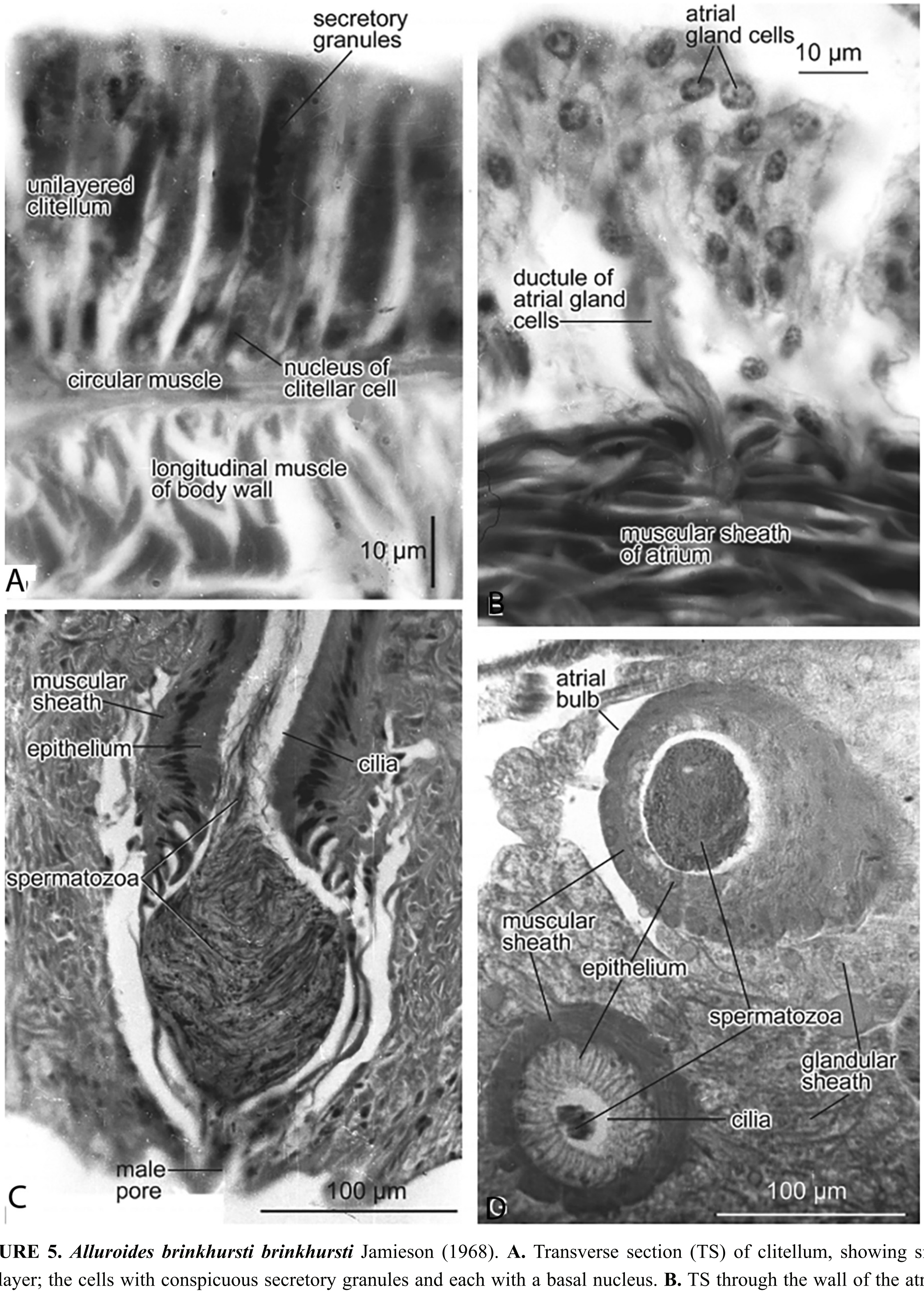


FIGURE 5. ***Alluroides brinkhursti brinkhursti*** Jamieson (1968). **A.** Transverse section (TS) of clitellum, showing single cell layer; the cells with conspicuous secretory granules and each with a basal nucleus. **B.** TS through the wall of the atrium, showing a group of atrial gland cells with ductule penetrating the muscular sheath of the atrium. **C.** Longitudinal section through the male pore, showing the ectal end of the atrium, which forms a penis with muscular sheath, ciliated epithelium and rope of spermatozoa in the lumen, forming in the ectal chamber a sperm mass. D. *Alluroides pordagei*. Oblique section through the atrial bulb, containing a large sperm mass, and the associated atrium. From Jamieson (2006).

Alluroides brinkhursti brinkhursti Jamieson 1968 (see Figs 4, 5)

Alluroides tanganyikae Beddard (part.) Brinkhurst 1964: 528, Figs. 1–3, Pl. 1, Fig. 1–2, Pl. 2, Fig. 1–2.
Alluroides brinkhursti brinkhursti Jamieson 1968:76, Fig. 13; Brinkhurst & Jamieson 1971: 711–712, Fig. 14. 3A, Frontispiece A–D.
(Non) *A. tanganyikae* Beddard 1906: 215. Michaelsen 1913: 7; 1914 a: 89; 1914b: 165; 1935: 36.

Length 35–45 mm, width 1–1.5 mm, segments 150. Length of a lateral seta from XV ental to the node, 0.109 mm. in XI, *aa*:*ab:bc:cd:dd*=3.7:1.0:3.1:1.0:3.6; dd=0.21*u*; *bc*:*aa*=0.8. Clitellum annular in 1/2XII to XV. Male pores ventrolateral in XIII, just dorsal to *b*. Female pores in line with the male pores immediately behind furrow 13/14. Spermathecal pore single, mid–dorsal on IX just behind 8/9 on a prominent papilla.

Septa very muscular from 4/5–9/10 inclusive; 3/4 not apparent; 10/11 dorsally partially thickened, mostly evaginated posteriad as a very thin–walled seminal vesicle; 11/12 and 12/13 only slightly thickened; 13/14 posteriad not appreciably thickened. Intestine beginning in XVI. Chromophil septal glands in V–VIII, attached to posterior septa. Nephridia commencing in XV or XVI. Testes ventral on the anterior wall of X. No testis–sacs apparent. Seminal vesicle almost filling XI. Sperm funnels posterior and ventral in X facing anteriorly and dorsally to serve both X and the seminal vesicle. Atria large and globular, almost filling XIII; 0.347 mm wide narrowing ectally to 0.204. mm. Each with lining epithelium surrounded by a thick muscular sheath outside which, but not closely adherent, are tongues of unicellular gland cells which communicate with the atrial lumen by a large number of small ductules which penetrate the muscular layer. Penis eversible and elongate. Ovaries in XIII, on its anterior wall; funnels on its posterior wall, penetrating 13/14. Ovisac extending posteriad into XVI. Mature oocytes large and yolky. Nephridia commencing in XV or XVI. Spermatheca 0.138 mm wide, single, lying recurved in IX.

Distribution. Uganda, Mt. Elgon, in tributaries of the Kiriki River, which flows into Lake Okolitorom.

Alluroides brinkhursti abyssinicus Jamieson 1968 (see Fig 6)

Alluroides brinkhursti abyssinicus Jamieson 1968: 77, Fig. 9–11, 14; Brinkhurst & Jamieson 1971: 712–713, Figs 4.1B, C, D, 14.3B.

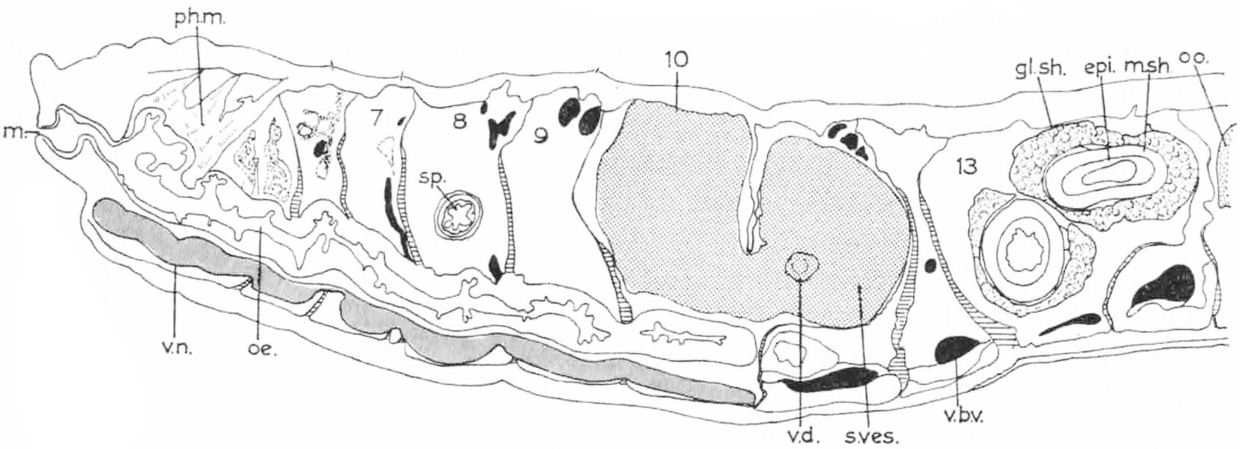


FIGURE 6. *Alluroides brinkhursti abyssinicus* Jamieson (1968). Longitudinal section of holotype. Abbreviations: epi, epithelium of atrium; gl sh, glandular sheath of atrium; m, mouth; msh, muscular sheath of atrium; oe, oesophagus; oo, oocyte: ph m, pharyngeal musculature; s.ves, seminal vesicle; sp, spermatheca; vbv, ventral blood vessel; vd, vas deferens; v n, ventral nerve cord. Slightly modified from Jamieson (1968).

Length 45 mm, width 1.6 mm, segments 144. Zygolobous. Body form slender, tapering uniformly to the somewhat pointed tail end; cylindrical throughout. A lateral line visible as a conspicuous white line running the length of the body on each side slightly above mid–*bc* and commencing at the lower limits of the peristomium. Ventral setal couples absent from XIII. Clitellum annular, over XII–XV but its limits not determinable with certainty; best developed in XII–XIV. Male pores one on each side in the setal arc of XIII immediately below the lateral line and thus almost exactly lateral. Each pore at the depressed centre of a very protuberant, transversely elliptical porophore which extends forwards to intersegmental furrow 12/13 and is preceded by a small tumescent crescent in XII. Female pores one on each side, each a small but conspicuous transverse slit, with minute elliptical lips, in intersegmental furrow 13/14 which is deflected posteriorly; slightly more ventrally located than the male pores. Spermathecal pore, a conspicuous unpaired mid–dorsal slit immediately in front of the posterior border of VII, with obvious but only slightly tumid lips which are surrounded by a transversely oval pale field. This field extending anteriorly almost to the setal arc and posteriorly impinging slightly on VIII.

Septa 4/5–12/13 fairly strong, with the exception of 10/11 which is very thin and is evaginated posteriad to form a bulbous seminal vesicle; 7/8–9/10 the thickest; 3/4 imperfect and very delicate; 13/14–15/16 thin but not as delicate as the succeeding septa. 13 /14 is deflected posteriad by the atria so as almost to touch 14/15 and is prolonged backwards to XVIII as the (unpaired?) ovisac. Chromophil glands extend posteriorly to the posterior wall of VII. The first nephridia with recognizable lumina in XVI, but peritoneal masses in XV and some more anterior segments possibly represent nephridia. The alimentary canal widens in XIII, but not until XV, which may be the segment of intestinal origin, is enlargement pronounced. Dorsal and ventral blood vessels well developed; subneural vessel absent. Sperm morulae in X form a compact mass suggesting the presence of a testis–sac and also contained in a narrow stalked seminal vesicle formed by backward evagination of septum 10/11 into XI which it almost fills. The sperm funnel situated in the spermatogenic mass at the neck of the seminal vesicle and directed dorsally so as to serve both X and the seminal vesicle. Atria each a bulbous tube with narrow lumen, restricted to XIII, with lining epithelium of eosinophil glandular cells surrounded in turn by a thick sheath of predominantly circular muscle and a layer of similar width and several cells thick of unicellular gland cells: total width of muscular tube (external surface) 0.38 mm, narrowing to 0.195 mm ectally. Ovaries and funnels in XIII. The ovisac almost occluded at the intersegmental septa but bulging dorsally to the gut in each segment and posteriorly containing large oocytes full of large eosinophil yolk granules. Spermatheca unpaired; a simple, narrow, blind tube, 0.14 mm wide, recurving at the ental third, widening ectally before opening, via a narrower section at its pore dorsally in VIII.

Distribution. Ethiopia: Stream at 10,500 feet (3,200 m) in Choke Mts (Mt. Tab). Senan District, Goj jam Province.

Alluroides lauzannei Ljungström,1971 (see Fig 7)

Alluroides tanganyikae, Lauzanne 1968. 107–109.
Alluroides lauzannei Ljungström 1971, nomen nov. pro *Alluroides tanganyikae*, Lauzanne 1968.
(Non) *Alluroides tanganyikae* Beddard 1906.

Length 20–60 mm. width 1.2–1.5 mm, segments 110–150. Colour rose to red. Prostomium conical and ciliated, divided into two parts. Setae 2 per bundle; simple–pointed and 150–170 um long; well demarcated and very thick in the anterior region; ventral setae absent in the region of the male pores. Clitellum poorly developed, in IX to XIII. Spermatheca single, with dorsomedial pore anterior in VIII forming a pad clearly visible on the body wall.

Septa strongly developed in the anterior region as far as XII. Mouth followed by a well-developed pharynx. Oesophagus extending to XII–XIII where it is followed by a straight intestine with strongly marked constrictions. Gizzard absent. Circulatory system consisting of a large contractile dorsal vessel and a smaller ventral vessel. In the midregion the commissures short and not ramifying and attached to the intestine. In the anterior region (II–XII) the commissures long, powerful, contractile, and coiled. The posterior region richly vascularized; the commissures ramify into numerous vessels; this region possibly functioning as gills. Nephridia two per segment; absent from the anterior region, commencing in VIII; in VIII very near to intersegment 7/8; constituted by a thin–walled ovoid pouch and a strongly muscular duct. Segments X and XI occupied by a conspicuous mass, constituting, very likely, the testes, in X, and a sperm sac. Segment XII occupied by a yellowish mass constituted by the ovaries and sexual products. At maturity the eggs occupying the posterior of segments XIII and XIV; voluminous and rich in yolk These products apparently included in an ovisac issuing from septum 12/13. Female ducts not observed. Male genital tract represented in XIII by two voluminous, pyriform, and very elongate atria each with a thick muscular part. For most of its length but particularly in the swollen region each covered on the largest part of its length by a glandular mass, very likely functioning as a prostate; this formation richly vascularised. A series of fine canaliculi traverses the muscular mass in the swollen region. In the swollen part of the atrium there are pyriform cells orientated longitudinally. Atrium opening ventrolaterally via a short pseudo–penis, in the form of a corolla which becomes a truncated cone on fixation. Male funnel issuing from septum 10/11 closely associated with the sperm mass. The narrow sperm duct is elusive and better seen in the living animal. It follows the length of the ventral body wall and reaches segment XIII in the region of the pseudo–penis. It remounts the atrium at the interior of the glandular bed where its course is lost, it has not been possible to detect its opening into the atrium and it is presumed that the sperm enter the atrium through the canaliculi already referred to. The single, voluminous spermatheca, projecting into IX; consisting of an ovoid pouch with thin walls and a well–developed muscular duct.

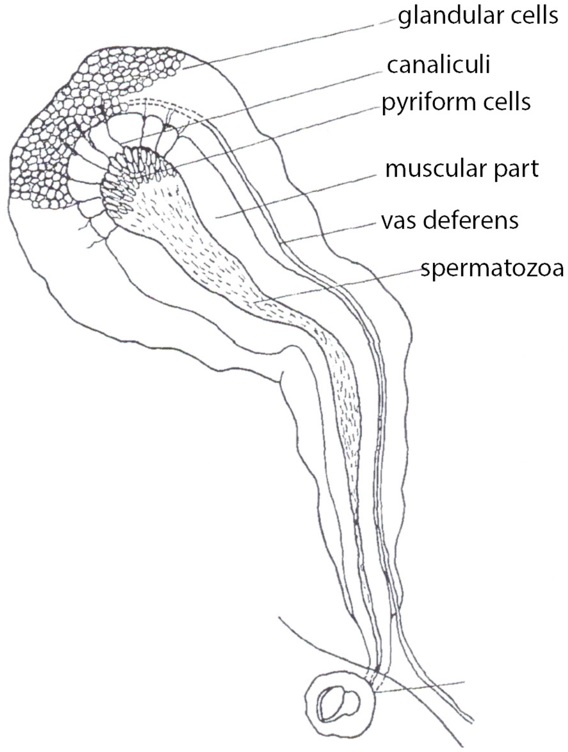


FIGURE 7. ***Alluroides lauzannei*** Ljungström, 1971. Detail of an atrium. Note the vas deferens entering the apex of the atrium via canaliculi. Relabelled from Lauzanne (1968).

Distribution. This worm forms the major part of the biomass of benthic oligochaetes in Lake Chad. It prefers sandy bottoms where currents give good oxygenation but is never found where vegetable debris predominates. The reproductive period is November to February. It is equally collected in Lakes Léré and Fianga (Mayo Kebi Region).

Alluroides pordagei Beddard 1894 (see Fig 8)

Alluroides pordagei Beddard, 1894: 244, Fig. 4, 5.
Alluroides pordagei Beddard, Michaelsen 1900: 106–107; Brinkhurst 1964: 527. Jamieson 1968: 75, Fig. 15–18; Brinkhurst & Jamieson 1971: 713–714, Fig. 14.3D, E.
? Alluroides tanganyikae Beddard. Michaelsen 1913: 7, Pl. XIX, Fig. 9; 1914 a: 89; 1914 b: 165, Pl. V. Fig. 13; 1915: 29; 1935: 36; 1936: 37 (part.)
(Non) *A. tanganyikae* Beddard 1906.

Length 25–48 mm, width 1.0 mm, segments 202. Prolobous. Form approximately cylindrical throughout, anterior segments at least biannulate with the transverse furrow shortly postsetal. Lateral line in *bc*, nearer to *b* than to *c*. Anus terminal. Ventral setal couples of XIII absent at maturity; all setae sigmoid, with approximately central, well–developed node; none modified as genital setae. Outer setal couples dorsal, *dd:u*=ca 0.2. Clitellum annular, XII–XVI. Male pores a pair precisely lateral, or slightly ventrolateral, nearer to *b* than to *c* lines in the setal arc of XIII, each surrounded by a circular tumescence almost filling the segment longitudinally. Female pores in 13/14 directly in line with the male pores, inconspicuous. Spermathecal pore paired or single, dorsal and anterior in VIII, in the type paired near the dorsal midline.

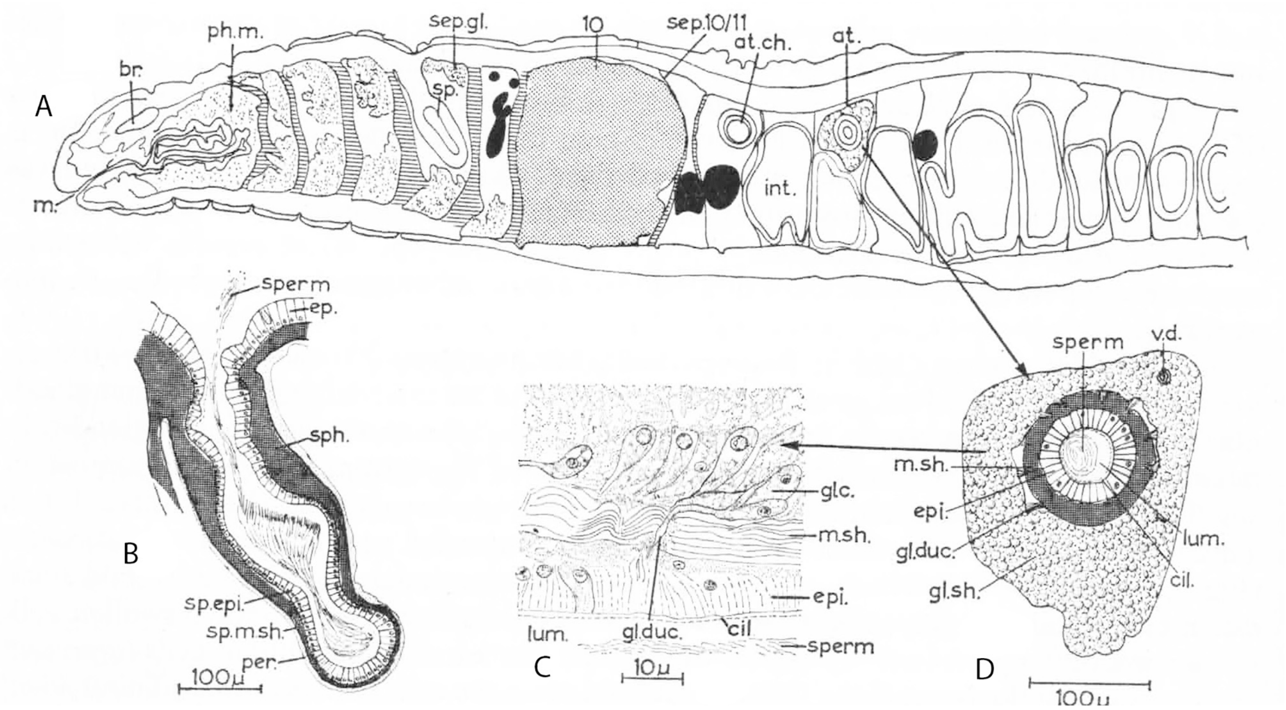


FIGURE 8. ***Alluroides pordagei*** Beddard 1894. **A**. Longitudinal section of the anterior region of the body of Beddard's paratype. **B**. Spermatheca. **C**. Longitudinal section of wall of atrium. **D**. Transverse section of atrium. Abbreviations: at, atrium; at ch, atrial chamber; br, brain; cil, cilia; ep, epidermis; epi, epithelium; gl duc, glandular ductule(s); gl sh, glandular sheath; int, intestine; lum, lumen; m, mouth; ph m, pharyngeal musculature; per, peritoneum; sep.gl, septal gland; sp, spermatheca; sperm, spermatozoa; sph, sphincter; sp epi, spermathecal epithelium; sp m sh, muscular sheath of spermatheca; v.d, vas deferens.. Slightly modified from Jamieson (1968).

Septa 4/5 (the first clearly developed), 9/10 exceptionally strongly thickened, 10/11 thin and attenuated, 11/12 and (though less so) 12/13 moderately thickened, the succeeding septa thin. Septal glands posterior in V–IX? Nephridia commencing in XII–XVI. Pharynx anterior to septum 4/5. Intestine commencing in XIII, internal epithelium with tall cilia; oesophagus similarly ciliated in XII in front of the oesophageal valve; ciliation not certainly present further anteriorly. Brown–granuled chloragogen cells commencing (always?) at 1/2 IX. Dorsal blood vessel large and adherent to the gut in XIII posteriorly; slender and freer anteriorly to this. Hearts (posterior commissural) very tortuous extending posteriorly into XI(XII?). Septum 10/11 bulging posteriorly far into XI to form a wide–mouthed (unpaired?) seminal vesicle. Muscular tubes of the atria forming slender somewhat coiled tubes extending from XIII into XIV or as far as XVI and widening immediately before opening at the male pores. With the exception of the terminal ectal chamber each tubular atrium surrounded by a sheath of unicellular prostate cells, which approximately doubled the width of the apparatus, the cells communicating with the atrial lumen by minute ductules. Vasa deferentia running in the glandular prostatic duct and presumably entering the atrium entally. Ovaries and funnels in XIII. Oviduct penetrating the body wall immediately behind septum 13/14. Female gonadial cells, at maturity, in XIII–XXI, probably in ovisacs. Spermatheca single or paired, dorsally in VIII.

Distribution. Kenya: swamp 4 miles inland from Mombasa (Type locality, Beddard 1894); lower forest region of Mt. Kenya at 2400 m (Michaelsen 1914 a, b; Michaelsen 1915, as *A. tanganyikae*); Kahawa stream, Athi River tributary, near Nairobi, collector B.G.M. Jamieson, 11 Dec. 1967. Republic of the Congo: Mulongo, Niunzu; Albertville (Michaelsen 1935); Leopoldville (Michaelsen 1936). Rhodesia: swampy earth, Zambezi River, near Victoria Falls (as *A. tanganyikae,* Michaelsen 1913).

Remarks. Because of the uncertain status of Michaelsen's material this account (from Jamieson 1968) was derived solely from Beddard's type–series, and his description, and incorporated results of examinations by Brinkhurst (1964) and Jamieson (Athi River material).

The extreme septal thickening, and its distribution, now emerge as diagnostic features of *A. pordagei* (condition still unknown, however, in *A. tanganyikae s*. Beddard and s. Michaelsen). Intraspecific variation from a paired to a single spermatheca (in VIII) is confirmed and reinforces Brinkhurst's conclusion (1964) that *A. tanganyikae s*. Michaelsen (spermatheca single in VIII), but not *s*. Beddard (spermatheca single in IX), should be included in *A. pordagei*.

The decision by Michaelsen (1936) to recognize three subspecies, *pordagei*, *tanganyikae* and *congicus*, has not been followed here though it still deserves consideration. *A. tanganyikae* has been retained as a distinct species but recognition of *congicus*, from Leopoldsville, as a subspecies appears reasonable. Michaelsen distinguished it by the spermatheca with a thin–walled, sac–like ampulla and sharply demarcated muscular duct. He added that *congicus* was 90–100 mm long, with *ca* 210 segments, the largest form, whereas the typical subspecies was 22 mm long, the smallest form, while *tanganyikae* had a length of 45 mm, with *ca* 150 segments, intermediate between the two other forms. Some of these figures no longer hold.

Alluroides ruwenzoriensis Brinkhurst 1964 (See Fig 9)

Alluroides ruwenzoriensis Brinkhurst 1964: 531, fig. 4; Jamieson 1968: 74; Brinkhurst & Jamieson 1971: 714.

Length 100 mm, width just exceeding 1 mm, segments 150. All segments, except first 2 or 3, triannulate. Setae broad, simple pointed; ventral couples absent from XIII at maturity. Spermathecal pores middorsal on VII and VIII (also on VI in one specimen). Sperm funnels, testes, seminal vesicles and ovaries as in *pordagei*. Atria elongate with glandular covering, standing vertically in XIII to which they are restricted. Vas deferens thin walled, joining the median face of the atrium about midway along the length of the latter. Each atrium narrowing distally and terminating in a well–defined penis which is visible externally on a raised papilla. Spermathecae single (in one case the spermathecal duct had 2 unequal ampullae).

Distribution. Uganda: Ruwenzori Mountains (lakes and stream at 3816 and 3930 m., Nyamagasani Valley).

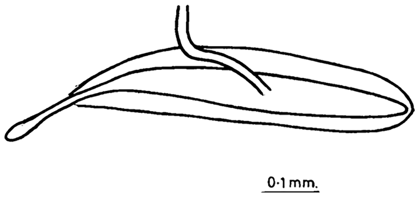


FIGURE 9. ***Alluroides ruwenzoriensis*** Brinkhurst 1964. Atrium and vas deferens entering at midlength. From Brinkhurst (1964).

Alluroides tanganyikae Beddard 1906

Alluroides tanganyikae Beddard 1906: 215.
Alluroides tanganyikae Beddard (part.) Brinkhurst 1964: 528; Brinkhurst & Jamieson 1971: 714–715.
(Non?) *Alluroides tanganyikae*; Michaelsen 1913: 7; 1914a: 89; 1914b: 165; 1915: 29; 1935: 36.

Taken from Brinkhurst and Jamieson (1971).

Length 30 mm, width 1·5 mm, segments 60. Prostomium long and pointed, transversely bisected by a constriction, but zygolobous. Ventral setal couples absent from XIII. Clitellum? Male pores on XIII in line with the ventral setae (of adjacent segments). Female pores in intersegment 13/14 in *ab*. Spermathecae single, pore middorsal in 8/9, with tumid periphery and very conspicuous. Septal glands obvious. Intestine beginning in XIX, transition from moniliform oesophagus abrupt. Chloragogen cells apparently beginning in IX. Nephridia? Atria a pair ending posteriorly in oval expansions; directed posteriorly to the pores.

Distribution. Lake Tanganyika at about 10 fathoms (18.3 metres).

Remarks. Since the last revision of this genus (Brinkhurst & Jamieson 1971) and owing to the fact that no new material has been collected and/or revised, the status of *A. tanganyikae* Beddard (1906) remains uncertain owing to omissions and contradictions in the type–description and the paucity of information yielded by the holotype (Brinkhurst 1964). Its inadequate characterization, together with an apparent difference in location of the male pores and in intestinal origin, have made it necessary to separate *A. tanganyikae* from the better–known material from Mt. Elgon referred to this species by Brinkhurst (1964), the latter being regarded (Jamieson 1968; 1971) as a distinct species*, A. brinkhursti*. The affinity between *tanganyikae* and *brinkhursti* cannot be settled until topotypic material of the former taxon is collected from Lake Tanganyika, a lake noted for the high endemicity of its fauna. Occurrence of *A. tanganyikae* in the lake at a depth of 60 feet (18.3 metres), whereas *brinkhursti* is a montane form, lends some support to taxonomic separation. Its affinities with *pordagei* are also uncertain but *A. pordagei* has been shown (Jamieson 1971) to be clearly distinguished from *A. brinkhursti* (Mt. Elgon and Ethiopian sub–species) in its extreme septal thickening. If this distinction is found to exist between *pordagei* and *tanganyikae* it will considerably strengthen the grounds for specific separation. They were merged as subspecies by Michaelsen (1936).

Genus *Barriejamiesonia* Ljungström 1971

Barriejamiesonia Ljungström 1971: 321. (Correction for *Barryjamiesonia* of Ljungström)

Alluroidinae in which the ‘atria’ are divided into three regions: an ectal muscular spindle–shaped chamber, a short narrow duct and an ental gland; vas deferens opening independently from the corresponding atrial duct and not thickened. Male pores ventral just in front of or slightly lateral to *a.* Setae *ab* of XIII present but not modified. Genital setae absent. Spermathecal pores lateral on extreme posterior margin of VIII. First septum 5/6; 10/11 not attenuated. First visible nephridia in VII. Intestine commencing in XIV. Seminal vesicles present.

Remarks. Ljungström distinguished this genus from *Alluroides* by the atria not being wide coiled tubes, the vasa deferentia opening ectally rather than entally; the atria being divided into a muscular duct and a glandular prostate; first septum 5/6 rather than 3/4; first nephridia in VII rather than in XIII–XIV. From *Brinkhurstia* in having a muscular rather than non–muscular chamber; the prostate cells not surrounding the muscular duct; penial setae absent; male pores ventral rather than ventro–lateral; setae *ab* present in XIII; spermathecal pores paired ventral on VII rather than ?IX or further back. From *Standeria* in having the atria divided into a glandular and muscular duct rather than a muscular duct lined internally with prostatic cells; vas deferens opening ectally rather than entally into the chamber; setae *ab* present in XIII; spermathecal pores on VIII rather than IX; first septum 5/6 rather than 4/5; 10/11 not attenuated; genital setae absent; first nephridia in VII rather than XI; intestinal origin in XIV rather than XV; seminal vesicles present.

Further differences from other alluroidine genera were that the atria are more like the prostates of the Ocnerodrilinae; the wide separation of the dorsal setae at 0.44 rather than 0.2 of the circumference; and the absence of a visible latero-muscular groove.

Barriejamiesonia aberratus Ljungström 1971

Barryjamiesonia aberratus Ljungström 1971: 322–323.

Maximum length 58 mm. Greatest width in front of clitellum 1 mm. Body round in cross–section, clitellar region dorsoventrally flattened. Colour, unpigmented white. Cuticle non–iridescent. Lateral grooves absent. Number of segments 127, 129 (plus about five undifferentiated and asetal segments) and 142, all segments smooth except VIII which is biannulate. Prostomium prolobous. Setae present from II and of equal size throughout; *cd* present on clitellum; no modified setae; *ab* present in XIII. Setal ratio on X: *aa:ab:bc:cd*=8.3:1:8.3:1, DD=0.44 C. Nephropores minute in straight lines in 1/2 *BC*, situated in intersegmental furrows. Dorsal pores absent. Clitellum pink reddish or whitish, smooth, saddle–shaped throughout down to B, intersegmental furrows obliterated down to B, on XII–XV or XII–XVI, ending at 11/12 and 15/16 or 16/17, anterior and posterior borders indistinct. Spermathecal pores one pair on extreme posterior margin of VIII in 1/2 BC. The pores big, slit–like and surrounded by glandular lips that form a transverse oval. Female pores minute, each visible as a black spot in 13/14 in A. Seminal grooves absent. Genital markings circular, 0.36 mm in diameter, low but protuberant from the body wall as glandular discs; post–setal and situated in file with protuberances around the atria in AB on XIII left, XIV and XV or XIV and XV.

First septum in 5/6 behind which all are present, 5/6–10/11 somewhat and equally thickened and conical with posteriad apex or 5/6–8/9 equally thickened and then gradually becoming thinner from 9/10 to 11/12 but 5/6–11/12 conical. Gizzard absent. Septal glands in V–VII depending from anterior face of 5/6–8/9, covering dorsal face of gut. Extra–mural calciferous glands absent.

Hearts (commissures) in X (not seen in XI) or in XI (not seen in X**)**. Nephridia holonephric, recognizable from VII. From VII to about XX they are big, leaf–shaped and surrounded by a layer of (? connective) tissue. Testes and their funnels, one pair, free in X. Male ducts running in A under peritoneum back to XIII where they fuse with the ectal end of the atrial chamber. Ovaries probably in XIII, ovisac, oviduct and ovifunnels not seen. Seminal vesicles two pairs. In one specimen the anterior are small, depending from 9/10 into IX and the posterior pair big depending from 11/12 into XII. In the other specimen both pairs are vestigial, the anterior pair depending from 9/10 into IX and the posterior pair from 10/11 into X. Prostates one pair originating in XIII. The prostatic duct swells up into a muscular (sheen present) bursa at parietes. The bursa somewhat spindle–shaped; from the bursa the duct gradually attenuates towards the gland from which it is not sharply demarcated. Prostate glands reaching to 19/20 on right and to 20/21 on left side in one worm. The greatest width of the bursa 0.25 mm, of the duct 0.1 mm and of the gland (in XIII) 0.27 mm. Genital marking glands, two pairs, circular, rather flat, acinous; free in the coelom in XIV and XV (specimen with GM on XIV, XV).

Parthenogenesis is suspected.

Distribution. Natal. N41. Scottsburgh, Port Shepstone road. Aquatic, just below and near water's edge.

Remarks. During the preliminary identification the specimens were thought by Ljungström to represent an aberrant ocnerodriline. No data on spermathecae were provided in the original description, and the only information refers to its empty nature. Distinction from *Standeria* is uncertain.

Genus *Brinkhurstia* Jamieson 1971

Type species: *Alluroides americanus* Brinkhurst 1964

Alluroidinae in which the atria are very slender, much coiled tubes, prostatic cells surround the muscular sheath of the atrium, and the openings of each atrium into the rounded terminal, non–muscular chamber is separate from that of the corresponding vas deferens. Male pores ventrolateral. Ventral setal couples of XIII absent. Penial setae present. Spermathecal pore single, dorsal in IX. First septum 3/4; 10/11 not attenuated. First nephridia in IX? Intestine commencing in XIII–XV. No distinct seminal vesicles.

Distribution. Brazil; Saint Lucia (Caribbean); Argentina; Guyana**.**

Remarks. Unique features within the Alluroidinae of *Brinkhurstia americanus* are the extreme attenuation of the atrial prostates, the ratio width muscular tube of the atrium: width body being only 0.036 at maturity, and the presence of penial setae. The generic significance of the penial setae, *per se*, is questionable, however, as their presence or absence varies intragenerically in other families.

Brinkhurstia resembles *Standeria*, and differs from *Alluroides*, in possessing at each male pore a distinct, rounded terminal chamber into which two ducts, positively identified as the atrium and vas deferens of the corresponding side, discharge (Fig. 3) but the chamber is exceptional in *Brinkhurstia* in being non–muscular. A particularly noteworthy difference from *Standeria*, shared with *Alluroides*, is the presence of prostatic cells ensheathing the atria.

Brinkhurstia americanus **(Brinkhurst 1964) (See Figs 3 & 10)**

Alluroides americanus nom. nud. Cernosvitov 1936: 19.
Alluroides americanus Brinkhurst 1964: 533–534. Figs.5–7.
Brinkhurstia americanus (Brinkhurst), Jamieson 1968: 80–81, Figs. 3, 12; Brinkhurst & Jamieson 1971: 716–717, Fig. 14.1E, F; Righi *et al*. 1978: 11–12, Figs. 11–21; Stacey & Coates 1996: Tables 1 and 2; Omodeo and Coates 2001: 39–40, Fig. 1 A, B.

Length 24–30 mm, width 0.56–0.75 mm, segments 100–130. Prostomium short or large and rounded. Ventral setal couples of XIII replaced by a single penial seta on each side; in the ovarian segments *aa:ab:bc:cd:dd*=4.7:1:5:1.1:6.2;

dd=0–25 u; length of a lateral seta from XI, base to node=87 µm. Clitellum annular, slightly less developed ventrally; segments 1/2XII–XV. Lateral lines present. Male pores ventrolateral in XIII. Female pores anterior in XIV. Spermathecal pore single, middorsal, anteriorly in IX.

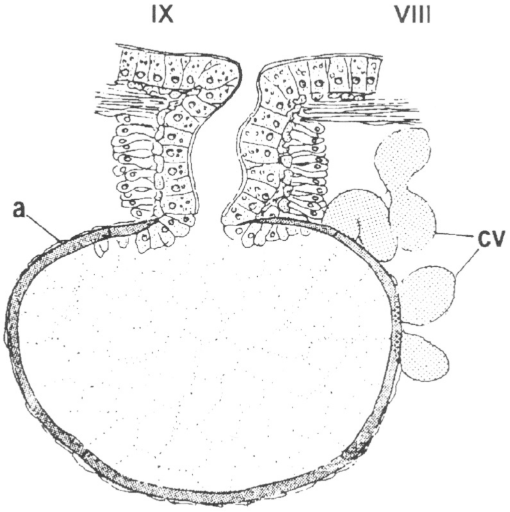


FIGURE 10. ***Brinkhurstia americanus***. (Brinkhurst 1964). Spermatheca opening mid–dorsally in the anterior of IX. Abbreviations: a, ampulla; cv, commissural vessel. From Omodeo & Coates (2001), reproduced with permission.

Septum 3/4 excessively delicate and doubtfully complete; 4/5 and 14/15 hardly appreciably, 6/7–8/9 fairly strongly thickened (two tiers of muscle fibres) the remainder intermediate; 10/11 has one tier of muscle fibres and is not backwardly deflected. Septal glands in V–VIII. Alimentary canal expanding greatly in XVI but no definite transition from oesophagus to intestine. Gizzard, oesophageal diverticula and typhlosole absent. Perienteric blood sinus in IX posteriad, not appreciable in front of this. Testes discrete elongated tongues of tissue dependent from the anterior wall of X. Gonadial tissue absent from XI. Seminal vesicles absent or present in XI. Vas deferens running on body wall in XI and XII. Atria very thin much coiled tubes extending from mid–XIII into XIV; discharging in the close proximity of the corresponding vas deferens through the posterior wall of a globular non-muscular ectal chamber; a simple, straight, unornamented penial seta in a follicle approximately twice the length of the chamber, penetrates the anterior wall of the chamber. Each prostate has a cuboidal lining epithelium surrounded in turn by a very thin muscular sheath and an external layer of prostatic cells only one to a few cells thick, though considerable masses of prostatic cells are formed between adjacent coils. Width muscular tube of atrium (external) 28 µm; width ectal chamber 37 µm; length penial seta 115 µm; greatest width 18 µm. Ovaries dependent from the anterior wall of XIII and extending posteriad into ovisacs formed by the backward evagination of septum 13/14 through as many as 8 segments: diameter of the largest oocyte–nuclei 33 µm. First nephridia (from peritoneal masses) in IX or X. Spermatheca in IX a simple elongated pouch, 87 µm wide, with no distinct ampulla, lined internally by a short columnar epithelium invested in a single layer of circular muscle and an outer glandular? peritoneal sheath.

Distribution. Brazil; Saint Lucia (Caribbean); Argentina; Guyana**.**

Brinkhurstia donaldi Omodeo & Coates, 2001 (see Figs 11, 12)

Brinkhurstia sp. Coates & Stacey 1994: 81, Table 1, Fig. 2.
Brinkhurstia sp. 2. Stacey & Coates 1996: Table 1 and Fig. 4D–F.
Brinkhurstia donaldi Omodeo & Coates 2001: 40–43, Figs, 2–3.

Length 30–32 mm, width 0.82–0.90 mm; segments 105, 109, 131, 135, 150, multiannulated. Lateral lines recognizable only on microscope slides: Body slender, cylindrical, tapering posteriorly; a series of buttons formed by 6–8 hyaline cells situated amid the longitudinal muscle fibres in a line included between setae *b* and *c*. Anus terminal.

Clitellum annular, 1/3XII–1/2XV, male pores in the middle of XIII aligned with setae *a*; in a few cases the terminal chambers and the penial setae protrude through them. Female pores in furrow 13/14, slightly ventral to setal line *a*. Spermathecal pore a mid–dorsal cleft in furrow 7/8. Setae sigmoid, slender, unsculptured; the longest ones in XI and measure respectively: *a* 328 µm*, b* 284 µm*, c* 164 µm*, d* 280 µm*;* their lengths decreasing anteriorly and posteriorly; in XX, *aa*:*ab*:*bc*:*cd*:*dd*=6.1:1.0:9.0:1.0:8.2. Cuticle about 2 µm thick.

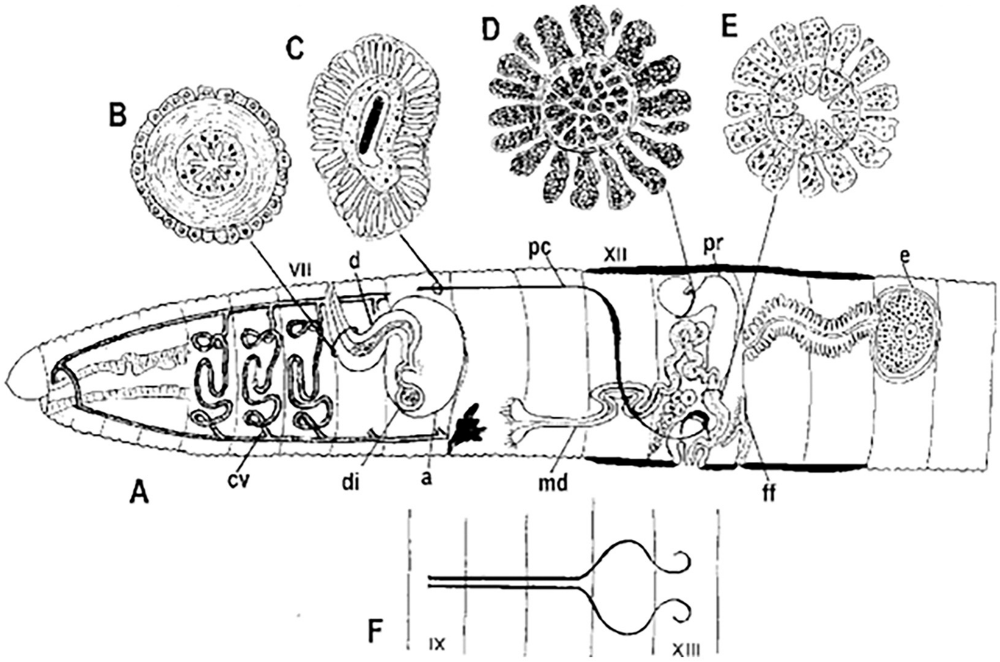


FIGURE 11. ***Brinkhurstia donaldi*** Omodeo and Coates (2001). **A**. Scheme showing arrangement of genital organs and vascular commissures. **B**. Cross section through spermathecal duct. **C**. Cross section of the muscular sac ensheathing penial seta. **D**. Section through ental part of prostate. **E**. Cross section of prostatic duct. **F**. Dorsal view of the arrangement of the penial setae within IX–XIII. Abbreviations: a, spermathecal ampulla, cv, commissural vessels, d, spermathecal duct, di, spermathecal diverticulum, e, egg, if, female funnel, md, male duct, pc, penial seta, pr, prostate. From Omodeo & Coates (2001), reproduced with permission.

Septum 3/4 incomplete, septa 4/5–12/13 fairly thick. Septal glands in V through VIII. Perienteric blood sinus commencing in IX. Nephridia avesiculate beginning in XI. Dorsal and ventral vessels with large diameters; commissural vessels in V–XI tortuous with thin walls, diameter *ca* 17 µm; their dorsal loops in V–VIII embedded in the septal glands; commissures in X and XI compressed and hidden by large gregarine gamonts; numerous capillaries beneath and among the epidermal cells, especially in the clitellar region, and among the glandular cells covering the prostates; diameter *ca* 3.5 µm. Muscular fibres of the body wall ribbon–shaped, 3 µm thick, 21 µm high.

Testes and seminal funnels in X; male ducts thin in XI and XII; in XIII becoming sinuous and filled with sperm, forming a highly convoluted epididymis, and finally connecting with the prostate at an intermediate point. Prostates long, convoluted, confined to XIII; with an inner layer of epithelial (glandular?) cells surrounded by a thick layer of muscle cells and covered by large, club–shaped gland cells which diminishes and then disappears near the outlet into the globular terminal chamber, which opens through as a small penial papilla. In each terminal chamber emerges a ribbon–like penial seta, whose proximal end lies in the anterior dorsal part of IX: the two penial setae, each ensheathed in a muscular sac, run parallel near the mid–dorsal line in IX, X and XI; then in XII they diverge sidewards and ventralwards, arcing around the terminal chamber in XIII and exiting through it. Ovaries in XIII; two egg sacs arise near the female funnels and extending backwards to XVI; the histology of the egg sac resembling that of *Kathrynella guyanae*. Ovaries and egg sacs disappear in fully mature specimens leaving two or three free large ellipsoid eggs (420 by 420 by 300 µm) in the coelom of XV and XVI.

Spermatheca with a thick, spindle–shaped muscular duct that runs forward to the middle of VIII abutting on a very large, free, globular ampulla that almost fills the cavity of this segment. Near the insertion of the duct is attached a pedunculated diverticulum. Sperm contained in the diverticulum and in the ental part of the duct.

Remarks. *B. donaldi* differs from *B. americanus*, the only described congener, in the form, size and peculiar insertion of the penial setae. Its spermatheca has a diverticulum and a much longer duct (correlated with the length of the penial setae) and opens one segment more anteriorly (Omodeo & Coates 2001).

Distribution. Guyana, Kurupukari creek, flowing into Essequibo River.

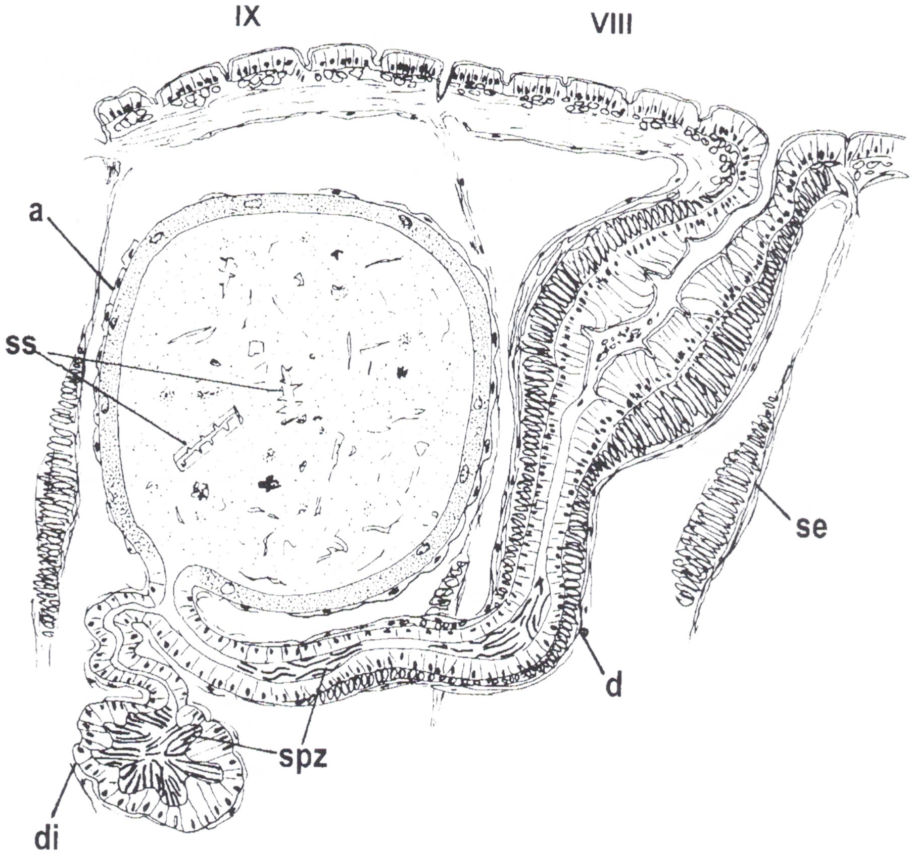


FIGURE 12. ***Brinkhurstia donaldi*** Omodeo & Coates 2001. Spermatheca, sagittal section. Abbreviations: a, ampulla; d, duct; di, diverticulum; se, septum with muscle fibres; spz, spermatozoa; ss, sponge spicules. From Omodeo and Coates (2001), reproduced with permission.

Genus *Kathrynella* Omodeo 1996

Type species: *Kathrynella guyanae* Omodeo 1996

Alluroidids with a cylindrical muscular atrium (euprostate); male pores paired, intraclitellar, opening ventrally and equatorial in XIV. Spermathecal pores a pair, opening in intersegmental furrow 6/7. Modified setae *a* and *b* in VII; grooved penial setae ventral in XIV. Circulatory apparatus strongly developed, showing in the anterior segments long lateral commissures between dorsal and ventral vessels rolled into a ball. *Kathrynella* shares with *Righiella* the metandric condition of the male apparatus. The presence of sperm sacs and the absence of glandular lining of the atria may also be diagnostic (Omodeo & Coates, 2001).

Kathrynella guyanae Omodeo 1996 (See Fig 13)

Kathrynella guyanae Omodeo 1996, 334. 11–15. Fig 1A–N, 2–5.

Body thread–like, flattened in clitellar and caudal regions, with deep intersegmental furrows conferring a moniliform appearance to the posterior half of worms. Longitudinal, latero–muscular grooves of body wall not observed but here recognized for Figure 13A.

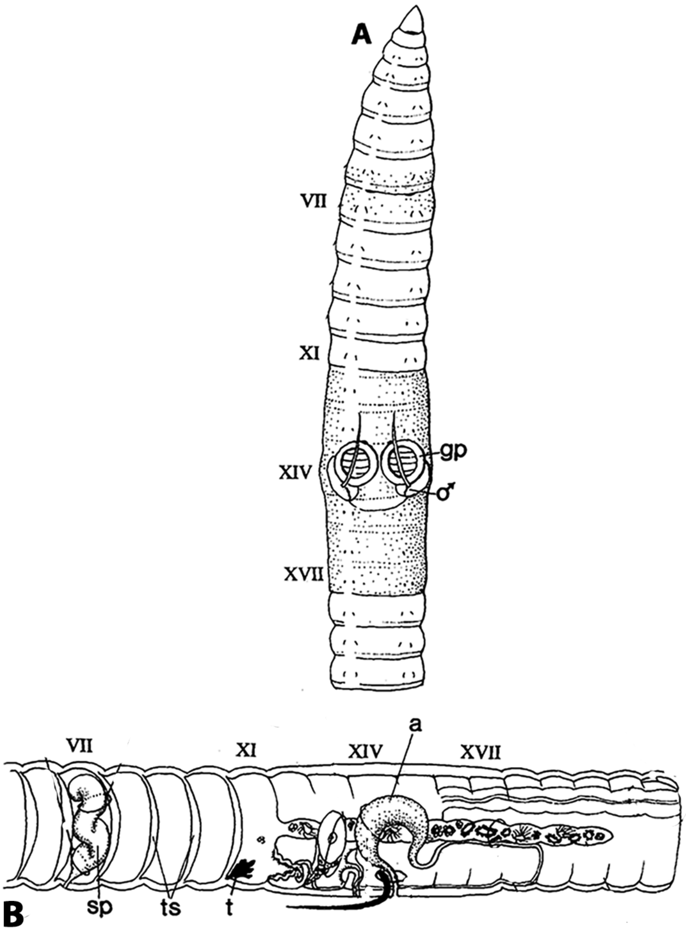


FIGURE 13. ***Kathrynella guyanae*** Omodeo 1996. **A**. Ventral view of anterior segments. Note the pale lateral line. **B.** arrangement of genital organs. Abbreviations: a, atrium; gp, genital papilla; ♂, male pore; sp, spematheca; t, testis; ts, thickened septum. The penial setae are seen projecting from the male pore. Modified from Omodeo (1996).

Length 85–89 mm; diameter 600 µm at X, 520 µm at mid–body, segments 282, 259. No cutaneous pigmentation, integument transparent. Prostomium zygolobous, conical; peristomium short. Setae paired with lumbricin arrangement. Pygidium small, anus a vertical cleft. Clitellum annular, extending from the posterior part of XI to XVII; the ventral side of XIV with two large, circular papillae with swollen borders and a very thick, whitish, central part crossed by 4–5 transverse furrows; behind and beside these papillae two crescent–shaped fields visible, each bearing a single, large, grooved, penial seta. In all specimens examined, penial setae were broken but their length estimated as longer than 300 µm. No other ventral setae visible in XIV. Dorsal setal couples of midclitellar segments slanting relative to the long body axis, setae *c* located more posteriorly than setae *d*. Male pore as a slit on hinder portion of each crescent–shaped field in XIV; paired female pores on anterior border of XIV, near midventral line. No dorsal pores. Nephridiopores inconspicuous. Spermathecal pores in furrow 6/7 on setal line *a*. Setal ratio *aa:ab:bc:cd:dd*=5.6:1.1:5.6:1:10 at segment X; 2.5:1:1.5:1:12 in posterior segments (where all setae are displaced ventrad). The length of setae increases from II, where it is 37 µm, to VII where setae *a* and *b* measure 92 µm and setae *c* and *d* 43 µm. Further posteriorly, the setal length decreases gradually (penial setae of XIV excepted), to become constant (*ca* 50 µm) behind the clitellum. Only caudal setae show distal ornamentation.

Body wall thin; cuticle approximately 0.5 µm thick; layer of circular muscles very thin. Septa 5/6–10/11 thickened, funnel–shaped. No pharyngeal pad distinguishable. Neither a gizzard, nor any apparent distinction between oesophagus and intestine present. Ciliated epithelium of intestine ending in clitellar region. Peri–intestinal blood sinus occurring from XII backwards. Holonephridia, apparently avesiculate, beginning in XII or XIII; initially poorly developed and acquiring normal size only behind clitellum. The circulatory apparatus exceptionally well developed. Dorsal and ventral vessels run the whole length of the worm and have very large diameters, only slightly less than that of the intestine. Seven pairs of long commissural vessels in V–XI, wound in balls whose size increases backwards; each ball covered with chloragocytes. A pair of large vessels originates in VII from the peri–intestinal blood sinus, and from XII to XVI run along the sperm sacs. Many lesser vessels seen everywhere, but no capillaries. Testes anterior in XI, facing the large seminiferous funnels, covered with sperm and bulging into segment XII. Sperm ducts coiled in XII in their proximal course, then running laterally within the body wall till XVII where they emerge again in the coelomic cavity, become thicker, and run forwards till XIV, where they form the atria. Atria possess thick muscular walls and appear as shining, bent, spindles which open in the middle of XIV, behind the penial setae; atria (which correspond to the 'euprostates' of Eudrilidae) with a thin external coating of non–glandular cells. Two long sperm sacs begin from septum 11/12 and run till XX, parallel to the egg sacs and to the posterior course of vasa deferentia. Ovaries located in the ventral forepart of XIII; two long cylindrical egg sacs, apparently beginning in XVII, extending as far back as XXXV; possessing thick glandular walls and containing up to a dozen large ripe eggs (*ca* 530 µm wide) between XXV–XXXV. Two large, convoluted spermathecae in VII; consisting of a short, partly ciliated duct and elongate ampulla; the ectal section of the latter containing the bulk of spermatozoa, whereas the ental section is filled with a hyaline secretion. The spermathecal length exceeds the body diameter and possibly the length of penial setae. It can be inferred that during copulation the sucker–shaped genital papillae in XIV help to fasten the two partners together, while at the same time the penial grooved setae are introduced into the spermathecae for sperm transfer.

Remarks. In his elegant paper, Omodeo (1996) considered that *Kathrynella guyanae* showed traits, discussed here in a previous section, which were reminiscent of various 'microdrile' taxa. Omodeo saw two main differences (autapomorphies) of *Kathrynella* from the Alluroididae previously described i.e. the location of male pores in XIV and the metandric condition of the male apparatus which contrasted with the proandric condition of the Alluroidinae and the holoandric, supposedly plesiomorphic (cf. Jamieson 1980), condition of the Syngenodrilinae. He noted a resemblance of the 'atria' of *Kathrynella* to the typical 'euprostates' of the Eudrilidae, an African family of unknown kinship.

Distribution. Known only from the type locality in Guyana.

Genus *Lacandodrilus* Fragoso & Rojas, 2023

Type species: *Lacandodrilus* Fragoso & Rojas 2023

Setae eight per segment, closely paired, *ab* ventral, *cd* dorsolateral, all setae simple, straight, with a node. Clitellum annular. Septal glands in perigonadial segments. Gizzard, oesophageal glands and typhlosole absent. Dorsal vessel simple. Long and contorted vascular commissures embedded within septal glands and located before XII. Holonephric, ovoidal nephridia covered by a granular peritoneal layer. Holandric, with testes and sperm funnels in X and XI and paired male pores in XIII. Male gonoducts intraparietal. Seminal vesicles long, extending several segments backwards within ovisacs. Genital paired lobular glands (prostates?) in XIII and XIV. Metagynous, with large ovaries in XIII and paired female pores in XIV, presetal to AB. Paired spermathecae before XI, without diverticula and with ventral pores. Segment XII lacking gonads.

Remarks: With the Alluroididae *Lacandodrilus* shares the pair of male pores and single pair of ovaries in XIII, presence of septal glands and (assumed) the single–layered clitellum. However, it differs in the absence of tubular or globular atria and the intraparietal nature of the male gonoducts; it also differs in the number of testes (holandric, two pairs in X and XI vs. proandric one pair in X or metandric–one pair in XI). Intraparietal male gonoducts also occur in Sparganophilidae (Jamieson 1971).

Distribution. Chiapas, Lacandon tropical rainforest southeastern Mexico.

Lacandodrilus paludosus Fragoso & Rojas 2023

Lacandodrilus paludosus Fragoso & Rojas 2023, 5255 (1), 136–156.

Maximal length 58 mm. width, midbody 0.64 mm; number of segments 248. Secondary annulation one pre– and one post–setal throughout the body. Pigmentless. Prostomium prolobious. Setae eight per segment, present from II; closely paired throughout. Setae of preclitellar segments conspicuous and with replacements. Setae *a* and *b* of preclitellar segments 130–150 µm long, almost straight, with a slight nodulus close to the basal end; without ornamentation. Setae *ab* of XI and XII larger, replacement setae 64 and 93 µm long; seta *c* (112 µm) and *d* smaller than seta *a* and *b*. Behind clitellum all setae similar (slightly curved and without ornamentation) measuring 105–117 µm. Setae *aa:ab:bc:cd:dd* at X: 3.7:1:4.7:0.9:9.2 and 0.54 *dd*; *dd*=½C (*cd* dorsal); at XXX: 5.7:1:5.3:1:14.2 and 0.7 *dd*=½C (*cd* slightly dorsal); ten segments before anus: 2.9:1:2.4:1:14.4 and 1.2 *dd*=½C (*cd* ventral). Clitellum annular, from ½XII–½XVI, very thin. Dorsal pores absent. Spermathecal pores not visible. Female pores in XIV, presetal in AB. Nephridial pores not visible. Lateral lines (latero–muscular grooves) in BC close to C, from II or III to XIV, XVI or XX and more posterior segments; in one individual in CD.

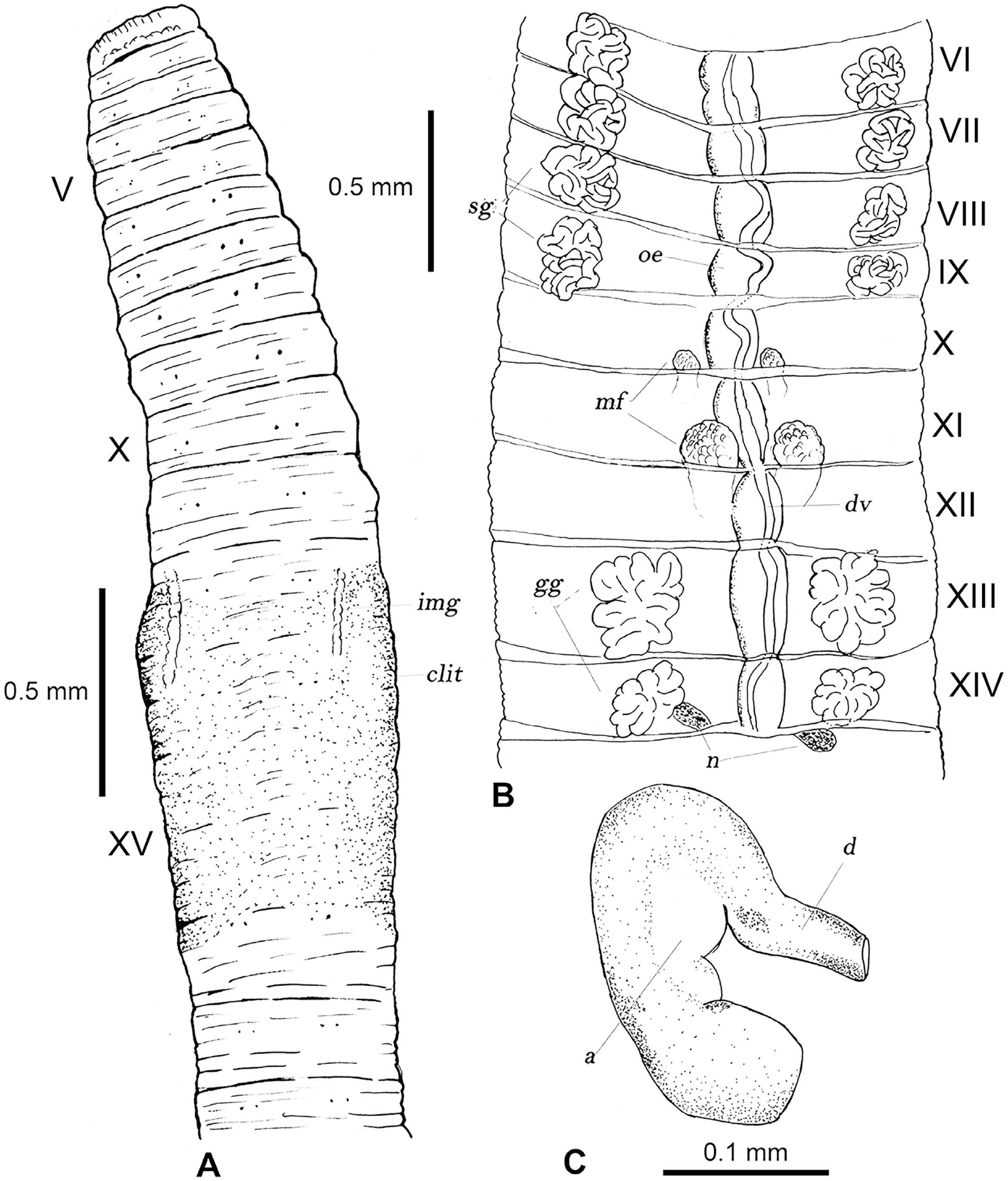


FIGURE 14. ***Lacandodrilus paludosus*** Fragoso & Rojas 2023. **A**. External view of the anterior ventral region of a clitellate adult. **B**. Internal view of the anterior region of an adult. **C**. Spermatheca. Abbreviations: a, ampulla: clit, clitellum; d, duct; dv, dorsal vessel; gg, genital glands (prostates?); img, internal male gonoducts; mf, male funnels; n, nephridia; oe, oesophagus; sg, septal glands. Modified from Fragoso & Rojas (2023).

Septa all thin and membranous. Paired septal glands in V, VI, VII, VIII and IX (in X incipient), attached to corresponding posterior septum, mixed with lateral vascular commissures. Gizzard, caeca and typhlosole absent. Oesophagus moniliform, with no distinct transition to intestine. Dorsal vessel single; sometimes increasing from XIV posteriad. Vascular commissures long and contorted in segments V?, VI–XI; embedded in septal glands. Ventral vessel present. Ventral holonephridia from XI backwards; covered by a granular peritoneal layer giving them an ovoid, flat appearance; this ovoid portion floating in the coelom, and not attached to septa. Nephridia gradually increasing in size and from XV attaining maximal size; exonephric (opening in *ab*) and probably open (stomate). Holandric; iridescent male funnels in X and XI; those of XI the larger; testes not seen. Both funnels enclosed in seminal vesicles. Male gonoduct coming from male funnels of X entering the body wall in XI; a second gonoduct coming from funnels of XI entering the body wall in XII. Both male ducts intraparietal over XI, XII and 3/4 of XIII (deduced from the externally observed, undulating cream band). Accordingly, male pore deduced to be in XIII, postsetal and in BC. One pair of sausage–shaped vesicles in XI; projecting in posterior direction from XII until segments XVIII or XX and running dorsolateral of the digestive tract, completely covering it. In X another pair of vesicles that also contain male funnels that run in anterior direction before turning over 180° and which, apparently, are limited to XII. Two pairs of lobulate, rosette–shaped glands internally on the ventral body wall XIII and XIV, the anterior the larger; composed of several short lobules, deduced to be prostatic glands. No tubular, atrium–like glands present. Large ovaries in XIII projecting from the ventral portion of 12/13 at AB and extending over the entire segment. Female funnels on the ventral wall of XIII very close to 13/14, in AB, and with a duct opening in XIV before setae *ab*. Septum 13/14 apparently modified as dorsolateral paired ovisacs that contain the corresponding seminal vesicles of XII and extending backwards until XVIII or XX. One pair of adiverticulate spermathecae in X opening ventrally in 9/10, at AB, the duct turned 180° to connect with a sausage–shaped ampulla. Total length of spermathecae 580 µm, 370 µm the ampulla, and 210 µm the duct.

Distribution. Mexico, Chiapas, Lacandon tropical rain forest in semi–inundated gley soils at 30–40 cm depth.

Remarks. This species was considered as gen.nov.sp.nov.4, but not named, by Fragoso & Lavelle (1987). Fragoso and Rojas (2033) suggest that future morphological and molecular evidence might render *Lacandodrilus* the type of a new family within the order Alluroidida. The absence of normal atria and presence of two pairs of prostates not associated with the male pores lend some support to this proposition.

Genus *Righiella* Omodeo & Coates, 2001

Type species: *Righiella jamieson*i Omodeo & Coates 2001

Alluroidinae with large, coiled prostates having a thin muscular sheath surrounded by a thick glandular sleeve. The vas deferens enters the prostate, not ectally but at the ental tip. Metandric, male pores lateral in XIII, in the place of the absent ventral setae. A large unpaired spermatheca formed by duct and ampulla situated in pregonadial segments, opening in the mid–dorsal line. Lateromuscular groove conspicuous.

Remarks. *Righiella* differs from the African genera and *Brinkhurstia* in being metandric, from *Kathrynella* by the position of the male and spermathecal pores, and from both American genera in the absence of penial setae (Table 1).

Righiella jamiesoni Omodeo & Coates, 2001 (see Fig 15)

Righiella jamiesoni Omodeo & Coates, 2001, 45–46, Figs 5B–7.

Length 35 mm, width 0.8 mm. Body slender, cylindrical, tapering posteriorly. Lateral lines evident in IV–XIV. Segments 105, multiannulated. Anus terminal. Clitellum annular XII–2/3XV. Male pores in XIII in the place of absent setae *ab*. Female pores in furrow 13/14 in setal line *a*. Spermathecal pore mid–dorsal in furrow 7/8. Setae sigmoid, slender, unsculptured, the longest in X, ca 180 µm, their length decreasing anteriad and posteriad, measuring 134 μm in V and 156 μm in XVI. At XX, *aa*:*ab*:*bc*:*cd*:*dd*=approximately 3.0:1.0:4.5:1.0:3.8. No penial setae. Cuticle 1.8 μm thick.

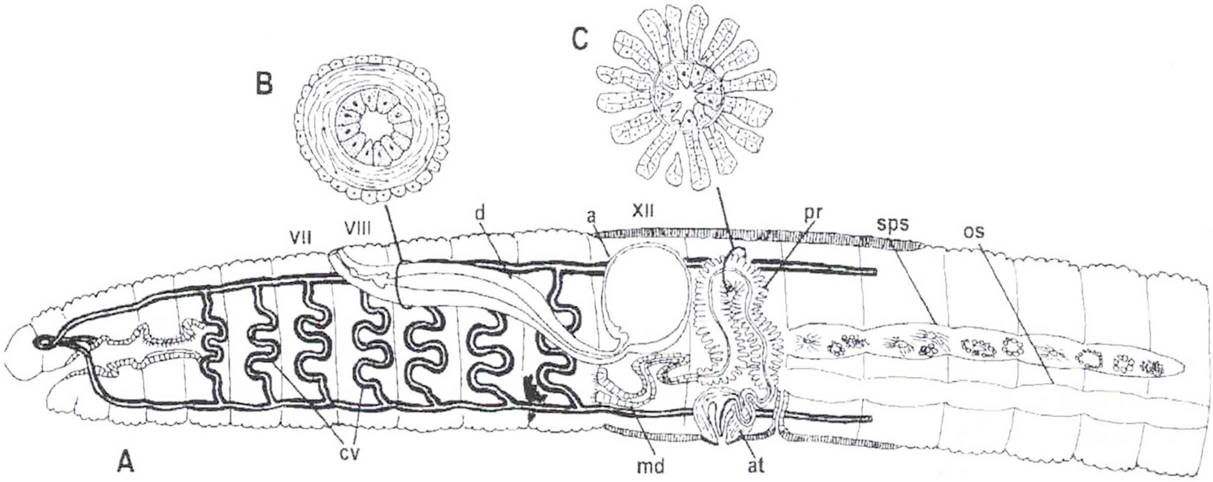


FIGURE 15. ***Righiella jamiesoni*** Omodeo and Coates 2001. **A**. Scheme showing arrangement of genital organs and vascular commissures. **B**. Cross section through spermathecal duct; **C**. Cross section through prostate. Abbreviations: a, spermathecal ampulla, at, male atrium, cv, commissural vessels, d, spermathecal duct, md, male duct, os, egg sac, pr, prostate, sps, sperm sac. From Omodeo and Coates (2001), reproduced with permission.

Septa 4/5–11/12 fairly thick. Septal glands in V–VIII moderately developed. Nephridia without bladders, beginning in XVII. Intestine moniliform beginning in XIV; maximum diameter in XVII. Perienteric sinus beginning in XIV; commissural vessels sinuous, moderately large (diameter 18 µm) in V–XI. Muscular fibres of the body wall ribbon–shaped, *ca* 3 *µ*m thick and 25 µm high. Sperm funnels in the posterior part of XI; testes regressed; sperm sacs in XIV–XVIII. Male ducts convoluted in XIII, inserting into the prostates at their ental tips. Prostates confined to XIII; formed by an inner epithelial layer surrounded by a thin layer of muscle fibres and covered by long digitiform glands formed by cells with small nuclei; this covering disappears in the convoluted ectal portion which terminates with a penis enclosed in the terminal globular chamber. Ovaries and female funnels regressed in the posterior part of XIII, egg sac regressed, in XIV–XXIII? Two eggs in XXII and XXIII, measuring 300 by 400 µm. The spermatheca with a large globular ampulla in XII and a long duct opening in 7/8; the ectal portion of the duct filled with sperm, the ental portion narrow. Ampulla contained mucous matter containing mineral particles, fragments of sponge spicules and young gregarine trophozoites.

Distribution. Collected in a pool, between buried roots, twigs, mud and silt, next to Kurupukari creek flowing into Essequibo River, Guyana.

Remarks. *Righiella jamiesoni* lacks penial setae, an absence otherwise peculiar to the African Alluroidinae, but it is metandric whereas all African species are proandric; it also has more complex spermathecae. *Righiella* also resembles the South American *Kathrynella*, but that metandric genus has the male pores in XIV, has penial setae and has two simple spermathecae and thick muscular euprostates (Omodeo and Coates, 2001).

Intestinal contents were organic matter and a few sand granules together with fragments of spiculae of fresh–water sponges. The gut lumen of XVI through XL harboured many astomatous ciliates attributable to *Anoplophrya*, a common commensal of oligochaetes.

Genus *Standeria* Jamieson 1968

Type species: *Standeria transvaalensis* Jamieson 1968

Alluroidinae in which the atria have narrow ducts and bulbous ental ends, the prostatic cells are solely internal to the muscular sheath of the atrium, and the opening of each atrium into the terminal chamber is separate from that of the corresponding vas deferens. Male pores ventral at the sites of the absent ventral setal couples of XIII. Genital setae present. Spermathecal pores paired, lateral in IX. First septum 4/5; 10/11 attenuated. First nephridia in XI. Intestine commencing in XV. No distinct seminal vesicles.

Distribution. Mpumalanga Province, in the former Transvaal, (Lake Chrissie).

Remarks. *Standeria* shows some notable resemblances to *Brinkhurstia* which distinguish the two genera from *Alluroides*. In both, rounded terminal male chambers each receive an atrial duct and a second duct which in *Brinkhurstia* is known to be the vas deferens and in *Standeria* is apparently so. Furthermore, in both genera the atria are significantly thinner relative to the body width than those of *Alluroides*.

Standeria transvaalensis **Jamieson 1968 (see Figs 16,17)**

Standeria transvaalensis Jamieson 1968: 82–84, fig. 1, 2, 4–8; Brinkhurst &Jamieson 1971: 717–718, fig. 14.1A; 14.2A–F.

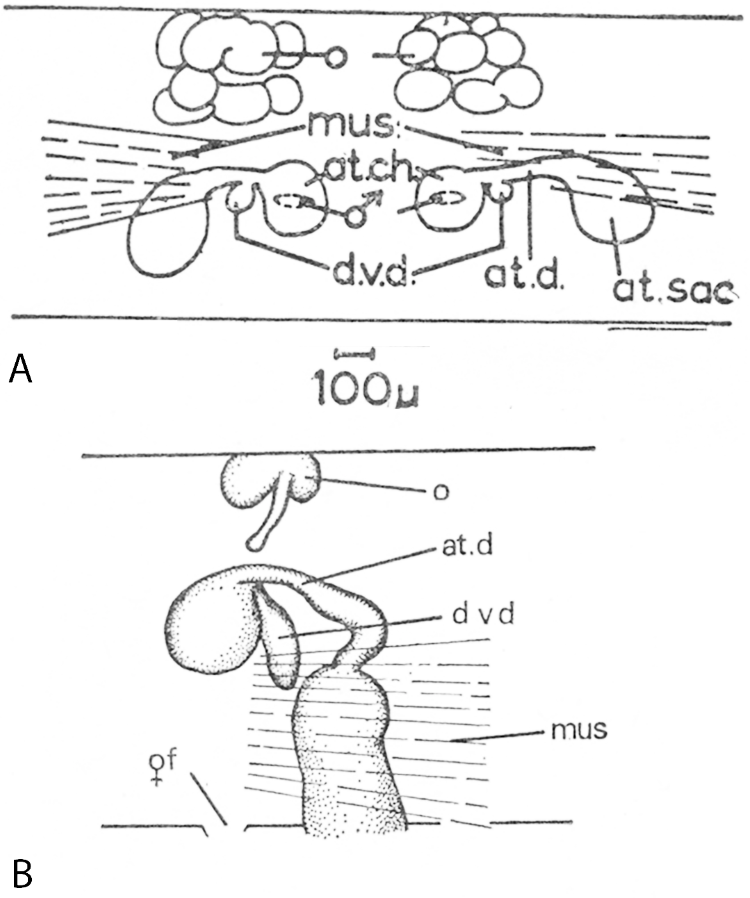


FIGURE 16. ***Standeria transvaalensis*** Jamieson 1968. **A**. Paratype 2. The two atria *in situ* in segment XIII, **B**. Paratype 1. Atrial duct and vas deferens opening into the ectal atrial chamber. Abbreviations: atd, atrial duct; atsac, saccular portion of atrium; atch, terminal chamber of atrium; dvd, dilatation of the vas deferens; mus, muscle fibres; of, oviducal funnel. Adapted from Jamieson (1968).

Length 25 mm, width 1.1–l.4 mm, segments 82. Prostomium epilobous 1/2 although lacking a separate dorsal tongue. Form cylindrical; somewhat flattened ventrally at the clitellum. Lateral lines conspicuous, in mid *bc*; the posterior third of IV and a number of more posterior segments set off as a distinct annulus. Intersetal ratios in XII; *dd*=0.2 *bc*=1.7 *aa*; ventral pairs absent in XIII; replaced in XIV and XV on each side by 6 enlarged genital setae located within paired papillae. Lengths of 4 of 6 genital setae on the left side in XIV=0.33–0.35 mm. Length of lateral setae from the same segment 0.19 mm. Neither type of seta with distinct node but both sigmoid with tapering extremities. Greatest widths: 15 µm for a genital seta and 10 µm for a lateral seta; ornamentation absent. Clitellum saddle–shaped; apparently extending from 1/2 XII–*ca* XV, 1/2 XVI, 1/2 XVII (=3 1/2, 4, 5 segments); ventral margins at *ca* 1/4 *bc*. Male pores crescentic slits on low porophores at the sites of the absent ventral setae of XIII.

Each porophore continuous posteriorly with a slight tumescence which extends to approximately midway between the former and the setal zone of XIV; female pores indentations at the posterior limits of each tumescence, anterior in XIV. Ventral setal couples of XVI and XVII each on slight but distinct protuberances. These protuberances confluent medially to form feebly developed transverse pads of glandular appearance. Spermathecal pores 1 pair, conspicuous in intersegmental furrow 8/9, lateral of setal lines *b* with very large tumescent anterior and posterior lips each of which occupies a third of the adjacent segment. Nephropores in setal lines *a* very close to the setal follicles.

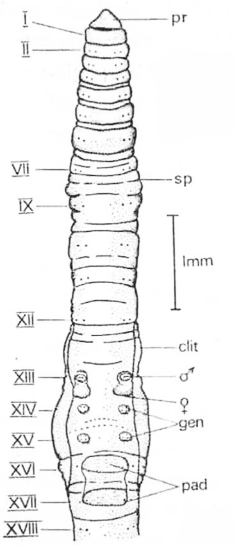


FIGURE 17. ***Standeria transvaalensis*** Jamieson 1968. Ventral view of forebody. Abbreviations: clit, clitellum; o, female pore; gen, papillae bearing genital setae; ♂, male pore; pad, ventral pads; pr, prostomium; sp, left spermathecal pore; From Jamieson (1968); Brinkhurst & Jamieson (1971).

Septa: 4/5 the first visible, it and 12/13 slightly thickened. 5/6, 7/8, 9/10 and 11/12 relatively strongly thickened; 6/7 and 8/9 moderately thickened; 10/11 and 13/14 unthickened and very delicate, as are 14/15 and succeeding septa. Septal glands attached dorsally to anterior faces of septa as far as 9/10 and also 11/12, 12/13? Oesophagus beginning in IV, widening to form the intestine, which is at least twice as wide, in mid–XV; longer and more slender in XIII than in other segments. Dorsal and ventral blood vessels single. No subneural vessel. A pair of commissural loops winding far laterally present in XII anteriad. Nephridia open holonephridia, at least as far anteriorly as XI; lacking bladders. Proandric; large lobed testes ventral and anterior in X embedded in free morulae and abundant spermatozoa which fill the remainder of the segment. Sperm funnels large, convoluted areas of septum 10/11, seminal vesicles absent. No reproductive organs or cells in XI. On each side, overlying the external male pore on XIII is a rounded muscular atrial chamber into which discharges the tubular entally dilated atrium of the corresponding side. Its ectal portion narrowed to form a slender duct which curves ventrally and medially to join the anterolateral aspect of the atrial chamber. This ectal region obscured by a web of muscle fibres, passing from the ventral to the lateral body wall, which bind it to the latter. A second, spindle–shaped sac about the width of the atrial duct, projects from the junction of the atrial chamber with the duct and apparently represents the thickened end of the vas deferens. The walls of the atria and of the appended sacs lined by cuboidal epithelium outside which is a layer of circular muscle fibres several times as thick. The wide lumen of the atrial chamber lined by columnar epithelium outside which is a thick sheath of radial and circular muscle fibres. Glandular investment of these male terminalia absent. Ovaries in XIII. Septum 13/14 evaginated posteriorly on each side as a broad funnel continuous into XIV as a slender oviduct. Spermathecae a pair of elongated, adiverticulate pouches in IX; their scarcely narrowed ducts being almost wholly embedded in the body wall.

Distribution. South Africa: Mpumalanga Province, in the former Transvaal, (Lake Chrissie).

SUBFAMILY SYNGENODRILINAE

Defintion as for the genus *Syngenodrilus*

Genus *Syngenodrilus* Smith & Green 1919

Type species: *Syngenodrilus lamuensis* Smith & Green 1919

Slightly modified from Jamieson (1968).

Lateral lines unknown. Genital and penial setae absent; the dorsal median intersetal distance=0.6 of the circumference of the body (dd=0.6 U). Clitellum commencing in XI; intraclitellar tubercula pubertatis present. Male pores one pair lateral and anterior in XIII. Prostate pores separate from the male pores on XI, XII and XIII. Female pores in the setal arc of XIV. Spermathecal pores two pairs, posterior in VII and VIII. Two gizzards present, one in each of VIII and IX. Nephridia with pyriform terminal bladders. Holandric, testes in X and XI enclosed in testis–sacs. Sperm funnels with their mouths directed ventrally. Seminal vesicles of the microdrile type, *i.e.* extending posteriad within the ovisacs through several segments. Sperm ducts simple, prostate glands entirely separate.

Distribution. Kenya; Martinique?.

Remarks: An aquatic worm found in Martinique by Chagné and Giani (1998) was identified as Syngenodrilinae *gen. sp.* However, the identification was made based on thickness of the clitellum (a single layer of cells) and its extent (XIII–XIX), dorsal location of the setae, presence of septal glands in V, VI, VII and VIII, holandry (testes and male funnels), a pair of ovaries in XIII and presence of lateral spermathecae in IX. Key characters such as position of male pores, number of gizzards, prostatic glands and penial and genital setae were not mentioned. Accordingly, this worm cannot be assigned with certainty to this subfamily. With the available information it might be considered more related to the alluroidid Mexican genus *Lacandodrilus* (but see Remarks to the Martinique species below).

Syngenodrilus lamuensis Smith & Green 1919

Syngenodrilus lamuensis Smith & Green 1919: 145, Fig. 1–8.
Syngenodrilus lamuensis Smith & Green. Gates 1945: 393; Pickford 1945: 397; Jamieson 1968: 85; 1971: 719.

Length 52 mm, width 4 mm, segments137. Clitellum annular 2/3 XI–XVI. A copulatory band extends from 11/12 to setal arc XIV and filling *bc*. Setae very small; *aa*:*ab*:*bc*:*cd*:*dd*=17: 1:17 0.9:92; *dd*=0.6 U, *bc*=1.0 *aa*; present in the clitellar region. Nephropores commencing at the anterior margin of IV; some midway between *cd* and the mid–dorsal line others in *cd*. Male pores at the anterior margin of XIII at about 3/5 *bc*. Prostate pores intrasegmental in XI, XII and XIII, slightly dorsal of setal line *b*, presumably paired. Female pores slightly anteriad and dorsal to setae *b* of XIV. Spermathecal pores two pairs immediately in front of intersegmental furrows 7/8 and 8/9, slightly ventral of setal lines *c*.

Septa 5/6–7/8 very strong. 8/9–12/13 very thin and imperfect. Strong gizzards in VIII and IX. Intestine commencing in XII or XIII, but oesophagus widened between it and the gizzard. No calciferous glands, intestine lacking typhlosole. Hearts in VI–XI (XII?), possibly absent from X. Nephridia paired; absent from I–III, XI and XII; with pyriform terminal dilatation. Testes and funnels paired in X and XI and enclosed in (unpaired?) testis–sacs containing hearts and nephridia. Seminal vesicles of the microdrile type, a pair extending backwards in the ovisacs to XX. Vasa deferentia lacking terminal atria. Three pairs of short tubular prostates, in XI, XII and XIII, opening separately from the male pores by very short ducts which are confined to the body wall. Penial and genital setae absent. Ovaries extensive in XIII; funnels broad and short on the anterior face of septum 13/14. Ovisacs extending posterior of XXII. Eggs yolky. Spermathecae two pairs, in VIII and IX, each with an irregular, simple tubular ampulla, *ca* 0.35 mm wide and somewhat longer than the duct which is 0.07–0.1 mm wide: lacking diverticula.

Remarks. Gates (1945) and Pickford (1945) rightly argued for exclusion of *Syngenodrilus* from the Moniligastridae, They recognized its affinity with the Alluroididae, Gates tentatively suggested inclusion in this family but Pickford advocated retaining a separate family Syngenodrilidae. Both authors noted that it differs from the Alluroidinae in possession of a well–developed, double oesophageal gizzard, in having simple *Sparganophilus*-

like prostate glands which are not related to the male opening and in the absence of a moniligastrid–like atrium at the ectal end of the vas deferens.

Distribution. Kenya: Lamu (Habitat unknown).

Syngenodrilinae gen sp. Chagné & Giani (1998)

Syngenodrilinae gen sp. Chagné & Giani 1998, 134, 21–32.

Four pairs of single pointed sigmoid setae, the dorsal setae in a very lateral position, close to the ventral setae. Setae present on the genital segments and no differentiation of genital setae. Clitellum with a single layer of cells, in segments XIII to XIX (XX?). Female pore just anterior to the setae of XIV.

Pharynx long, well–developed in IV and V. Septal glands 4 pairs, in V, VI, VII and VIII. Septa from 4/5 strongly developed and bulging posteriad (excepting 10/11), Testes in X and XI, with corresponding sperm funnels. Male genital tract not determinable. Ovaries one pair, in XIII; female funnel well–developed on septum 13/14. One pair of lateral spermatheca in IX. A second individual with the genitalia shifted 2 segments anteriorly (testes in VIII and IX, female pores in XII).

Remarks. The lateral position of the dorsal setae and the presence of two pairs of testes (in X and XI) led Chagné & Giani to place the specimens in the subfamily Syngenodrilinae which included the single monospecific genus (*Syngenodrilus*) but they regarded it as a new, unnamed genus. They stated that of 82 specimens only two were mature but that their state of conservation did not permit identification. As they did not report on prostate structures the identification as Syngenodrilinae must remain uncertain. The holandric condition is also seen in *Lacandodrilus* but is a symplesiomorpy widespread in oligochaetes and may not indicate close relationship (for further discussion, see previous remarks).

Ecological aspects of Alluroidida

When the first species of this Order was found and described, Beddard (1894) considered *Alluroides pordagei* to be *"... a water worm with affinities to the terrestrial worms"* and also suggested that the genus *Alluroides "... rendered the distinction between the old groups Limicolae and Terricolae untenable."* The discovery of additional species of this genus and several new genera, has supported Beddard's point of view, in the sense that alluroidids are aquatic, but close to the terrestrial habitat. Of the 14 species hitherto assigned to Alluroidida (including one unidentified syngenodrilid from Martinique), ten species were exclusively found in rivers and lakes, mainly in bottom sandy sediments, two were found in both freshwater and swampy environments (*B. americanus* and *A. pordagei*), one was recorded exclusively in swamps (*L. paludosus*) and one was not linked to any habitat. Until now, no marine alluroidids have been found. The apparent absence from most of the African great lakes may be due to ignorance (Martin 1996).

In general, alluroidids are found in pristine sites. Except for the African *Alluroides lauzannei* (Lauzanne 1968), which it is mentioned comprised the main component of the benthic oligochaete biomass in Lake Chad, and the Martinique Syngenodriline with 82 individuals found (Chagné & Giani 1998), from the other records it seems that they are scarce. Quantitative data are mentioned only in one case: *L. paludosus*, 1.6 individuals per square meter, in swampy soils (Fragoso & Rojas 2023). Are these low abundances reflecting a group which is actually scarce in nature or, as Ljungström (1971) mentioned, they inhabit rare sampling habitats, they have been affected by human activities or sampling techniques have not been adequate? Quite probably the answer is a combination of all.

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