NEW RECORDS OF OCNERODRILIDAE AND LUMBRICIDAE (OLIGOCHAETA) FROM SOUTH AFRICAN RIVERS

B. G. M. JAMIESON

Zoology Department, University of Queensland, Australia

SYNOPSIS

Two species of Ocnerodrilidae and three species of Lumbricidae collected during a survey of South African Rivers by the National Institute for Water Research, Pretoria, are described and illustrated.

Recognition by Gavrilov (1952) of infra-specific taxa of *Eukerria saltensis* (Beddard, 1895), namely *typica*, *gatesi* and *bellavistensis*, is not upheld. *Pygmaeodrilus arausionensis* Michaelsen, 1910*a* is shown to have male copulatory bursae which suggest affinities with the three Zambesi species, *P. paulae*, *quilimanensis* and *rhodesiensis*.

Disposition of the gizzard in segments xvii and xviii in material of *Eiseniella tetraedra tetraedra* (Savigny, 1826) removes the sole distinction noted by Stephenson (1930) between *Eiseniella* and *Eisenia* but the evidence of Omodeo (1956) for placing the two genera in separate subfamilies must at present be accepted. *Dendrobaena rubida* (Savigny, 1826), is described. Inclusion in this species of *Bimastos tenuis* (Eisen) is accepted but the validity of separation of *Dendrobaena* and *Bimastos* (s. strict.) on the grounds presented by Omodeo is questioned. Material here described as *Allolobophora caliginosa trapezoides* intergrades with the typical subspecies and attention is drawn to the need for a critical investigation of the discreteness of the two forms. *A. iowana* Evans, 1948 is synonymised with *A. c. trapezioides*.

INTRODUCTION

In 1949 the South African Council for Scientific and Industrial Research initiated a programme of detailed chemical and biological studies on South African rivers and other inland waters. The chief object of these studies was to assess chemically the extent of domestic, industrial and agricultural pollution of South African waters and to obtain a knowledge of the composition and ecology of the fauna and flora with a view to determining the biotic effects and biological indicators of pollution.

The present paper deals with the megadrile oligochaetes of the C.S.I.R. survey which have been collected and made available by the National Institute for Water Research, Pretoria. Megadrile is a loose epithet for those families of oligochaetes which are partly or predominantly terrestrial and contain species of relatively large body-size. Available collections and hydrological data are sufficient neither for determination of the environmental requirements and tolerances of the megadriles concerned nor for establishing any value they may have as biological indicators of pollution but the survey has substantially augmented our knowledge of the distribution and morphology of the five species of megadriles collected. Specimens of the microdrile genus *Alluroides* in the collections sent to the author will be described in a later paper. The remaining microdriles of the survey have been described by Brinkhurst (1964, 1965). A bibliography of publications based on the survey, from which ecological data may be obtained, is given in appendix 1 of the latter paper. An explanation of the terms used in oligochaete taxonomy is provided by Stephenson (1930).

SPECIES REPRESENTED AND THEIR DISTRIBUTION

The following species are recognisable in the present collection. The remaining material is unidentifiable owing to immaturity or desiccation.

Family Ocnerodrilidae*

Eukerria saltensis (Beddard, 1895)	Circum-mundane	p. 61
Pygmaeodrilus arausionensis Michaelsen 1910*a*	S. African endemic	p. 66
Family Lumbricidae.		
Eiseniella tetraedra (Savigny, 1826) *tetraedra*	Cosmopolitan	p. 70
Dendrobaena rubida (Savigny, 1826).	Cosmopolitan	p. 74
Allolobophora caliginosa (Savigny, 1826) *trapezoides* (Dugès, 1828)	Cosmopolitan	p. 77

Table 1 indicates the occurrence of these species in those South African rivers from which identifiable material has been obtained in the present survey. Details of distribution are given in the systematics section (p. 61).

TABLE 1

NEW RECORDS OF MEGADRILES IN SOUTH AFRICAN RIVERS

+ = present — = not collected

	Eukerria saltensis	Pygmaeodrilus arausionensis	Eiseniella tetraedra tetraedra	Dendrobaena rubida	Allolobophora caliginosa trapezoides
CAPE PROVINCE					
Krom River	+	—	+	—	+
Gt. Berg River	+	—	+	+	—
NATAL					
Bushmans River	+	—	—	—	—
Umgababa River	+	—	—	—	—
Umbilo River	+	—	—	—	—
TRANSVAAL					
Jukskei—					
Crocodile River	—	—	+	—	—
Vaal River	+	+	—	—	—
Sabie River	—	+	+	—	—
ZULULAND					
Tugela River	+	—	—	—	—

*The Ocnerodrilinae were removed from the Megascolecidae and elevated to family rank by Gates (1959) but the justification for this step remains questionable.

The most widespread megadrile species in the nine South African rivers listed thus appear to be the South American *Eukerria saltensis*, recorded from seven of the rivers, and the palaearctic *Eiseniella tetraedra tetraedra*, from four of the rivers. Both these circum-mundane species were previously known to be amphibious and had been reported from South Africa.

The restricted distribution of *Dendrobaena rubida* and *Allolobophora caliginosa trapezoides*, which were found in one river only, and the small numbers of specimens of these in each sample, reflect the typically terrestrial nature of these species which have only occasionally been recorded from limnic habitats. Both species are practically cosmopolitan and appear from previous records to be well represented in South African soils.

Pygmaeodrilus arausionensis, a little known South African endemic, now known from limnic habitats as far apart as South West Africa and the Eastern Transvaal, and occurring in the Kalkspruit, a somewhat polluted tributary of the Vaal River, would seem to be successfully withstanding invasion of non-indigenous species and modification by human activities of the composition of river waters. The absence of other previously reported limnic endemic species from the present samples possibly indicates that they are being less successful.

It is probable that both *Eukerria saltensis* and *Eiseniella tetraeda tetraedra* have considerable resistance to pollution. *Eu. saltensis* was collected shortly before and after extreme mineralisation of the Great Berg river (station 12) when total dissolved solids, normally 18 to 91 ppm, rose to 220 ppm (Harrison and Elsworth, 1956). *Eiseniella tetraedra* occurs in the Jukskei River which receives continuous effluence from sewage works at source and concentrated inorganic nitrogen from a factory and is stated by Allanson (1961), p. 32, to be chemically more severely polluted than any other system in South Africa, with the possible exception of the Krom River at Stellenbosch, from which this species is also recorded. The proportion of the two species in the total biomass and in the specific composition of the fauna as a possible index of pollution, especially in the case of the abundant *Eukerria saltensis*, appears worthy of investigation.

SYSTEMATICS

Family Ocnerodrilidae

Eukerria saltensis (Beddard, 1895)

(Fig. 1, A–C)

Kerria saltensis Beddard, 1895, p. 225; Beddard, 1896, p. 46; Michaelsen, 1898, p. 479; Michaelsen, 1900, p. 371; Michaelsen, 1907, p. 23; Pickford, 1928, p. 3; Gates, 1942, p. 73; Gavrilov, 1952, p. 692.

Acanthodrilus sydneyensis Sweet, 1903, p. 124.

Kerria gunningi Michaelsen, 1913*b*, p. 1; Michaelsen, 1913*c*, p. 419; Michaelsen, 1913*e*, p. 276. (Named in Michaelsen, 1913*a*, p. 139, which formed part I of 1913*b*.)

Kerria nichollsi Jackson, 1931, p. 121.

Kerria nichollsi Jackson, 1931, was added to the synonymy by Michaelsen, 1935; *sydneyensis* Sweet and *gunningi* were first included by Pickford, 1928, in a thorough revision of its types.

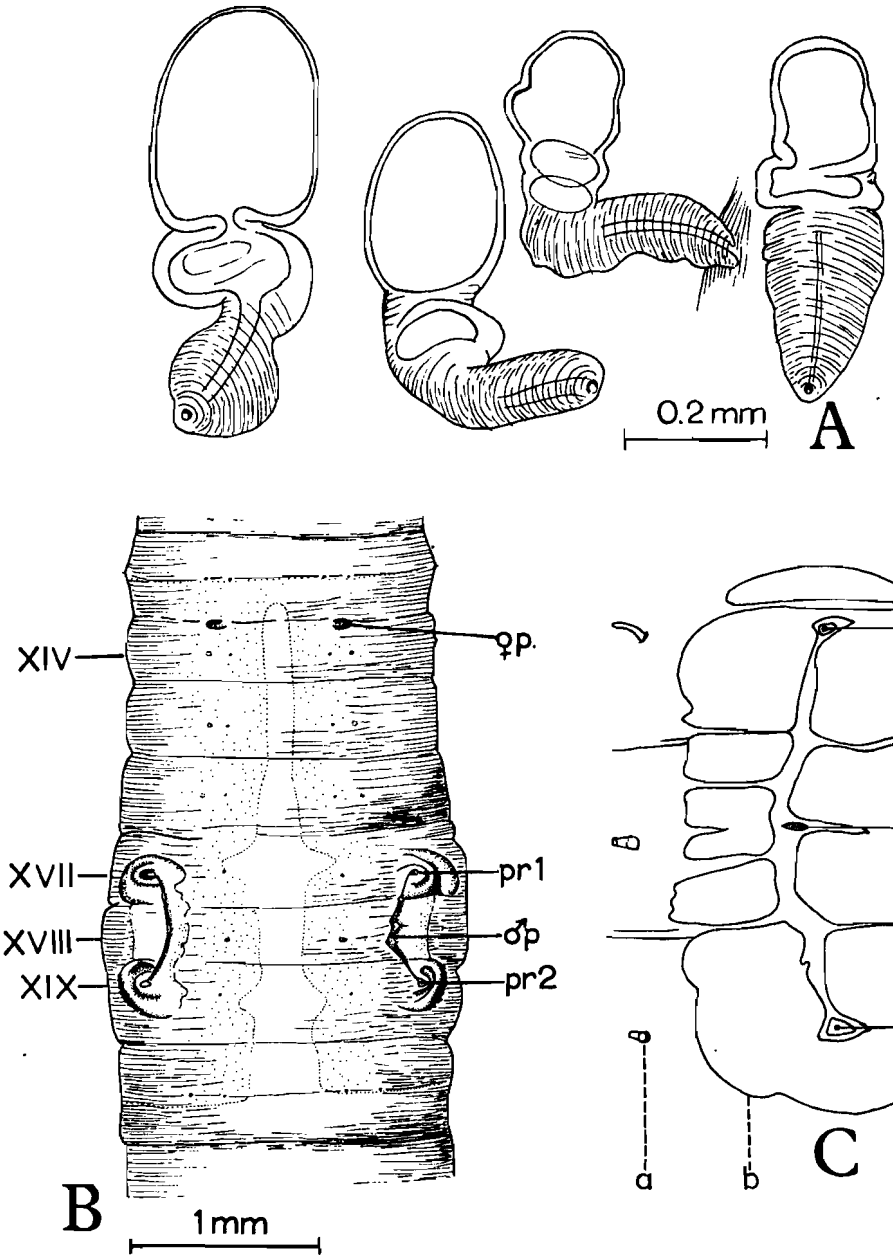

Figure 1. *Eukerria saltensis*. A, camera lucida drawings of spermathecae from four different individuals from the Great Berg, Krom and Vaal Rivers. B, male and female genital fields of specimen 1, (11–X11–52), from the Krom River. C, camera lucida drawing of left seminal groove of same, showing male and prostate pores. ♀ p, female pore; ♂ p, male pore; pr 1 and pr 2, prostate pore of segment xvii and xix respectively.

Distribution. Aquatic or terrestrial, recorded sporadically throughout the southern hemisphere though almost certainly originating from S. America where, alone, endemic species of the genus occur. *S. America:* Chile; Juan Fernandez Is.; Argentina. *Burma, New Caledonia, Australia:* New South Wales, S. Western Australia and (author's collection, unpublished) Queensland.

Previous South African Records. *Cape Province:* Stellenbosch. (*v.* Gavrilov, 1952). *Natal:* Durban; Howick (Michaelsen, 1913*c*). *Transvaal*: Pretoria (Michaelsen, 1913*b*).

New Records. *Western Cape Province.* Upper Great Berg River at the Driefontein Bridge, lower forest reserve, stony bottom, 13. ix. 1950, several; French Hoek Stream (tributary of the Berg River), bridge at La Motte, stones in current, 30. x. 1950, 3; Great Berg River at the farm Watergat, Simondium, stones in current, 14. ix. 1951, 1; Great Berg River at Daljosaphat, near Paarl sewage works, stones in current, 14. xi. 1951, 5, and 24. ix. 1952, 1; Great Berg River at Lady Loch Bridge, Wellington, stones in current, 12 specimens taken at approximately 2 month intervals from 14. v. 1952—29. iv. 1953; Great Berg River at Piquetberg, gravel bottom, 31. x. 1951, 1, and stones in current, 28. i. 1952, 1. Krom River, a tributary of the Eerste River near Stellenbosch, habitat not recorded, many specimens collected from 15. ix. 1952—23. iii. 1953.

Transvaal/Orange Free State: Vaal River—Barrage—Vereeniging area, stones in current, 29. v. 1958, 3; Vaal Dam catchment area, Kalkspruit at Grootvlei Coal Mine, Ekman bottom grab, 12. i. 1959, 3; Klein Vaal River near its confluence with the Vaal River, aquatic vegetation, 19. xi. 1958, 3.

TABLE 2
DISTRIBUTION OF SOME TAXONOMIC CHARACTERS
IN 29 CLITELLATE SPECIMENS OF *Eukerria saltensis*
(*Modes)

Prostomium	No.	Clitellum	No.	Spermathecal Pores				No.
Epilobous	27*	xiii—xix	1	Readily seen				21*
Zygolobous	1	½ xiii—½ xx	4	Inconspicuous				4
Tanylobous	1	½ xiii—¾ xx*	18*	Not visible				4
Length (mm)		½ xiii—xx	5	All approx. mid *bc*				3
		Indistinct	1	All ⅔ *bc*				18*
35—44·5	2	Female Pores		Rt.		Left		
45—54·5	7	Setal line *a*	1	Ant.	Post.	Ant.	Post.	
55—64·5	11*	*ab*	6					
		b	19*		Absent	⅔ *bc*	Absent	1
65—74·5	5			⅓ *bc*	⅓ *bc*	⅔ *bc*	⅔ *bc*	1
		Lateral of *b*	1	⅔ *bc*	⅔ *bc*	mid *bc*	mid *bc*	1
75—84·5	4	Left *ab*, right *b*	2	mid *bc*	mid *bc*	⅔ *bc*	mid *bc*	1

Natal: Umgababa River, Natal South Coast, bottom sample, 15. vi. 1964, 2. Umbilo River, Durban, bottom sample, 17. viii. 1964, 3. Little Bushmans River just above its confluence with the Bushmans River, stones in current, 29. x. 1956, 1. Tugela River at Hart's Hill, marginal vegetation, 16. xii. 1953, 1, and 30. xii. 1953, 1 specimen.

EXTERNAL ANATOMY

Dimensions. Length 35 to 83 mm (mean of 29 = 56 mm). Greatest width, at the clitellum, 1·4 to 2 mm (3 specimens); 133 to 135 segments (2 specimens). Colour (in life blood red (Gavrilov, 1952)) in alcohol variable, whitish to pigmented grey, sometimes with greenish iridescence; clitellum pale buff, yellowish brown, red-brown or purple-grey (29 specimens).

Prostomium. Epilobous 1/3 to 1/2, dorsal tongue open, or closed and convergent posteriad; usually indistinctly demarcated and sometimes appearing zygolobous; in one specimen apparently tanylobous (29 specimens, Table 2).

Setae. Eight per segment, closely paired; conspicuous only on the anterior-most segments. On the clitellum setae *a* are visible but setae *b* are almost obscured on xiv to xvi and are absent from xvii to xix. Lateral setae in the forebody ornamented by minute teeth; ventral setae lacking this ornamentation, but apparently eroded. In segment xii, *dd* = 0·38*u*, *bc* = 1·1 *aa* (mean of 4, Table 3).

TABLE 3

Eukerria saltensis. SETAL DISTANCE RATIOS IN SEGMENT XII.

(4 specimens).

aa : *ab* : *bc* : *cd* : *dd*	*dd* : *u*	*bc* : *aa*
17 5 17 4 40	0·37	1·0
18 5 21 5 50	0·38	1·2
14 5 17 4 43	0·39	1·2
16 4 14 4 38	0·39	0·9
Mean	0·38	1·1

Form: Attenuated. Often much-coiled on fixation. Slightly swollen at the clitellum. No secondary annulation. **Clitellum:** Ring-shaped but interrupted ventrally by a very narrow pale, less tumescent strip which is considerably median of the ventral setae except in xvii where it extends lateral of these. Usually embracing 1/2 xiii to 3/4 xx, less commonly extending to 1/2 xx or xx, in one specimen embracing xiii to xix (= 7, 7 1/4, 7 1/2 segments, Table 2).

Male genital field (Fig. 1 B, C): Prostate pores two pairs, on minute papillae lying considerably lateral of setal lines *b* of adjacent segments and encircled by a seminal groove which passes to segment xviii where it is medially convex, and connects the papillae of each side. Each prostatic papilla and its encircling groove situated on the summit of a transversely oval prominence which is not clearly defined medially and is in turn borne on a low ear-like prominence which is only laterally raised (26 specimens). Male pores in the setal arc of xviii (Fig. 1 C), one in each seminal groove (2 specimens).

Female pores (Fig. 1 B). Conspicuous relative to most megadrili (23 specimens) or inconspicuous (6 specimens); situated on minute cones, or bounded anteriorly and posteriorly by very narrow lips, immediately behind the anterior border of xiv in setal lines *b*; much less commonly in *ab* or lateral of *b*, sometimes asymmetrically disposed (Table 2, see Remarks). **Spermathecal pores.** A pair of transverse slits in each of intersegmental furrows 7/8 and 8/9 mostly situated at 2/3 *bc*, occasionally at approximately mid *bc*, or asymmetrically disposed or invisible (29 specimens, Table 2). Usually readily observed on close examination but never conspicuous (see Remarks).

INTERNAL ANATOMY

Unless otherwise stated this account is derived from a single specimen from the Krom River, Stellenbosch, 11.ii.1952). Other specimens are referred to in the discussion.

Septa. 6/7 to 8/9 strongly, 5/6, 9/10–11/12 moderately thickened (5/6 being the strongest of these); the remainder thin. Conspicuous septal glands as far back as vi. **Alimentary Canal:** A broadly fusiform gizzard in vii, about three times the width of the adjacent oesophagus; highly muscular yet easily deformed by pressure. Anteriorly directed ocnerodrilin paired oesophageal diverticula in ix. Intestine commencing in xii (see Remarks).

Blood vascular system. Dorsal vessel single; very large in xii and behind. Dorsoventral hearts well developed in x and xi. A pair of commissural vessels in ix resemble the hearts in connecting the dorsal and ventral vessels but are thinner and receive a large branch on each side from the ventral body wall, being very thin below the junction. **Nephridia:** Large holonephridia. Commencing in vi (?); apparently avesiculate and discharging at mid *bc*. **Anterior male organs:** Proandric: testes and funnels in x only. Large, lobed seminal vesicles in ix and xi (see Remarks). **Posterior male organs:** Prostate glands very slender (0·1 mm. wide), and long, winding backwards through several segments; discharging in xvii and xix nearer the posterior than the anterior septum by slightly more slender ducts, which are clearly demarcated by their muscular sheen. Vasa deferentia posteriorly at least tightly coiled, ending at mid xviii; much thinner than the prostate ducts. Neither prostatic nor male ducts ectally thickened.

Female organs. A pair of large palmate ovaries and small, cup-shaped funnels on the anterior and posterior walls, respectively, of xiii.

Spermathecae (Fig. 1 A). A pair in each of segments viii and ix opening at the anterior border. No diverticulum. Ampulla large and oblong-ovoid with thin walls. In dissection the duct, which is often bent at a right angle to the ampulla, appears longer than the ampulla but in cleared mounts the ental portion of this "duct" is seen to be thin walled relative to its ectal portion and may be regarded as a chamber of the ampulla, though its walls may be convoluted. The duct proper is tubular with a narrow lumen and thick muscular walls and is as long as, or shorter than, the ampulla plus chamber (4 worms).

Remarks. Gavrilov (1952), in a valuable paper demonstrating uniparental reproduction in *Eukerria saltensis*, recognized three "varieties" (subspecies?): forma *typica*, circum-mundane and including all records for S. Africa; var. *gatesi*, from Burma, erected for two clitellate specimens described by Gates (1942); and var. *bellavistensis* established for numerous specimens which he examined from between Garcia Fernandez and Bella Vista, in Tucuman Province, Argentina.

Although gene-flow between allopatric populations of this small and therefore presumably easily transported worm may be high, some morphological divergences between them are to be expected. Many of the differences noted by Gavrilov are not, however, confirmed in the present study. Lengths of 35 to 83 mm. in the present account nullify the apparent difference in lengths of the three taxa; absence of seminal grooves (like other features) cannot be considered constant for Burmese worms as only two specimens were taken and a suggestion of a groove was seen in one of these (Gates, 1942, p. 73). Spermathecal pores are indistinct in some clitellate specimens of S. African populations, a distinguishing character of *bellavisten.sis* Inconspicuous pores in the latter are perhaps correlated with uniparental reproduction, which Gavrilov has demonstrated for the population, and may represent a true morphological as well as cytogenetic departure from the normal form. The possibility of unisexual reproduction in "*typica*" cannot, however, be excluded.

Indistinctness of the female pores in *bellavistensis* cannot be ascribed to parthenogenesis but is not uncommon in the new S. African records. Characterisation of the gizzard is highly subjective and from Gavrilov's figure it does not appear that this organ is better developed in *bellavistensis*, for which its large size is supposedly a distinguishing feature, than in the new material. Distinction of *typica* by intestinal origin in xiii is not confirmed as it is in segment xii in 4 specimens, as in the other two taxa. Nephridial size (small in *gatesi*, large in *bellavistensis*l not previously recorded for *typica*) is of doubtful significance, varying with environmenta, conditions. Seminal vesicles, said to be restricted to ix in *typica*, occur in the new material in ix and xi (3 specimens) as in *gatesi* and *bellavistensis*, or in ix only (1 specimen). In *bellavistensis*, the spermathecal duct is always longer than the ampulla, and in illustrations, appears to be relatively thinner than that of South African specimens.

Former distinctions between the three taxa are, thus, considerably reduced and their elevation to subspecific rank does not appear warranted. As the variety is no longer a recognized taxonomic rank, these subdivisions must be dropped while recognizing that the Bellavista worms, as might be expected in a geographically homogeneous and at least partly parthenogenetic population, show a constant and possible distinctive combination of certain characters (indistinct spermathecal and male pores and longer, more slender spermathecal ducts).

Pygmaeodrilus arausionensis Michaelsen, 1910

(Fig. 2A–D)

Pygmaeodrilus arausionensis Michaelsen, 1910a, p. 114; Michaelsen, 1914, p. 172.

Distribution. Amphibious and aquatic; endemic in S. Africa.

Previous Records. *Orange Free State:* Bothaville (Michaelsen, 1910a).

South West Africa: Grootfontein (Michaelsen, 1914).

New Records. *Transvaal:* Sabie River at Lower Sabie Rest Camp, Kruger National Park, eastern Transvaal, stones in current, 1.vii.1960, 6 clitellate specimens. Vaal Dam catchment: Kalkspruit at Grootvlei Coal Mine, Ekman bottom grab, 12.i.1959, 2 mature specimens (1 clitellate).

The following description of the new material incorporates Michaelsen's data (1910a, 1914) and therefore summarizes all known information on the species.

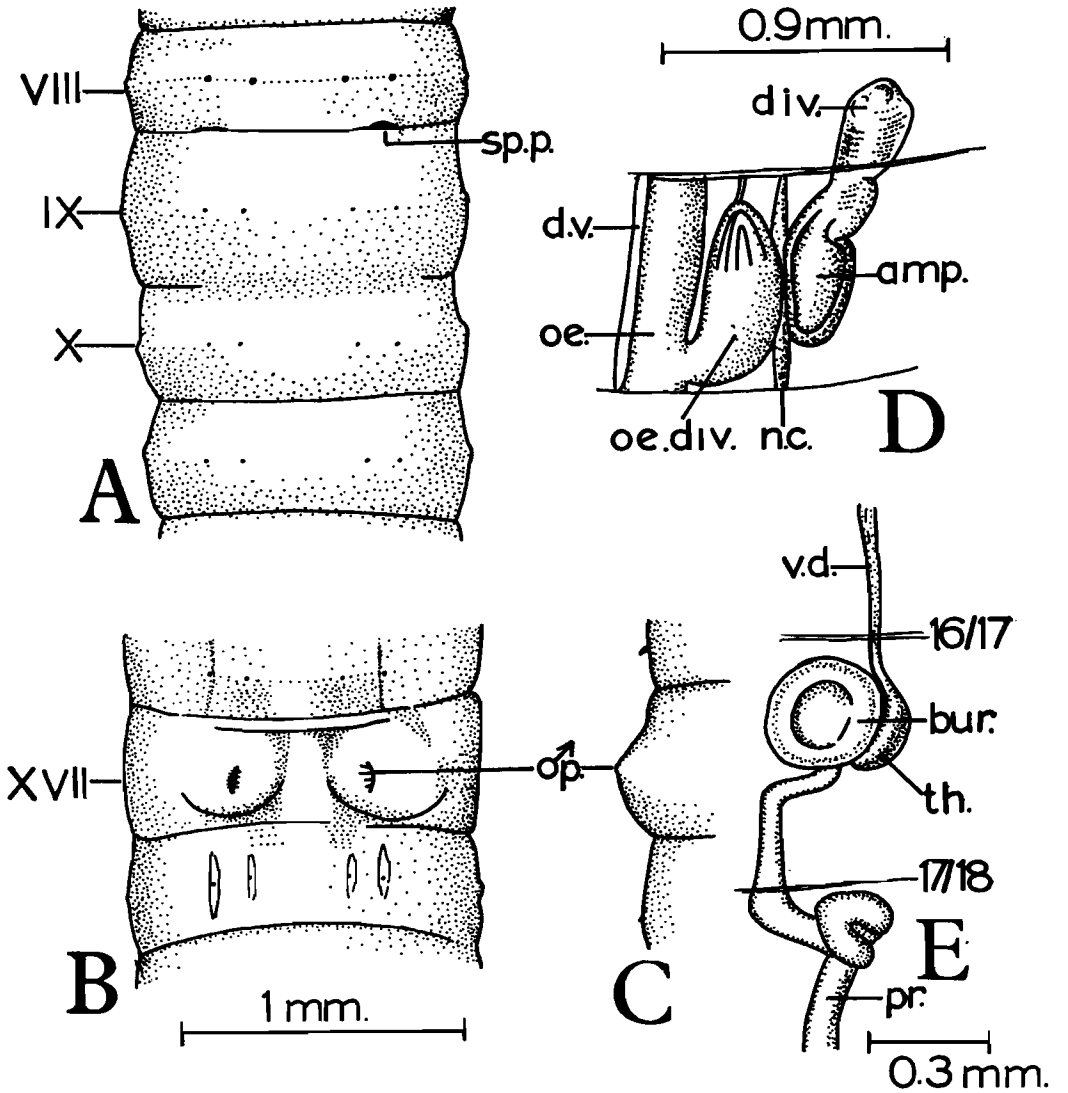

Figure 2. *Pygmaeodrilus arausionensis.* Sabie River specimen. A, spermathecal pores (sp.p.). B, male pores (♂ p.) on porophores, ventral view. C, left male porophore, lateral view. D, oesophageal diverticulum (oe.div.) and spermatheca *in situ*; amp., spermathecal ampulla; div., spermathecal diverticulum; d.v., dorsal blood vessel; o.e., oesophagus; n.c., ventral nerve cord; E, male terminalia, bur., copulatory bursa; pr., prostate gland; th., spindle-like thickening of v.d., vas deferens.

EXTERNAL ANATOMY

Dimensions. Length 27 to 40 mm. Maximum width (forebody or clitellum) 1·3 to 1·6 mm. Number of segments 80 to 106. Means: 35 mm. × 1·4 mm., 97 segments (5 specimens). Max. 45–65 mm. × 1–2 mm., 110–128 segments (Michaelsen, 1910, 1914).

Prostomium. Indistinctly epilobous, appearing zygolobous (confirmation Michaelsen, 1910a, 1914), dorsal tongue broad, slightly narrowing posteriorly, closed (3 specimens) or apparently open (2 specimens), extending over 1/3 (1 specimen) or 1/2 (5 specimens) of the peristomium.
Colour. In preservative, whitish (confirmation, Michaelsen, 1910a) with the clitellum pale brownish yellow (new material). Grey or yellow-brown (preserved) and dusky orange-yellow to brownish in life (Michaelsen, 1914).
Form. Slender; the first two or more segments abruptly narrowed; the peristomium approximately as long as wide; segment ix (containing the oesophageal diverticula and spermathecae) appreciably widened, it and x usually significantly elongated relative to adjacent segments.
Setae. Comparatively large, lumbricine, closely paired, $aa = bc$ (confirmation), $dd = 0{\cdot}4\ u$ (Table 4), ca. $= 0{\cdot}5$ u (Michaelsen, 1910a, 1914).

TABLE 4

Pygmaeodrilus arausionensis. SETAL DISTANCE RATIOS IN SEGMENT XII (3 specimens).

aa :	*ab* :	*bc* :	*cd* :	*dd*	*dd* : *u*	*bc* : *aa*
18	5	20	5	50	0·4	1·1
15	5	15	5	40	0·4	1·0
21	5	21	5	50	0·4	1·0
Mean					0·4	1·0

Clitellum. Saddle-shaped, dorsally extending from xiii, 1/3 xiii, 1/2 xiii to xviii, 1/2 xix, xix (= 5 1/2, 6, 6 2/3 segments) its ventral margins in setal lines *b* (5 specimens). Limits uncertain apparently commencing at 1/2 xii (Michaelsen, 1910a), xiii–xix (= 7) (Michaelsen, 1914).
Male genital field (Fig. 2 B, C): Male pores longitudinal slits in xvii in setal lines *ab* slightly behind the setal arc at the summit of two large, circular prominences which are continuous laterally with the clitellum, medianly are separated by a narrow unmodified tract of the epidermis, and almost fill the segment longitudinally (1 specimen). Male fields in the other five specimens essentially similar though in some less developed. Male pores in all specimens directed slightly towards the midventral line and in some cases extending as grooves to the posterior, or anterior borders of the porophores.

In one specimen the left bursa copulatrix (*v.inf.*) is everted as a muscular, medially indented vesicle through the corresponding male pore which its proximal stalk forces open as a wide circular orifice (see Remarks).

The ventral pairs of setae of xvii are absent (confirmation of Michaelsen, 1910a, 1914, from 6 specimens) but the male pores lie immediately posterior to the setal arcs and not, contrary to Michaelsen, at the sites of the absent setae.
Female pores. Visible in all specimens as dark points, with narrow whitish margins, in front of setae *b* of xiv, (located here or a little mediad, on tiny papillae in glandular fields, Michaelsen, 1914) varying in position from immediately anterior to the setal arc to midway between this and intersegmental furrow 13/14.

Spermathecal pores (Fig. 2A). A pair of transverse slits, a little narrower than a setal couple, with their centres in setal lines *b* (confirmation of Michaelsen, 1914) or immediately medial or lateral to these (6 specimens). In some specimens their anterior and posterior borders are differentiated as apparently glandular, but not protuberant, fields extending for about one fourth of the length of each neighbouring segment. Michaelsen (1914) found these fields to be raised in some cases.

Dorsal pores. Absent (6 specimens).

INTERNAL ANATOMY

Unless otherwise stated the following description refers to specimen 1.

Septa. 6/7 to 9/10 relatively strongly thickened, 5/6 and 10/11 hardly appreciably (new material); 6/7 and 7/8 rather strongly; 5/6, 8/9, 9/10, very slightly thickened, the remainder thin, 4/5 distinctly developed (Michaelsen, 1914, correction of 1910 account); lobed septal glands in iv to vii, largest in v, smallest in vii (Michaelsen, 1910a, 1914).

Alimentary canal. Gizzard absent; a pair of lateral oesophageal diverticula in ix (confirmation); each ovoid (Fig. 2D), with the blind end directed forwards and attached by a blood vessel to septum 8/9; proximal stalk short and fairly stout, the lumen constricted by longitudinal folds of the walls (confirmation). Oesophagus widening abruptly in xii to form the intestine (confirmation; Michaelsen, 1910a, 1914) but not attaining its full width until xiii.

Blood vascular system. Last hearts in xi (confirmation; Michaelsen, 1910, 1914), a further pair in x; dorsal vessel single.

Nephridia. Holonephridia (confirmation); not certainly observed in front of xiii. Absent from xiii (Michaelsen, 1914).

Anterior male organs. Free sperm masses and a pair of large sperm funnels in each of x and xi (specimen 1); testes large and flattened in these segments (Michaelsen, 1910a); seminal vesicles lobed, a pair in each of ix and xii (specimen 1, Michaelsen, 1914) or in xii only (Michaelsen, 1910).

Posterior male organs (Fig. 2E). Prostates a pair of slender tubes without distinct ducts; ca. 1·5 mm. long and, depending on the degree of convolution, occupying four or less segments (confirmation); greatest width entally 90 μ (Michaelsen, 1910a) to 130 μ (specimen 1); at the ental end only 60 μ (Michaelsen, 1910a). A large hemispherical though centrally depressed copulatory bursa present on each side at the site of the male pore, in segment xviii; prostate gland ending at the posterior border of this bursa; vas deferens 0·05 mm. wide ending at its posterolateral aspect; the terminal portion of the vas deferens thickened in the form of a spindle 0·1 mm. wide (specimen 1); terminalia similar in other specimens (see Remarks).

Female organs. Ovaries and oviducal funnels paired in xiii (confirmation). Apparently mature oocytes ca. 70 μ wide (Michaelsen, 1910a).

Spermathecae (Fig. 2D). A pair in ix. Each with a transparent ovoid ampulla 0·4 mm. long and a shorter, almost equally wide duct; the latter discharging ventrally, in furrow 8/9, at the spermathecal pore, but also continuous through the anterior septum into viii as a diverticulum which has approximately the dimensions of the ampulla. Iridescence of duct and diverticulum suggests the presence of sperm; the ampulla contains a whitish homogeneous mass, presumably

nutritive in function. Length of spermatheca including diverticulum, ca. 0·9 mm. (specimens 1; see Remarks).

Remarks. The new series shows that the species has a pair of copulatory bursae into which discharge the terminally thickened vasa deferentia and the prostate ducts, a condition described elsewhere in the genus only for *P. paulae* Michaelsen, 1913b and *P. quilimanensis* Michaelsen, 1890. Both of these species inhabit the Zambesi and are clearly distinct from *P. arausionensis*, being readily distinguished from the latter by their numerous small diverticula arranged in a wreath around the spermathecal duct. In *P. quilimanensis* the bursa is associated with an external "penis". In *P. rhodesiensis* Michaelsen 1913b, also from the Zambesi but distinguishable from all three species by its spermathecae, the prostate and male ducts open at the tip of a "penis" which in Michaelsen's illustration has the appearance of the everted bursa seen in one specimen of *arausionensis*.

The four species thus appear to form a southern division of the genus probably possessing intromittent organs evaginable into spermathecal orifices of partners in copulation. Copulation has yet to be observed in the genus, however. They are among the smallest megadrili, the range in maximum length for the group being 25 to 40 mm. and in width 1·5 to 1·6 mm.

P. arausionensis is unique among the known species of the genus in having a single spermathecal diverticulum, in the large size of the latter, equalling that of the ampulla, and its location in the segment in front of the ampulla.

Family LUMBRICIDAE

Eiseniella tetraedra (Savigny, 1826) *tetraedra*

(Fig. 3A–C)

Enterion tetraedrum Savigny, 1826, p. 176.
Eiseniella tetraedra (*typica*); Michaelsen, 1900, p. 471.
Eiseniella tetraedra f. *typica;* Gerard, 1964, p. 42.

The long and confused synonymy of this species is dealt with by Michaelsen (1900, p. 471), Tétry (1937, p. 142), Pool (1937, a detailed morphological monograph) and Omodeo (1956, p. 187).

Distribution Amphibious or aquatic and almost cosmopolitan.

Previous South African Records *Cape Province:* Port Elizabeth (Michaelsen, 1899), Knysna, rain forest (Michaelsen, 1913f), Cape Flats (Pickford, 1937).

New Records. *Cape Province:* Krom River, a tributary of the Eerste River, just north of Stellenbosch, habitats not recorded, 22.viii.1952, 3 clitellate specimens; 15.ix.1952, 3 clitellate; 8.x.1952, 1 clitellate. Great Berg River tributaries: French Hoek Stream, bridge at La Motte, stones in current, 30.x.1950, 1 clitellate; Wemmers River at road bridge, stones in current, 14.xi.1951, 1 clitellate.

Transvaal: Jukskei River near Bryanston, Johannesburg, habitat unknown, 17.xi.1954, 1 clitellate.

EXTERNAL ANATOMY

Dimensions. In mm., five clitellate specimens (means in parentheses): length 34–59 (48); maximum width, 2·0–3·3 (2·8); number of segments 58–89 (79).

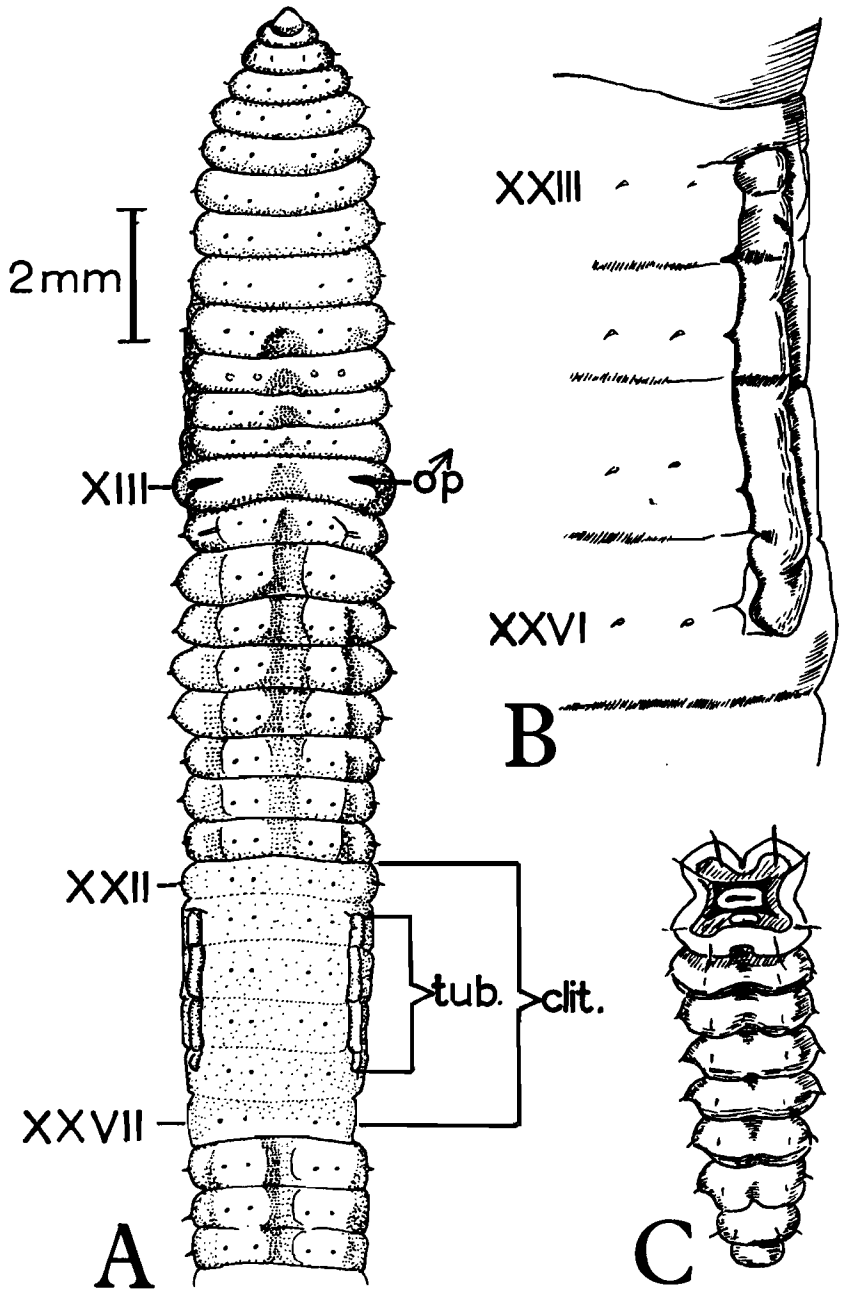

Figure 3. *Eiseniella tetraedra tetraedra.* Specimen from French Hoek Stream, Great Berg River. A, ventral view of clitellar end, clit., clitellum, ♂ p., male pore; tub., tuberculum pubertatis. B, detail of left tuberculum of same; C, tail end showing quadrangular cross section.

Colour. Greyish to buff in alcohol; pigmented. *Prostomium:* Epilobous 1/4 (1) to 1/2 (5 specimens).

Form. Relatively stout; quadrangular in cross section behind the clitellum (Fig. 36).

Setae. Eight per segment; large and distinctly visible; closely paired throughout. In xii *dd* = 0·4 *u*, *bc* = 1·0 *aa* (mean of 4, Table 5).

TABLE 5

Eiseniella tetraedra. SETAL DISTANCE RATIOS IN SEGMENT XII.

	aa	:	*ab*	:	*bc*	:	*cd*	:	*dd*	*dd* : *u*	*bc* : *aa*
	32		10		31		10		104	0·44	0·97
	25		9		28		8		84	0·42	1·12
	20		6		21		6		60	0·43	1·05
	20		5		20		7		70	0·45	1·00
Mean	24		8		25		8		80	0·44	1·03

Ventral setae of at least some of segments ix, x, xii, xiii, xiv, xxii and xxvii modified as genital setae and almost or completely obscured by slight tumescence (4 specimens). Modification deduced from examination of ventral setae of ix (2 specimens) and xxii (1 specimen), which are elongated and spear-shaped with 'lateral' blade like expansion of the slightly curved ectal end; otherwise straight. Length of one from ix, 0·92 mm. Genital seta glands present (*vide infra*).

Clitellum (Fig. 3A). Appears saddle-shaped but ventrally the clitellar region is tumescent and its intersegmental furrows are indistinct; embracing xxii (1), 1/2 xxii (4), xxiii (1) to xxvi(1), 1/3 xxvii (1), 1/2 xxvii (4) = 4 1/3—5 segments.

Tubercula pubertatis (Fig. 3A, B). A pair of narrow longitudinal ridges of uniform width transversely incised or indented by the intersegmental furrows; extending from xxiii (1), 1/2 xxiii (5) to 1/2 xxvi (6) and lying at 1/3 *bc*.

Male pores (Fig. 3A). A pair in the setal arc of xiii, each apparent as a deep transverse cleft which has its median extremity immediately lateral of *b* and has swollen anterior and posterior tips; these tips pushing furrow 13/14 backwards, so that it is arched, but not encroaching on xiv (6 specimens). Male clefts closed laterally by a small oval tubercle in which are located setae *cd*; male pore nearer *c* than *b*, within cleft (detailed examination of one specimen).

Female pores. Usually invisible. Observed in one specimen in the setal arc of xiv immediately median to seta *a;* inconspicuous, without fields.

Nephridiopores. Not externally visible.

Spermathecal pores. Two pairs, apparent as minute dome-like anterior protrusions of segment x and xi which slightly indent furrows 9/10 and 10/11, a little lateral of the middorsal line, at about 3/4 *d* to MD (1 specimen).

Dorsal pores. Commencing in 4/5 (5 specimens), 5/6 (1 specimen). Visible but imperforate on the clitellum.

INTERNAL ANATOMY

Unless otherwise stated the following account is based on a single specimen (Krom River, 22.viii.52). Some points were checked on a further specimen (French Hoek Stream, 30.x.50) referred to as specimen 2.

Septa. 8/9–14/15 thickened, 8/9 only slightly, none strongly.

Alimentary canal. Pharynx terminating posteriorly in vi. Oesophagus occupying vii to xiv with a pair of distinctly visible ovoid laterodorsal pouches in x but no external protuberances or widening in xi and xii; soft and without sheen in x to xii, presumably owing to presence of calciferous glands (see Smith, 1924); elsewhere glossy, though thin-walled, and intersegmentally constricted; very short in xiv as septum 14/15 is pushed forward by the crop which is thin-walled, several times the width of the oesophagus and occupies xv and xvi. Gizzard in xvii and xviii approximately as wide as crop and intestine; poorly demarcated from the crop, but distinguished by its sheen and narrow, transverse muscular striations; its walls muscular but thin relative to the large lumen; demarcated from the intestine, which begins in xix, by an intersegmental constriction. Gut similar in specimen 2.

Blood vascular system. Last hearts in xi.

Nephridia. Lacking definite muscular end-tubes; each terminating in a slender tube which penetrates the parietes in setal line *d*.

Male organs. Testes and sperm funnels free in x and xi. Male ducts sinuous, iridescent and unusually wide in xi and xii where they presumably act as epididymes; straight in xiii in which each penetrates an internal swelling, the anterior lip of the male cleft, near the lateral extremity of the latter. Seminal vesicles 3 or 4 pairs each with several lobes in ix, (x), xi and xii, the second pair very small (specimen 1) or absent (specimen 2). Empty transparent homologues of the seminal vesicles, resembling the latter in shape and size, present in xiii and xiv, dependent from the anterior walls of these segments (specimen 1).

Female organs. Ovaries and funnels in xiii; compact multiloculate ovisacs in xiv dependent from the anterior septum; (specimens 1 and 2); oviduct entering parietes immediately median to setal line *a* in xiv.

Spermathecae. A pair in each of x and xi opening at the anterior septum; ampulla spherical and apparently sperm-filled; duct very short, conical (specimens 1 and 2); width ampulla 0·5 mm.

Accessory glands. Ventrolateral parietal glandular masses in ix–xii, xxii and xxvii coincide with ventral setae which are externally obscured by glandular areas; these are presumably genital setae and their glands. Glands in xiii correspond with the anterior and posterior lips of the male porophore and are transversely divided by its cleft; masses in xiv are evidently posterior extensions of these.

Remarks. The following features of the new material accord with previous descriptions or fall within known variation for the species: dimensions, number of segments, form of the prostomium, location of male and female pores, segmental limits of the clitellum and tubercula pubertatis, number and location of spermathecae and their pores, location of first dorsal pore and of seminal vesicles (see, however, below).

Absence of seminal vesicles from segment x, in one specimen, is typical of *E. balcanica* Cernosvitov. Location of female pores median to setal lines *a* which Omodeo (1956) observed to be unique to *E. tetraedra*, of all Lumbricidae, is stated by Pool (1937) to be general in the genus.

Intersetal ratios in the new material conform with the types (see Pool, 1937) with the exception of *dd* which averages 10 *ab* against 6 *ab* reported for the latter. The observation of Michaelsen, 1900 that *dd* is only slightly larger than *bc* is clearly an error as is his location of spermathecal pores in 8/9 and 9/10.

The clitellum, here recorded as ending at 1/2 xxvii reached 27/28 in the types (Pool, *l.c.*), but ventrally some modification as far as this intersegmental furrow is visible in the new material.

Septal thickening to 14/15 is characteristic of *Eiseniella lacustris ochridana* (Cernosvitov) (*vide* Pool, *l.c.*) which differs in having male pores in xv, among other respects. Assessment of septal thickening is highly subjective and the difference from the usual distribution of thickening in *E. tetraedra* (7/8–11/12) is of doubtful significance.

The genus *Eiseniella* has been stated to be isolated from the rest of the Lumbricidae by restriction of the gizzard to a single segment, i.e. xvii (Michaelsen, 1910b; Stephenson, 1930). This was the sole distinction from *Eisenia* noted by Stephenson (*l.c.* p. 908) who doubted the validity of separating the two genera. In the present material the gizzard occupies both xvii and xviii a disposition also noted by Omodeo (1956), by Jackson (1931) (for *E. intermedia*, regarded by Pool, 1937 as a synonym of *E. tetraedra typica*) and by Cernosvitov, 1931 for *E. lacustris* (Cernosvitov) a species retained by Pool (*l.c.*). Omodeo (1956) found fresh grounds for distinguishing *Eisenia*, however. He placed it in a distinct subfamily, the Eiseninae, differing from the Lumbricinae, in which *Eiseniella* and all other lumbricids were placed, in having more than one fertile egg in the cocoon, no excretory blastomeres in the embryo, and in possessing a globular embryo. *Eiseniella* was said to differ from it in having lateral pouches to the Morren's glands (calciferous glands) and a basic chromosome number of 18 as against 11 in *Eisenia*. Whether the distinguishing features of *Eisenia* merit subfamily status or even generic distinction is, perhaps questionable though the low basic genome appears to set it apart from the Lumbricinae, in which 15 is the lowest basic number recorded by Omodeo (*l.c.*).

Dendrobaena rubida (Savigny, 1826)

(Fig. 4D)

Enterion rubidum Savigny, 1826, p. 182.
Allolobophora tenuis Eisen 1874b, p. 44.
Helodrilus (*Dendrobaena*) *rubidus;* Michaelsen, 1900, p. 490.
Allolobophora constricta Rosa 1884, p. 38.
Helodrilus (*Bimastus*) *constrictus;* Michaelsen, 1900, p. 503; Michaelsen, 1908, p. 41; Michaelsen, 1913f, p. 552.
Dendrobaena rubida; Omodeo, 1957, p. 14.
Dendrobaena (*Dendrodrilus*) *rubida;* Omodeo, 1956, p. 175.

Allolobophora subrubicunda; Eisen, 1874a, p. 51.
Dendrobaena rubida; Gerard, 1964, p. 40.

Omodeo (1956) includes *B. norvegicus* (Eisen, 1874a), in addition to these taxa, in *D. rubida*. The partial synonymy listed above may be augmented by reference to Omodeo, 1956; Pop, 1947 and Michaelsen, 1900.

Distribution. Terrestrial, occasionally limnic. One of the commonest species of earthworms. Known from Gt. Britain; Europe; Siberia; North, Central and South America, including Tierra del Fuego and Hawaii; Falkland Islands; N. Africa; N. India; Australia; New Zealand.

Previous South African Records. *Cape Province:* Cape Flats in the south west (Michaelsen, 1908); Table Mountain; Knysna, Main Forest (Michaelsen, 1913d, f); also from Table Mountain, Skeleton Gorge (Pickford, 1937).

Natal: Howick, near foot of Umgeni Falls (Michaelsen, 1913c). Recorded in all three of Michaelsen's accounts as *Helodrilus* (*Bimastus*) *constrictus* (Rosa) and by Pickford as *Bimastus tenuis*.

New Record. *Cape Province:* Great Berg River at Cecilia's Drift, National Road bridge, above Paarl, in vegetation, 10.vii.1951, 1, desiccated except for the clitellum.

EXTERNAL ANATOMY

Dimensions: Length 11 mm., clitellar width 1·5 mm., 93 segments.

Colour: In preservative pigmentation remains only ventral to the clitellum.

Prostomium: Narrow, parallel sided, tanylobous but lateral borders indistinct behind a transverse furrow at 2/3 peristomium.

Form: Cylindrical? Possibly somewhat quadrangular behind the clitellum.

Setae. 8 per segment, the ventral couples moderately closely paired, the lateral couples relatively widely; in xii, $dd = 0{\cdot}42\ u$, $bc = 1{\cdot}2\ aa$ (Table 6).

TABLE 6

Dendrobaena rubida (*tenuis* morph.?) SETAL DISTANCE RATIOS IN XII

aa	:	*ab*	:	*bc*	:	*cd*	:	*dd*	*dd* : *u*	*bc* : *aa*
11		5		13		9		48	0·42	1·2

Ventral setae of xvi elongated as genital setae, each couple lying mediad to a circular shallow depression with tumescent margins. This segment tumid ventrally and impinging on xv medially.

Clitellum (Fig. 4D). Distinctly saddle-shaped; very protuberant, pale greyish buff; embracing xxvi to 1/2 xxxii dorsally, xxvii to xxxi laterally. Ventral borders immediately lateral to setae *b*. Intersegmental furrows and setae visible throughout.

Tubercula pubertatis (Fig. 4D). Rudimentary; represented by two longitudinally contiguous, slightly tumescent darkly pigmented strips on each side, one in xxix, the other in xxx.

Male pores. A pair in the setal arc of xv, each apparent as a deep transverse cleft bordered by broad, protuberant lips which extend from *b* to *c* but do not impinge on adjacent segments.

Female pores. A minute pore was seen on the left side immediately lateral of *b*.

Spermathecal pores. Absent.
Dorsal pores. Not visible.
Nephridiopores (Fig. 4D). Minute transverse slits between the setal arcs and the anterior borders of the clitellar segments, a little lateral of setal lines *b* and just included within the borders of the clitellum are presumably nephridiopores.

INTERNAL ANATOMY

Very little can be discerned owing to the poor condition of the specimen.
Alimentary canal. Large, longitudinally multilamellate calciferous glands in xi (and xii?). Crop in xiv and xv, gizzard well developed, in (xvi?) xvii to xviii.
Anterior male organs. Seminal vesicles apparently only in xi and xii.
Spermathecae. Absent.
Remarks. Omodeo (1956) made *Dendrobaena rubida* the sole member of a subgenus *Dendrodrilus*. Although *Bimastos tenuis*, to which the present material conforms in lacking spermathecae and, apparently, a third pair of seminal vesicles, was placed in this species, the genus *Bimastos* was retained. Supposed distinctions of *Dendrobaena* (*Dendrodrilus*) from *Bimastos* s. strict. were:

	Dendrobaena (*Dendrodrilus*)	*Bimastos* (s. strict.)
Setae:	Unpaired, rather large.	Paired, rather small.
Clitellum:	5 to 15 segments.	6 to 12 segments.
Longitudinal musculature:	Pennate.	Fasciculate.
Seminal vesicles:	3 pairs.	2 pairs.

Taking these distinctions in turn, intersetal ratios recorded by Omodeo, 1957 indicate that setae are paired in *Dendrobaena*, though widely; the significance of the difference in clitellar extent is questionable; fasciculate longitudinal musculature has been shown in *Bimastos* only for *B. eiseni* and *B. minisculus* and has been demonstrated in *D.* (*Dendrobaena*) *veneta* and *D.* (*Dendrobaena*) *hortensis*. In *D. rubida* it is pennate (Pool, 1937). Omodeo (1956) admits that the genera are not uniform in this character. Lastly, although *Dendrobaena rubida* is said to differ from *Bimastos* in having three pairs of seminal vesicles, Omodeo (1957, p. 16) states that in specimens of *rubida* from four localities in Greenland there were usually only two pairs of seminal vesicles, in the "*Bimastus* (sic.) disposition" (segments xi and xii) but that in specimens from Godhavn, vesicles showed the "*Dendrobaena* disposition" (segments ix, xi and xii). Previously (1956, p. 146) Omodeo pointed out that the taxonomic value of the number of seminal vesicles in *D. rubida* and in some other species showing reduction owing to parthenogenesis, was almost nil.

Separation of *Dendrodrilus* and *Bimastos*, at least on the characters given, therefore appears to be unjustified though valid grounds may yet be found for distinguishing them. It may be noted that the only clear distinction between *Dendrobaena* and *Bimastos* (including *tenuis*) given by Cernosvitov and Evans (1947) is the very questionable one of numbers of seminal vesicles. Gerard (1964) adds to this setal ratios $aa : ab = 1{\cdot}8$ in *D. rubida* and 3 in f. *tenuis*. The ratio in the present material, 2·2, is intermediate but may have been affected by desiccation.

The *tenuis* morph in the present collection is placed in *Dendrobaena rubida* in accordance with Omodeo (1956) but the subgenus *Dendrodrilus* is discarded. The latter subdivision was not used by Omodeo (1957).

Allolobophora caliginosa (Savigny, 1826) *trapezoides* (Dugès, 1828)

(Fig. 4A–C, 5A–D)

Lumbricus trapezoides Dugès, 1828, p. 289.
Allolobophora caliginosa trapezoides Rosa, 1893, p. 443.
Helodrilus (*Allolobophora*) *caliginosus trapezoides* Michaelsen, 1900, p. 483.
Allolobophora iowana Evans, 1948, p. 515.
?Allolobophora caliginosa forma *trapezoides* Cernosvitov and Evans, 1947, p. 14.
?Allolobophora caliginosa (Part.); Gerard, 1964, p. 27.

Michaelsen (1900) gives a comprehensive bibliography of the numerous synonyms of this species. Other major references for the species are Tétry (1937, p. 146), a re-examination of Savigny's types; Khalaf el Duweini (1940), a detailed morphological account of *trapezoides;* and Omodeo (1952, 1956).

Distribution (for the species). *A. caliginosa* is almost cosmopolitan, though rare in the tropics, and is probably the most widely distributed and abundant earthworm. It frequently replaces endemic earthworms in newly cultivated land and pastures and is relatively infrequent in limnic habitats. The new record from a purely aquatic habitat is therefore of interest although it is possible that occurrence of the specimens in water was accidental.

Previous South African Records. (Terrestrial unless otherwise stated. An asterisk indicates *trapezoides*).

Cape: Port Elizabeth* (Michaelsen, 1899, 1913f); Stellenbosch; Knysna* (Michaelsen, 1913f); Kamaggas in Little Namaland*; Cape Town* (Michaelsen, 1908); Cape Flats and Paradise Estate, Kirstenbosch (Pickford, 1937).

Natal: Howick*, in detritus near foot of Umgeni Falls, associated with the aquatic *Eukerria saltensis* (Michaelsen, 1913c).

South West Africa: Usakos*, Windhoek* (Michaelsen, 1914).

Transvaal: Witpoortje Falls, Krugersdorp District (Pickford, 1937).

New Record. *Western Cape Province**

Krom River, a tributary of the Eerste River just north of Stellenbosch, habitat not known, 15.ix.1952 and 23.iii.1953. One clitellate anterior amputee and one complete specimen with rudimentary clitellum, referred to as specimens 1 and 2, in this order, throughout the following account.

EXTERNAL ANATOMY

Dimensions: Length 128 mm. (specimen 2); greatest width, at clitellum, 3·5, 3·3 mm. 94 and 107 segments.

Colour: In alcohol, pigmented, brownish grey. In specimen 2 intersegmental furrows and setal arcs are paler and there is a greenish cuticular iridescence.

Prostomium: Epilobous 1/3, dorsal tongue narrowing posteriad, closed by a transverse furrow (specimen 2).

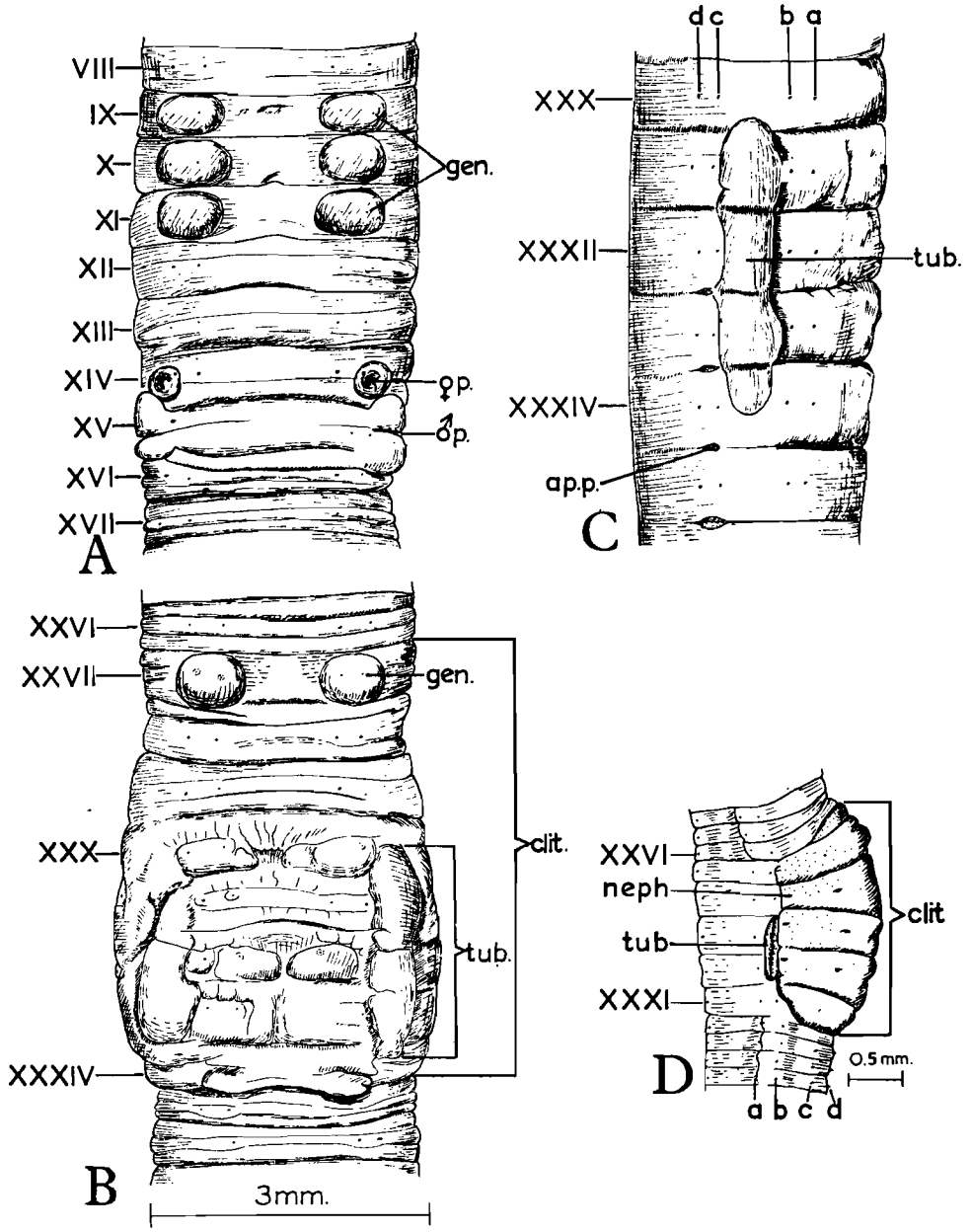

Figure 4. *Allolobophora caliginosa* (*?trapezoides*), Krom River. A and B, ventral views of male and female genital fields in specimen 1. C, lateral view showing tuberculum pubertatis of specimen 2.

Dendrobaena rubida, Great Berg River. D, latero-ventral view of clitellar region. ap.p., epidermal modification with appearance of a pore; clit., clitellum; ♀ p., female pore; ♂ p., male pore; neph., nephridiopore; gen., tumescence bearing genital setae; tub., tuberculum pubertatis.

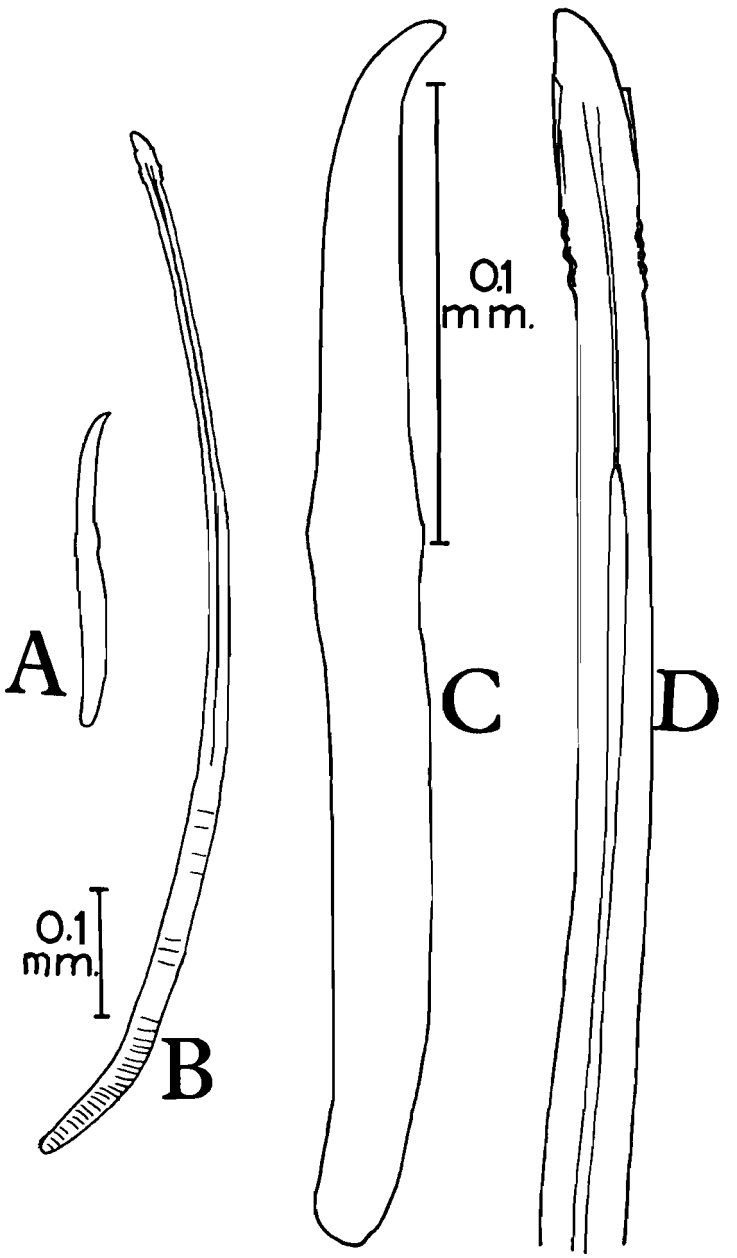

Figure 5. *Allolobophora caliginosa* (*?trapezoides*), Krom River. A, unmodified seta for comparison with B, a genital seta at the same magnification. C and D, enlarged views of these setae. (All by camera lucida).

Form: Fairly slender, circular in cross section throughout.
Setae: Eight per segment, very closely paired throughout; in xii *dd* = 0·5–0·6 *u*, *bc* = 0·6–0·8 *aa* (Table 7).

TABLE 7

Allolobophora caliginosa trapezoides. SETAL DISTANCE RATIOS IN SEGMENT XII

	aa	*ab* : *bc* : *cd* : *dd*	*dd* : *u*	*bc* : *aa*
Specimen 1	35	9 : 22 : 6 : 100	0·48	0·6
Specimen 2	16	5 : 12 : 3·5 : 70	0·55	0·8

Ventral setal couples of ix to xi, and also xxvii, xxx and xxxii to xxxiv, on tumescences (Fig. 4A, B). At least some of these modified as genital setae (Fig. 5B, D) which are elongated, gently curved, and lack a node. The ectal portion is longitudinally grooved on the concavity of the curvature and is flanked by very narrow lateral expansions which are not always apparent. Viewed in the plane of curvature, the ectal end of the seta appears slightly spatulate. Ornamentation near the tip, shown in Fig. 5D, is absent or less developed in other genital setae examined. Length of a genital seta of ix and xxxii = 0·9 mm. and of xxvii = 1·2 mm. Unmodified setae are sigmoid with prominent node and are not ornamented (Fig. 5A, C): length of one from xviii = 0·27 mm. (specimen 1).

In specimen 2, in which the clitellum is rudimentary, only the ventral setae of ix to xi are circumscribed by tumescent areas; genital setae in ix resemble those described.

Clitellum. Embracing xxvii to xxxiv (both specimens) appearing saddle-shaped but the clitellar region ventrally tumescent with partial obliteration of intersegmental furrows (specimen 1).

Tubercula pubertatis. A pair of longitudinal ridges extending from 1/2 xxx, 3/4 xxx to xxxiii or xxxiv and almost filling *bc* (Fig. 4B, C). Transversely incised by intersegmental furrows 31/32 (specimen 1) or showing, faintly, all the corresponding intersegmental furrows (specimen 2).

Male pores. A pair in xv; each apparent as a deep transverse cleft, filling *bc* approximately in the setal arc, between large swollen lips which encroach on xiv and xvi; segment xv and adjacent halves of xiv and xvi tumid ventrally (specimen 1, Fig. 4A). The lips are rudimentary in specimen 2 and the male pores are therefore exposed as minute orifices nearer *c* than *b*.

Female pores. A pair very slightly lateral of setae *b* on xiv, with circular lips which include these setae and are contiguous with the male porophores (specimen 1, Fig. 4A). Minute holes in the same location but lacking fields in specimen 2.

Spermathecal pores. A pair in each of intersegmental furrows 9/10 and 10/11; minute, with hardly if at all appreciable fields, in *cd* (specimen 2). Similarly located in specimen 1 (internal examination).

Dorsal pores. Commencing at 11/12, 8/9. Minute on the clitellum.

Nephridiopores. A straight intersegmental series at *b* (specimen 2).

Pore-like modifications of the epidermis which are visible on the right side only in most of intersegmental furrows 24/25 to 36/37 in specimen 2 (Fig. 4C) are apparently imperforate and do not coincide with any internal organ. Their nature remains obscure.

INTERNAL ANATOMY

Septa. 7/8 to 10/11 (specimen 2) or to 11/12 (specimen 1) strongly thickened, the remainder to 14/15 considerably but less thickened. Last septal glands a pair of large, grey, smooth lobes dependant from the anterior septum of *v* which is the first recognizable septum (specimen 2).

Alimentary canal. Pharynx terminating posteriorly in iv. Oesophagus in v to xiv, with slight hemispherical, laterodorsal protuberances (calciferous glands) in x. Crop in xv and xvi, thin-walled, about twice the width of the oesophagus. Gizzard in xvii and xviii, moderately muscular, passing almost imperceptibly into the intestine which begins in xix. Typhlosole, commencing in xxi as a low dorsal two ridged fold which soon enlarges to a U-shaped structure occupying about half the height of the intestinal lumen; lacking in a few posterior terminal segments (specimen 2). Divisions of the gut in specimen 1 appear externally the same but, although the oesophagus is widened in x (and xi), calciferous glands were detectable only by transverse sectioning when lamellae of calciferous glands were seen in x.

Blood vascular system. Dorsoventral hearts in (vi?) vii to xi (both specimens). Dorso-intestinal vessels two pairs in xv and posterior segments except xvi in which only a single pair was observed (specimen 2). Dorso-(subneural?) vessels from xii posteriorly.

Nephridia. Funnels long-necked; tubules long and conspicuous; terminal muscular tubes capacious, usually bent in a U with very short ental and long ectal limbs, in the intestinal region dilated and thin-walled but never forming a distinct bladder; passing into the parietes anteriorly in *b*.

Male organs. Testes and large iridescent sperm funnels free in x and xi. Seminal vesicles paired in ix, x, xi and xii. Male ducts coiled as epididymes behind their funnels, in xi and xii (both specimens), those of a side uniting at septum 12/13 and continuing posteriorly in a straight line to enter the parietes, without enlargement, beneath the retractor muscle joining the ventral and lateral setal couples of xv (specimen 2).

Female organs. Compact ovaries and small, flattened funnels paired in xiii. Ovisacs about as large as the ovaries, on the posterior face of septum 13/14 (both specimens).

Spermathecae. Two pairs, in x and xi, spherical, adiverticulate, and almost sessile (specimen 1). Very small (presumably not inseminated) in specimen 2.

Genital seta glands. In ix (x, xi?) and xxvii the ventral setal follicles are enlarged as whitish digitiform bodies. In xxix to xxxiv they form a pair of very large cushion-like glands in each segment. In the midline the latter glands are contiguous and are covered by the ventral nerve cord, which arches over them, and by the longitudinal musculature (specimen 1). They are present in xxxi, where the ventral setae are not on protuberances; whether the setae are enlarged in this segment is not determinable. In specimen 2 no genital seta glands are developed presumably because of immaturity, although genital setae are present.

Remarks. Two forms of *Allolobophora caliginosa* are currently recognised. These are 'forma *typica*' and 'forma *trapezoides*' which are designated *A. c. caliginosa* and *A. c. trapezoides* in this discussion.

The whereabouts of Savigny's types of *caliginosa* are unknown but Tétry (1937) has proved that the specimens for which Savigny (1828) erected *Enterion carneum* are referable to *caliginosa*, the sole supposed difference, the number of seminal vesicles, having been shown by her to be fictitious. Cain (1955) made a detailed investigation of the types of *carneum*

which merited alterations of the diagnosis by Cernosvitov and Evans (1947) of *A. caliginosa* 'f. *typica*'. The emended description of Cain gives us a very full knowledge of the typical form based on material which Savigny saw.

Lumbricus trapezoides Dugès 1828 (type locality Montpellier) was made a subspecies of *A. caliginosa* by Rosa (1893) without reference to the type specimens which had apparently been lost at a very early date. Our knowledge of material certainly assignable to *trapezoides* rests solely on the brief and somewhat confused accounts of Dugès, 1828 and 1837. Very precise descriptions of a new species, *Allolobophora iowana*, were, however, given by Evans (1948) and further data on this taxon, based on the types and Algerian material, were provided by Cain (1955) who presented convincing evidence that *iowana* should be suppressed as a synonym of *trapezoides*. He avoided this step, however, because the types of *trapezoides* were lost and because of the possibility that they may have included material of *caliginosa*, features of which might have been incorporated in the description of *trapezoides*. A further though less cogent reason was the belief that specimens of *caliginosa* with a *trapezoides* arrangement of the tubercula pubertatis had frequently been wrongly assigned to *trapezoides*. It seemed 'contrary to good practice' to suppress *iowana* which was clearly defined by its author and is supported by available type material.

These arguments could equally well have been used to support making the types of *iowana* neotypes of *trapezoides*. In support of union of these entities it may be argued that it is unlikely that Dugès found at Montpellier a species which has never again been collected. It seems probable that most of the frequent records of *trapezoides* and records of *iowana* itself do in fact refer to Dugès' taxon to which they so closely conform. It nevertheless seems acceptable that some records of *trapezoides* accord better with the diagnosis of *caliginosa* though having a *trapezoides* configuration of the tubercula pubertatis. Certainly too much emphasis has formerly been placed on the tubercula as a means of distinguishing between the two taxa, as Cain (1955) has suggested.

That the tubercula alone do not permit satisfactory distinction of *caliginosa* and *trapezoides* was recognised by Pop (1947, p. 2). Corsican specimens from single stations showed gradations in the form of the tubercula pubertatis between the two pairs of "*typica*" and the ridges of "*trapezoides*". Specimen 1 in the present collection is also not clearly referable to either taxon on this and other criteria (see Table 8).

Although Cain (*l.c.*) admits to gradations in the configuration of the tubercula between *caliginosa* and *iowana* (i.e. *trapezoides*) he emphasizes that no true intermediates, taking other characters, exist between the two forms. He recognises a number of differences which he regards as constant. The lack of intermediates between the forms and the constancy of their supposedly diagnostic features require firmer demonstration than any author has yet given, however.

Table 8 indicates that distinction in the literature between *caliginosa* and *iowana* is not as clear as Cain (*l.c.*) has suggested. A comparison of the features of specimen 1 from the present South African collection will serve to emphasise the lack of clear distinction.

Intermediates between *caliginosa* and *trapezoides* exist with regard to pigmentation, clitellar extent, distribution of genital cushions and tumescence of segment xv in addition to the configuration of the tubercula. Other supposed differences are unconfirmed.

TABLE 8.

Comparison of *Allolobophora caliginosa caliginosa* and *A. c. trapezoides* with specimen 1 (Present study).
T = SIMILAR TO *trapezoides* C = SIMILAR TO *caliginosa* I = INTERMEDIATE.

Character	*caliginosa;* Cernositov & Evans 1947, Cain emend. 1955. *A. caliginosa caliginosa*	*iowana* Evans 1948 Cain emend. 1955 *A. caliginosa trapezoides*	*trapezoides?* Present study		Remarks
Pigment	Absent	Brown	Brown	T	*iowana* rarely lacks pigment (Cain 1955).
Tail	Circular in t.s.	Distinctly flattened	Circular in T.S.	C	Posterior extremity of *iowana* somewhat flattened (Evans, 1948).
Clitellum	½ 28, 29–34.	27, ½ 27–34	27–34	T	27–34 in some *caliginosa* from Iowa (Evans, 1948).
Tubercula	On 31 and 33, extending over 32 but usually, not always, separated by a transverse furrow	Bands on 31–33, apparently always continuous	Bands on ½ 30, ½ 30–33 or 34, transversely incised by furrow 31/32	I?	*caliginosa* sometimes has *trapezoides* configuration (Cain, 1955).
Genital cushions	30, 32, 33 and 34	30, 32 and 33. Only occasionally on 34.	27, 30, 32, 33 and 34.	C	Also on 27 in *caliginosa*, see Fig. 6 in Cernosvitov and Evans, 1947 (similarity of *trapezoides* implied) and in *carneum;* Cain, 1955.
Male porophores	Pear-shaped	Rectangular	Intermediate	I	Dubious distinction, not noted by Evans, 1948.
Ventrally tumid segments	14 and 16 but not 15	14, 15 and 16	15 and adjacent halves of 14 and 16	T	15 tumid in *caliginosa* in Evans, 1946, fig. 1.
First dorsal pore	11/12 or 12/13	8/9 or 9/10	11/12	C	Difference not confirmed by Cain, 1955.
Septal thickening	5/6–9/10, not strongly	6/7–9/10 strongly	7/8–11/12 strongly	?	No difference demonstrable (Cain, 1955).

Existence of intermediates between two forms does not preclude regarding them as distinct subspecies but it is the purpose of this discussion to indicate that previously recognised distinctions between *caliginosa* and *trapezoides* require substantiation by far more rigorous investigation than has previously been accorded these taxa. The geographical distribution of the two forms also requires further investigation. Cernosvitov and Evans (1947, p. 14) state that *trapezoides* is prevalent in southern Europe and the Mediterranean region and is replaced in the north by the typical form. Pending such investigations *trapezoides* is retained as a trinomial within *caliginosa*.

REFERENCES

ALLANSON, B. R. 1961. Investigations into the Ecology of Polluted Inland Waters in the Transvaal. Part 1. The Physical, Chemical and Biological conditions in the Jukskei–Crocodile River System. *Hydrobiologia* 18, 1: 2–76 + appendix.

BEDDARD, F. E. 1895. Preliminary Account of new Species of Earthworms belonging to the Hamburg Museum. *Proc. zool. Soc. London*, 1895: 210–239.

BEDDARD, F. E. 1896. Naiden, Tubificiden und Terricolen. *Erg. Hamb. Magal. Samm:* 1–64.

BRINKHURST, R. O. 1964. A Taxonomic Revision of the Alluroididae (Oligochaeta). *Proc. zool. Soc. Lond.* 142, 3: 527–536.

BRINKHURST, R. O. 1966. A contribution towards a revision of the aquatic oligochaeta of Africa. *Zool. afr.* 2 (2): 131–166.

CAIN, A. J. 1955. The taxonomic status of *Allolobophora iowana* Evans 1948 (Oligochaeta, Lumbricidae). *Ann. Mag. nat. Hist.* (ser. 12) 8, no. 91: 481–497.

CERNOSVITOV, L. 1931. Zur Kenntnis der Oligochaeten–Fauna des Balkans.ii.Die wasserbewohnenden Lumbriciden aus dem Ochridsee. *Zool. Anz.* 95: 96–103.

CERNOSVITOV, L. and EVANS, A. C. 1947. Synopses of the British Fauna, No. 6, Lumbricidae. Linnean Society of London: 1–36.

DUGÈS, A. 1828. Recherches sur la circulation, la respiration et la réproduction des annélides abranches. *Ann. Sci. nat.* 15: 284–337. Cited by Cain.

DUGÈS, A. 1837. Nouvelles observations sur la zoologie et l'anatomie des annelides abranches sétigères. *Ann. Sci. nat.* (2) 8: 15–35. Cited by Cain *l.c.* (1955).

EISEN, G. 1874a. Om Skandinaviens Lumbricider. *Oefv. Ak. Förh.* 1873, 30, no. 8: 43–56.

EISEN, G. 1874b. Bidrag till kannedomen om New Englands om Canadas Lumbricider. *Oefv. Ak. Förh.* 1874, 31, no. 2: 41–49.

EVANS, A. C. 1946. A new Species of Earthworm of the genus *Allolobophora*. *Ann. Mag. nat. Hist.* (ser. 11), 13: 98–101.

EVANS, A. C. 1948. On some Earthworms from Iowa, including a description of a new Species. *Ann. Mag. nat. Hist.* (ser. 11), 14: 514–516.

GATES, G. E. 1942. Notes on various peregrine earthworms. *Bull. Mus. comp. Zool. Harv.* 89, no. 3: 63–144.

GATES, G. E. 1959. On a taxonomic puzzle and the classification of the earthworms. *Bull. Mus. comp. Zool. Harv.* 121, no. 6: 229–261.

GAVRILOV, K. 1952. Sobre *Eukerria saltensis* (Beddard) y su reproducctión. *Acta zool. lilloana*, 10: 673–716.

GERARD, B. M. 1964. Synopses of the British Fauna, no. 6, Lumbricidae. Linnean Society of London: 1–58.

HARRISON, and A. D. ELSWORTH, J. F. 1956. Hydrobiological Studies on the Great Berg River, Western Cape Province. Report No. 1. General description, chemical studies, main features of the flora and fauna. South African C.S.I.R., Pretoria.

JACKSON, A. 1931. The Oligochaeta of South-Western Australia. *J. Proc. R. Soc. West. Aust.*, 17, 1930–1931, 4: 71–136.

KHALAF EL-DUWEINI, A. 1940. The anatomy of *Allolobophora caliginosa* (Savigny) f. *trapezoides* (Dugès). *Bull. Fac. Sci. Egypt. Univ.*, 21, 1940: 61–151.

MICHAELSEN, W. 1890. Beschreibung der von Herrn. Dr. Franz Stuhlmann im Mundungsgebiet des Zambesi gesammelten Terricolen. *Mitt. naturh. Mus. Hamburg*, 7: 3–50.

MICHAELSEN, W. 1898. Die Oligochaeten der Sammlung Plate. *Zool. Jb. Syst.* Suppl. 4 (Fauna Chilensis): 471–480.

MICHAELSEN, W. 1899. Terricolen von verschiedenen Gebieten der Erde. *Mitt. naturh. Mus. Hamburg*, 16: 1–22.

MICHAELSEN, W. 1900. Oligochaeta in Das Tierrich, 10, Berlin. Friedländer und Sohn.

MICHAELSEN, W. 1907. Oligochaeten von Australien. *Abh. naturw. Ver. Hamburg*, 19: 1–25.

MICHAELSEN, W. 1908. Oligochäten aus dem westlichen Kapland. *Denkschr. med.-naturw. Ges. Jena*, Bd. 1, Syst. Tiergeog. 26: 31–43.

MICHAELSEN, W. 1910a. Oligochäten von verschiedenen Gebieten. *Mitt. naturh. Mus. Hamburg*, 27, 2: 47–169.

MICHAELSEN, W. 1910b. Zur Kenntnis der Lumbriciden und ihrer Verbreitung. *St. Petersburg Ann. Mus. Zool.* 15: 1–74.

MICHAELSEN, W. 1913a. Oligochäten vom tropischen und südlichsubtropischen Afrika. Tl. 1. *Zoologica, Stuttg.*, 67: 139–170.

MICHAELSEN, W. 1913b. Oligochäten vom tropischen und südlichsubtropischen Afrika. Tl. 2. *Zoologica, Stuttg.*, 68: 1–63.

MICHAELSEN, W. 1913c. The Oligochaeta of Natal and Zululand. *Ann. Natal Mus.*, 13: 397–458.

MICHAELSEN, W. 1913d. Report upon the Oligochaeta in the South African Museum at Cape Town. *Ann. S. Afr. Mus.* 13: 43–62.

MICHAELSEN, W. 1913e. Die Oligochäten von Neu Caledonien und den benachbarten Inselgruppen. In *F. Sarasin* and *T. Roux, Nova Caledonia, Zoologie*, Bd. 1, H.3. Wiesbaden. C. W. Kreidel.

MICHAELSEN, W. 1913f. Die Oligochäten des Kaplandes. *Zool. Jb. Syst.* 34: 473–556.

MICHAELSEN, W. 1914. Oligochaeta. In *Beitrage zur kenntnis der Landund Susswasserfauna Deutsch-Südwestafrikas.* 1, Hamburg. L. Friederichsen & Co.

MICHAELSEN, W. 1935. Earthworms from south-western Australia. *J. Proc. R. Soc. West. Aust.*, 21: 39–43.

OMODEO, P. 1952. Cariologia dei Lumbricidae. *Caryologia* 4 2: 173–275.

OMODEO, P. 1956. Contributo alla revisione dei Lumbricidae. *Archo Zool. ital.*, 41: 125–212

OMODEO, P. 1957. Lumbricidae and Lumbriculidae of Greenland. *Meddr. Grnland Komm. vid.*, 124, 6: 1–27.

PICKFORD, G. E. 1928. Synonymy in the genus *Kerria* (Oligochaeta, Ocnerodrilinae). *Ann. Mag. nat. Hist.* (ser. 10) 2: 378–382.

PICKFORD, G. E. 1937. *A Monograph of the Acanthodriline Earthworms of South Africa.* Cambridge. Heffer.

POOL, G. 1937. *Eiseniella tetraedra* (Sav.), Beitrag zur vergleichenden Anatomie und Systematik der Lumbriciden. *Acta zool.* Stockholm 18: 1–110.

POP, V. 1947. Lombriciens de la Corse. *Archs. Zool. exp. gén.*, 85, 1: 1–18.

ROSA, D. 1884. I Lumbricidi del Piemonte. Torino (cited by Omodeo, 1956).

ROSA, D. 1893. Revisione dei Lumbricidi. *Memorie Accad. Sci. Torino*, ser. 2, 18: 399–476.

SAVIGNY, J. C. 1826. In Cuvier, G. Analyse des travaux de l'Académie royale des Sciences pendant l'année 1821, partie physique. *Mém. Acad. r. Sci. Inst. France*, 5: 176–184.

SMITH, F. 1924. The Calciferous Glands of Lumbricidae and Diplocardia. *Illinois Biological Monographs*, 9, no. 1: 1–54.

SWEET, G. 1903. On the Structure of the Spermiducal Glands and Associated Parts in Australian Earthworms. *J. Linn. Soc.*, 28: 109–139.

STEPHENSON, J. 1930. *The Oligochaeta.* Oxford. Clarendon Press.

TÉTRY, A. 1937. Révision des Lombriciens de la collection de Savigny. *Bull. Mus. Hist. nat.*, Paris, 9 (ser. 2): 140–155.