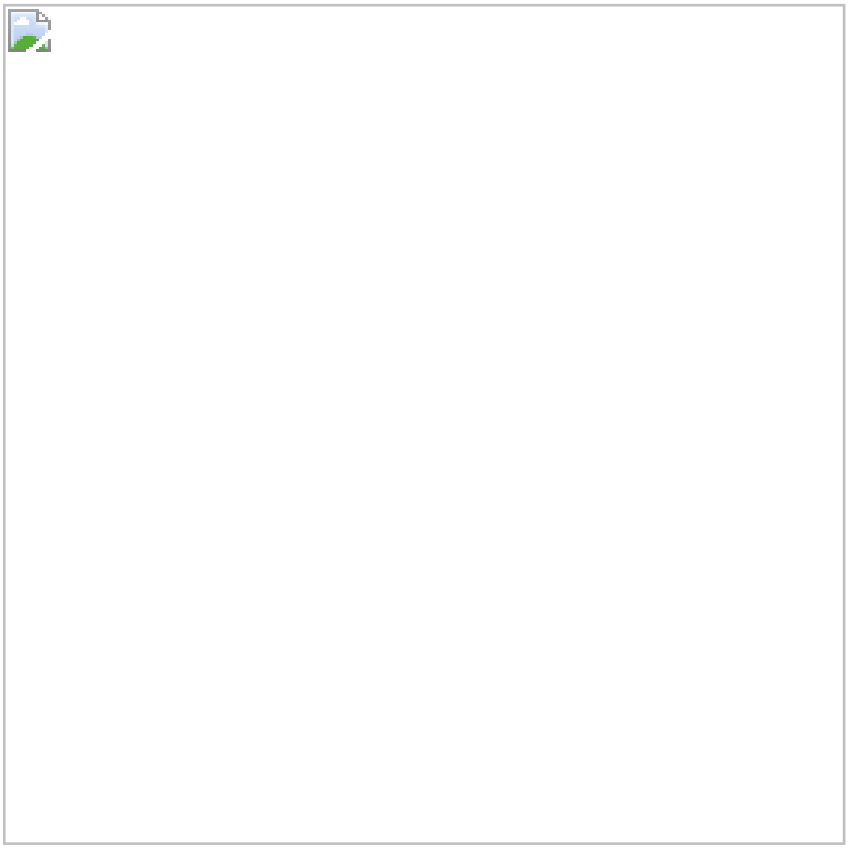

A New Family Tritogeniidae for the Genera Tritogenia and Michalakus, Earlier Accredited to the Composite Microchaetidae (Annelida: Oligochaeta)

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A new family Tritogeniidae for the genera *Tritogenia* and *Michalakus*, earlier accredited to the composite Microchaetidae (Annelida: Oligochaeta)

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ABSTRACT

Two genera, *Tritogenia* Kinberg, 1867 and *Michalakus* Plisko, 1996, are separated from the composite family Microchaetidae Beddard, 1895 (s.l.), and the Tritogeniidae fam. nov. is erected to accommodate them. The genera *Microchaetus* Rapp, 1849, *Geogenia* Kinberg, 1867, *Proandricus* Plisko, 1992, and *Kazimierzus* Plisko, 2006, are left in the Microchaetidae (s. str.). The diagnoses for both families as they now stand are given and keys to all the genera are provided. Species accredited to the Tritogeniidae fam. n. are listed, and distribution of *Tritogenia* and *Michalakus* is discussed. Revision of *Tritogenia zuluensis* (Beddard, 1907) is advised.

KEY WORDS: Oligochaeta, indigenous megadriles, earthworms, South Africa, new family.

INTRODUCTION

The taxonomic history of the South African megadriles accredited to the composite family Microchaetidae and its genera has a complex and sometimes confused record. Attention was first paid to indigenous earthworms in South Africa by Rapp (1849), who described *Microchaetus microchaetus* from the Cape (a locality name that was later doubtfully understood to be the Cape Peninsula). Two species, *Geogenia natalensis* and *Tritogenia sulcata*, collected in Port Natal (= Durban, KwaZulu-Natal), were subsequently described by Kinberg (1867). The evident external differences observed between the large-sized (*ca* 1900 mm) *microchaetus*, known from the southern part of the country, and from a distant locality, *natalensis*, which is of moderate size (85 mm), and also a very small, compact (55 mm) *sulcata*, confused the researchers who attempted to allocate these species and their genera at the higher taxonomic level. After short debates (Beddard 1884, 1886*a*, 1891, 1895; Perrier 1886; Benham 1888), all these taxa were placed to Microchaeta (the group proposed for the known (at that time) South African endemics, other than acanthodrilines), and later recognized as the family Microchaetidae. A 'calm' suggestion regarding the separation of *T. sulcata* from the other microchaetids, with a proposal for its affiliation to the Eudrilinae (suggesting Megachaeta) by Beddard (1886*a*) and Michaelsen (1891*a*) was not considered, even by the authors in their subsequent publications. Information on a specimen similar to *sulcata* and named by Benham (1888) as *Brachydrilus* [sp.] was not noticed until Michaelsen's (1900) redescription as *Brachydrilus benhami*, and only later was it placed in synonymy with *Tritogenia* (Michaelsen 1918: 332). New microchaetid species added by Rosa (1891, 1893, 1897, 1898), Benham (1892) and Michaelsen (1899) were placed in the genus *Microchaetus,* indicating assignment to 'Microchaeta', Geoscolecidae or Glossoscolecidae (Perrier 1886; Beddard 1886*a*; Benham 1886*a–c*, 1890, 1892; Vaillant 1890; Michaelsen 1891*a*, 1899), and to the Microchaetidae Beddard 1895 or later

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Microchaetinae. During the years that followed, some of the non-South African genera (*Alma* Grube, 1855; *Brachydrilus* Benham, 1888; *Glyphidrilus* Horst, 1889; *Callidrilus* Michaelsen, 1890; *Kynotus* Michaelsen, 1891*b*; and *Drilocrius* Michaelsen, 1918) were included in the subfamily Microchaetinae together with *Microchaetus*, *Geogenia* and *Tritogenia*. After synonymy of *Brachydrilus* with *Tritogenia* and withdrawal of the foreign genera from the Microchaetinae, only the South African endemics *Microchaetus*, *Geogenia* and *Tritogenia* were left. In subsequent years, more species were described, but all were placed in *Microchaetus* (Rosa 1891, 1893, 1897, 1898; Michaelsen 1902, 1907, 1908, 1913, 1933; Beddard 1907; Sciacchitano 1960; Pickford 1975). The description of *Tritogenia morosa* by Cognetti de Martiis (1906) with well-defined specific and generic characters was censured by Michaelsen (1908: 41) and the species sent to synonymy with *sulcata* (Michaelsen 1918: 338) until its resurrection and confirmation of *Tritogenia* validity (Michaelsen 1928*b*: 108) and allocation of its five species.

Further study on the South African microchaetids resulted in the discovery of more new species, all of which were placed in *Microchaetus*. However, Reinecke and Ryke (1969) described a new species, *lesothoensis*, in *Geogenia* (it was later transferred by Plisko (1994) to *Proandricus*). Plisko & Zicsi (1991) and Plisko (1992, 1997) paid attention primarily to the genus *Tritogenia*, redescribing it and adding new taxa. Plisko (1991, 1992, 1993*a*, *b*, 1994, 1996*b*, 1998) enlarged the number of species in *Microchaetus* and described two new genera (*Proandricus* in 1992 and *Michalakus* in 1996*a*). During the past few decades, more new species have been described in *Microchaetus* and *Proandricus* (Plisko 2000, 2002*a*, *b*, 2003, 2005); and to the known genera, the new *Kazimierzus* Plisko, 2006 was added; *Geogenia* was reinstated (Plisko 2006*b*); and the value of the features applied in microchaetid taxonomy was debated (Plisko 2006*a*, 2009, 2012). At the time that this paper was written, there were 136 species in the family Microchaetidae, all indigenous to the southern part of the African continent and accredited to six genera, namely: *Microchaetus* Rapp, 1849 (8 species), *Geogenia* Kinberg, 1867 (21 species), *Proandricus* Plisko, 1992 (50 species), *Kazimierzus* Plisko, 2006 (21 species), *Tritogenia* Kinberg, 1867 (35 species), and *Michalakus* Plisko, 1996 (1 species).

Considering the earlier history surrounding the misleading omission of the generic characters of *Tritogenia*, their taxnomic value and the distinct correlation between a cluster of specific characters, the position of the genus *Tritogenia* and its species was looked at more closely. The distinctive characteristics of *Tritogenia* are re-established to their correct importance and used to support the taxonomic validity of the genus. Closer evaluation of these features and assessment of the genera accredited to the Microchaetidae revealed family-related inconsistencies, and the familial taxonomic position is discussed. There are features of *Tritogenia* and *Michalakus* that are evidently exclusive, differing from those in the other four genera. The original and subsequent descriptions of the type species were re-considered and broadened by the observations made on the type and new material. It was also noted that although the apparent generic characteristics were observed earlier, inadequate attention was paid to them.

The present assessment of the diagnostic features observed in the genera accredited to Microchaetidae (s. l.) was based on: the excretory system; the gizzard(s)—how many there are and their location; the dorsal blood vessel—whether or not it has an enlargement in some of its anterior segments; the septa—whether or not they are enlarged in some

of the anterior segments; and the setae—their location. Other characters that were also considered are body size, shape, peculiarity of bodily contraction; and the total number of segments found. After comparative validation, selected features were accepted as diagnostic at the family level. The species accredited to *Tritogenia* and *Michalaku*s were found to share certain characters, and a new family Tritogeniidae is erected to accommodate them. The other genera, viz. *Microchaetus*, *Geogenia*, *Proandricus* and *Kazimierzus* are left in the family Microchaetidae (s. str.).

A history of taxonomic publications dealing with *Tritogenia* and *Michalakus* can be summarised as follows:

Kinberg (1867: 97–98), working on the earthworms deposited at the Royal Museum of Natural History in Stockholm that were collected by J.A. Wahlberg in the area of Port Natal (= Durban, KwaZulu-Natal), described *Tritogenia* with *T. sulcata*, writing: '*Genera hic descripta...: Setae, junioribus exceptis, segmenti cujusque ... 6 ... Tritogenia, ... TRITOGENIA n. Lobus cephalicus transversus, brevis, longitudinaliter striatus; setae corporis anterioris dorsuales singuae, ventrales binae, corporis posterioris nullae; tuberculum ventrale singulum.* T. sulcata *n. Segmenta 80, plurima biannulata; tuberculum ventrale segments 17–19 praebens; longitude 55 mm*' [Genera described here: … 6 setae in each segment, juveniles excepted ... *Tritogenia ... Tritogenia* n. [gen. n.]: Prostomium transverse, short, longitudinally striated; dorsal setae of anterior body region single, ventral setae doubled, no setae in posterior body region; ventral tuberculum single. *T. sulcata* (sp. n.): 80 segments, most segments biannulate; tuberculum ventral, present in segments 17–19, length 55 mm].

Perrier (1886: 875) inspected the *sulcata* type material, but did not provide accurate species description, although he corrected Kinberg's statement: 'six setae per segment', to eight setae; also noting that the specific shape and size of the body differed significantly from the other species (*microchaetus* and *rappi*, discussed by Beddard (1884)). The generic status of *Tritogenia* was re-confirmed.

Beddard (1886*a*: 63, 1886*b*: 306) followed the name 'Microchaeta' proposed by Perrier (1886) for the two South African earthworms known at that time, viz. *M. microchaetus* Rapp, 1849 and *M. rappii* Beddard, 1886, but did not include *Tritogenia sulcata* Kinberg, 1867.

Benham (1886*a*: 216, 219, 242, 1886*c*: 100) debated Beddard's omission of *Tritogenia sulcata* from the 'Microchaeta' (with no conclusion concerning its generic status mentioned), also Perrier's correction of Kinberg's 'six setae per segment' to eight setae, and commented on the absence of the clitellum in *Tritogenia*.

Benham (1888: 72) reported on a specimen from an unknown type locality, with two pairs of nephridia per segment and the gizzard in segment 6, and named it *Brachydrilus* [sp.]. This information was debated by Benham (1890) and Michaelsen (1900), suggesting similarity to *Tritogenia*, although these genera only later accepted as synonyms by Michaelsen (1918) and Stephenson (1930), and consequently by other authors.

Benham (1890: 306–308) remarked on the similarity of *Brachydrilus* [sp.] to other 'Microchaeta' species. The attached figures clearly showed two pairs of nephridia, the gizzard in segment 6, and holandry as the generic characters for *Brachydrilus*, although a pair of spermathecae in 12/13 was evaluated as being

in an 'abnormal position'. These descriptions (Benham 1888, 1890), later discussed by Michaelsen (1918), confirm meronephridial occurrence in the species accredited to *Brachydrilus*.

Michaelsen (1891*a*: 57) considered *Tritogenia sulcata* characteristics to be divergent from those observed in other microchaetids and debated *sulcata*'s relationship with the Eudrilinae (possibly with species of the genus *Megachaeta*), although later (1899: 415) he did not support it.

Beddard (1895: 573, 624, 664) discussed the taxonomic position of the South African earthworm species accredited earlier to the 'Microchaeta', placed in the Geoscolecidae at the subfamilial level Microchaetinae, although he also used the family name Microchaetidae (p. 664). The genus *Tritogenia*, with its species *sulcata*, was disputed: '*In addition to the genera of which adequate descriptions exists, there are a few of the worms so imperfectly described by Kinberg, which may possibly belong to the same family* [Glossoscolecidae] *and these are* Tritogenia *and* Geogenia.' The above declaration reflected an unclear systematic position of *Tritogenia* in 'Microchaeta' that persisted for many years.

Michaelsen (1899: 415–420) revised the *sulcata* type material under the generic name *Tritogenia*, accrediting it to the 'Microchaeta-Forms' group. He pointed out that the excretory system differs from that of known microchaetids: '*Auch von den Nephridien sind nur noch Spuren vorhanden. Trotzdem lässt sich die systematische Stellung der Art genau feststellen, und auch die noch erkennbaren artlichen Charaktere sind zur Wiedererkennung der Art vollkommen ausreichend.*' [And also the nephridia are present only as rudiments. It is nevertheless possible to establish the exact systematic position of the species, and the species-level characters that can still be recognized, and are entirely sufficient to recognize the species.] The comprehensive descriptions of the external and internal characters clearly revealed the specific status of this species, although the location of septa 6/7 and gizzard in segment 7 were mistakenly noted. Subsequently, this led to erroneous characterization of the genus *Tritogenia* (Michaelsen 1900), and an assessment that resulted in placement of a few other *Tritogenia* species (Michaelsen 1902, 1913) in *Microchaetus*. It should be noted that location of the gizzard in segments 6 and 7, with a thickened septum 6/7 attached to part of the gizzard, occurs in the South African species characterized by other generic *Tritogenia* features. The fact that these characters were overlooked in generic diagnosis led to incorrect evaluation of *Tritogenia* as a genus for a number of years, and also to inaccurate descriptions of some new species later (*howickianus* and *griseus*).

Michaelsen (1900: 447–454, 462) redescribed *Brachydrilus* sp. as *B. benhami* (p. 462), the only species in this genus. Unfortunately, its similarity to *Tritogenia* was not perceived. The genus *Tritogenia* was accepted for *sulcata* and placed, together with *Microchaetus*, *Kynotus*, *Callidrilus*, *Geogenia*, *Brachydrilus* and *Glyphidrilus*, in the subfamily Microchaetinae under Glossoscolecidae. Diagnostic characters for *Tritogenia* were limited to those observed only in *sulcata*, with the location of the gizzard erroneously given as being in 7. Moreover, the occurrence of nephridial pores was likewise incorrectly stated. The earlier, incomplete species redescriptions (Beddard 1895; Michaelsen 1899) and inaccurate data

supplied by Michaelsen (1900), together with overall existing knowledge of microchaetids that was generally inadequate, cast doubt on the validity of this genus for many years.

Michaelsen (1902: 33) described *Microchaetus griseus*, focusing on external characters, mainly the annulation and position of setae, omitting a description of the excretory system and dorsal blood vessel, although observing the much-thickened septa 5/6–8/9, and a gizzard in segments 6–7. (For a redescription and transfer of this species to *Tritogenia*, see Plisko & Zicsi 1991: 121.)

Cognetti de Martiis (1906: 601), in describing *Tritogenia morosa*, evidently portrayed morphological characters, accepting resemblance to and differences from *sulcata.* A note '*Non potei rintracciare i nefridiopori*' [I could not find the nephridiopores] (p. 602) drew attention to the characteristic absence of nephridial pores in *Tritogenia*.

Beddard (1907: 297) and Michaelsen (1907: 6) almost simultaneously described *Microchaetus zuluensis* and *M. zulu*, respectively. Both authors indicated a proandric condition (later not confirmed) and did not observe nephridia. Michaelsen (1913: 437) accepted Beddard's priority for *zuluensis*, making his *zulu* synonymous therewith.

Michaelsen (1908: 32), when referring to his earlier published (1891, 1899, 1900) data on *Tritogenia sulcata*, incorrectly synonomized *T. morosa* Cognetti de Martiis, 1906 with *sulcata*.

Michaelsen (1913: 431–436), after a second revision of the *T. sulcata* type material, redescribed it as *Microchaetus sulcatus* f. *typicus*. For the new material, collected from a locality over 100 km away, he gave the name *M. sulcatus* var. *howickianus*. The species descriptions, besides well designated, important external and internal characteristics, include the description that: '*The dorsal* [blood] *vessel is single in the middle portion of the body ... it is double in segments 11–9. The doubling is complete, there being no union of the two vessels at the septa. ... Excretory organs consist of small meganephridia*'. This observation highlighted certain characters occurring in *sulcatus* and *howickianus*, although the excretory system, named as 'small meganephridia' [two pairs] would be referred to as '*sehr klein*' [very small] later by Michaelsen (1918: 336). However, Michaelsen overlooked the fact that these characteristics are specific to the *Tritogenia* species [*sulcata* and *morosa* at that time], as well as to the revised type species, *sulcata*, with its variation *howickiana*, thus erroneously locating it in *Microchaetus*.

Michaelsen (1918: 332), in synonymizing the genus *Brachydrilus* under *Tritogenia*, accepted duplication of nephridia as the exclusive generic character for this genus, and wrote '*... vor allem die Verdoppelung der Nephridien (2 Paar in einem Segment). Dieser Charakter, einzig in der Fam. Lumbricidae s.l. dastehend, ist so hervorragend, daß er eine generische Sonderstellung seiner Träger verlangt.*' [… above all, the duplication of nephridia (2 pairs in one segment). This character, unique in the family Lumbricidae s.l., is so outstanding that it requires a separate generic position of its holders.]. He moved the South African species *sulcata* and *morosa* (resurrected from synonymy) to *Tritogenia*, as well as *Brachydrilus benhami*, of unknown provenance, and raised *howickiana* to species level. To this genus he also added his new species *T. crassa*, which was

described on a single, not fully mature specimen with no clitellum, having two pairs of nephridia per segment, with the gizzard in segment 7(!), and a single dorsal blood vessel. Plisko and Zicsi (1991), after examination of two fragments of the type material, declared *crassa* to be of doubtful validity because of the described characteristics: the position of the gizzard (in 7) and of the dorsal blood vessel (single) conflicted with the then-established diagnosis for *Tritogenia*. No similar earthworm specimens have been collected in the meantime.

Michaelsen (1928*a*: 7) described *Microchaetus melmothanus*, with the gizzard in segments 6–7 (characteristic for *Tritogenia*), although not observing nephridia. Reynolds and Cook (1976: 135) recorded this species under *Tritogenia*. (Plisko (1992) revised the type material.)

Michaelsen (1928*b*: 107) placed *Tritogenia* in the Microchaetidae, together with the other terrestrial genera *Microchaetus*, *Geogenia* and *Kynotus*, and the aquatic *Alma*, *Glyphidrilus*, *Callidrilus*, and *Drilocrius* (some of the these genera later, at different times, were raised to family level after consideration of various generic characters). The excretory system for *Tritogenia* was described as following: '*... Exkretionsorgane in der Regel meganephridisch, bei Tritogenia 2 gleichartige Meronephridien an Stelle eines Meganephridiums.*' [Excretory organs [in Microchaetidae] usually meganephridial; in *Tritogenia* two meronephridia of similar type in place of one meganephridium]. No similar meronephridia were noted in other genera, either aquatic or terrestrial, including *Microchaetus, Geogenia* and *Kynotus*. Five species, namely *sulcata*, *benhamia*, *morosa*, *howickiana*, and *crassa*, were placed in *Tritogenia*.

Stephenson (1930: 899–903), following Michaelsen (1928*b*), accepted the synonymy of *Brachydrilus* with *Tritogenia*, and placed *benhami*, *sulcata*, *morosa*, *howickiana*, and *crassa* in *Tritogenia*, in the Microchaetinae (under Glossoscolecidae), justifying this by drawing attention to generic characters, namely: '*... more than one pair of nephridia small and fairly simple in constitution ...*' (p. 235).

Brinkhurst & Jamieson (1971: 740): In the authors' understanding, *Tritogenia* was a member of the tribe Microchaetini of the subfamily Glossoscolecinae in the broadly-defined family Glossoscolecidae. No clear comprehension of the taxonomic position for this and of the other taxonomic units was apparent. For *Tritogenia*, the 'reduplicated nephridia' were mentioned, with no broader evaluation of their taxonomic value.

Reynolds & Cook (1976: 62) followed Michaelsen (1928*b*) in placing *Tritogenia* into the Microchaetidae. They erroneously attributed Michaelsen's authorship to *Microchaetus zuluensis* (p. 192), which was corrected by Plisko (1992).

Plisko & Zicsi (1991: 111–123) redescribed the genus *Tritogenia* and added five new species: *curta*, *karkloofia*, *kruegeri*, *mucosa*, *shawi*. Type material of *sulcata* var. *howickiana* was revised, and the species status of *howickiana* was confirmed. After a revision of *Microchaetus griseus* type material and some other newly collected samples, this species was transferred to *Tritogenia*. A small fragment of the oesophagus and calciferous gland of the *Tritogenia crassa* type specimen, kept in the Zoological Museum in Hamburg, has been found unsuitable for a revision. A single dorsal blood vessel and a gizzard location in segment 7 given in the original description could not be found in the existing fragment. The

description not being in accord with *Tritogenia* generic characters resulted in species placement in this genus not being confirmed. As no new material was known, *crassa* was considered to be a *species inquirenda*.

Plisko (1992: 366–375) emended *Tritogenia*, and commented on *Brachydrilus benhami*: '*because no type material* [for *B. benhami*]*, no new material known, the taxonomic position of this species cannot be established*' (p. 367). Considering that no material is available and the type locality is unknown, it is not possible to define the systematic position of *B. benhami.* Accordingly, it was placed as a *species inquirenda*. The description of *Microchaetus zuluensis* and new material collected in the vicinity of the type locality was reviewed, and the species transferred to *Tritogenia*. Paratype material of *Microchaetus melmothanus* was studied, meronephridia noted, and the species was transferred to *Tritogenia*. Furthermore, a key for the 13 species then known, viz. *crassa*, *curta*, *grisea*, *howickiana*, *karkloofia*, *kruegeri*, *melmothana*, *mucosa*, *ngomensis*, *shawi*, *sulcata*, *zuluensis*, and *B. benhami*, was given. The species name *zuluensis* was incorrectly printed as *zululensis* but was later corrected by Plisko (1997).

Plisko (1996*a*: 287–293) erected a new genus, *Michalakus*, for the only species, *Michalakus initus* Plisko, 1996; the new genus shared a complex of *Tritogenia*'s generic characteristics but differed by having two gizzards. For reasons of similarity, a relationship of this genus to the Hormogastridae was suggested, but this notion was later retracted (Plisko 2006*a*).

Plisko (1997) described 18 new *Tritogenia* species: *alveata*, *annetteae*, *ataxia*, *curiosa*, *diversa*, *douglasi*, *herbana*, *insolita*, *koilia*, *liversagei*, *lunata*, *miniseta*, *monosticha*, *ngelensis*, *palusicola*, *silvicola*, *soleata*, *turneri*, and a key for 31 species was provided. New characters were added and their taxonomic value discussed. The position of spermathecae and their pores were used as criteria for species-groups assemblage. The questionable taxonomic position of *Tritogenia* in the Microchaetidae was emphasized.

Plisko (2003: 308–321, 2005: 112) added new *Tritogenia* species: *debbieae*, *hiltonia*, *qudeni*, *tetrata*.

Plisko (2005: 112) described *T. phinda*, exceptional in this genus for spermathecae located in intersegmental furrows 9/10, 10/11.

Plisko (2006*a*) discussed the systematic position of *Tritogenia*, its relationship with *Michalakus*, and systematic position of both genera in Microchaetidae (s.l.).

Plisko (2006*c*) listed *Tritogenia* type material of the 29 species housed at the Natal Museum.

Plisko (2008) re-assessed the taxonomic position of species constituting *Tritogenia zuluensis* species-group, which resulted in its dissolution. The designation of *Tritogenia crassa* as a *species inquirenda* was confirmed.

James & Davidson (2012: 225) found *Tritogenia lunata* basal to other studied representatives of the Microchaetidae, pointing out the morphological distinctions observed in this genus.

Plisko (2012: 8) debated the position of *Tritogenia* in the Microchaetidae, commenting that expected information from a molecular study might yield positive data confirming that the decision to separate *Tritogenia* and *Michalakus* from the Microchaetidae and place them in a family of their own would be the right one.

A review of the historical and recent taxonomic undertakings concerning the indigenous South African megadriles of the genera *Tritogenia* and *Michalakus*, suggested that this group of 36 species evidently differs from the other members of the family Microchaetidae and deserves a family of their own. Revision of their type material, together with observations made during many years of research on southern African earthworms, prompted systematic reconsideration of the whole family Microchaetidae and accredited genera. The findings and opinions of earlier authors were compared with a new evaluation of the characteristics used for specific and generic determinations in the composite family Microchaetidae (s.l.). Species identification is based primarily on preserved material, but when live earthworms were available, observation of them was taken into account. The geographical distribution of species was also considered, partly in comparison with microchaetid distributional information (which provides an indication of *Tritogenia* and *Michalakus* dispersal) given in the earlier publications of Plisko (2006*a*, 2012). The Microchaetidae (s. str.) as it now stands is characterized here as well, and the clear differences between these two families, Tritogeniidae and Microchaetidae, are set out.

MATERIAL AND METHODS

The studied material covers a wide range of South African Microchaetidae (s.l.) (including type material of *Tritogenia* and *Michalakus* species) housed in the following institutions:

BMNH – The Natural History Museum, London, UK;
NMSA – KwaZulu-Natal Museum, Pietermaritzburg, South Africa;
NHMW – Natural History Museum in Vienna, Austria;
NHRS – Royal Natural History Museum, Stockholm, Sweden;
ZMUH – Zoological Museum in Hamburg, Germany;
ZMUN – Zoological Museum, University of Oslo, Norway.

The following material was examined:

The NMSA collection of Microchaetidae (s.l.), consisting of over 2000 samples, including the type material of 29 species of *Tritogenia* and one species of *Michalakus*. The large Oligochaeta collection was built up mainly by myself with the great help of the late Dr Brian Stuckenberg, Director of the Natal Museum for many years.

Tritogenia sulcata Kinberg, 1867, type material (NHRS 157): the photo of the frail specimen pieces, with small, separated parts of internal organs (Fig. 1), was made available to me by courtesy of Dr E. Sigvaldadóttir. The species was described by Kinberg (1867) and seen by Perrier (1886) and Michaelsen (1899, 1913); and these descriptions are accepted as valid for the species, and type species of the genus *Tritogenia*.

Tritogenia morosa Cognetti de Martiis, 1906, type material (NHMW 4818, registered as 'A.N. 16723 – tipo, *Musei vindobonensis*'): fragments of the type material were examined during my visit to the NHMW in 1994, thanks to Prof. Dr H. Schifter (NHMW).

Microchaetus microchaetus Rapp, 1849, lectotype (designated by Plisko (1999: 272), NHMW 4813, registered as 'A.N. 5525, *Coll. Musei Vindobonensis evertebrata varia*'). The type locality, incorrectly indicated as 'Cap d. Gut. Hoffnung' [=Cape of Good Hope], is probably the Grahamstown area in the Eastern Cape (see Plisko 1999).

Fig. 1. *Tritogenia sulcata* Kinberg, 1867, type material fragments (NHRS 157; photo by E. Sigvaldadóttir).

T. zuluensis (Beddard, 1907), two syntypes (ZMUN), abscised post-clitellarly, labelled '*Microchaetus zuluensis* – Zululand', presently on loan to the NMSA, courtesy of C. Vollev and Ann-Helén Rønning. The material will be redescribed in a separate paper.

Material in the ZMUH: (1) Fragments of the type material of *Tritogenia crassa* Michaelsen, 1918 (ZMUH V-8501): one small piece of the dissected specimen with no internal structures, and a small fragment of the gizzard; both decomposed parts were reviewed by Plisko & Zicsi (1991); loaned by courtesy of P. Stiewe. (2) The holotype of *Tritogenia melmothana* (Michaelsen, 1928) (ZMUH V-10434): abnormally extended, poorly preserved, with missing inner parts; loaned by courtesy of P. Stiewe. The species was redescribed by Plisko (1992) on the basis of two paratypes (NMSA/Olig. 00260). (3) A syntype of *Tritogenia howickiana* (Michaelsen, 1913) (ZMUH V-7658; Fig. 2), designated as the lectotype by Plisko & Zicsi (1991); loaned by courtesy of H. Roggenbuck.

Tritogenia soleata Plisko, 1997, the holotype (BMNH 1893:12:16:3), which had been loaned to me in 1997 for species description, courtesy of M. Lowe.

Fig. 2. *Tritogenia howickiana* (Michaelsen, 1913), lectotype (ZMUH V-7658). Scale bar = 5 mm.

TABLE 1
Characters that distinguish genera in the composite family Microchaetidae (s. l.).

Characters	*Tritogenia* & *Michalakus*	*Microchaetus*	*Geogenia*	*Proandricus*	*Kazimierzus*
Male funnels	Holandric	Holandric	Holandric	Proandric	Holandric / metandric
Excretory system	Meroic	Holoic/V-shaped nephridial bladders	Holoic/V-shaped nephridial bladders	Holoic/V-shaped nephridial bladders	Holoic/J-shaped nephridial bladders
Oesophageal gizzard(s)	Either one or two. One in 6–7; two: one in 6–7, the second in 9	One in 7	One in 7	One in 7	One in 7
Dorsal blood vessel	Double in some pre-clitellar segments, incl. where passing septa	Double in some preclitellar segments, simple where passing septa	Double in some preclitellar segments, simple where passing septa	Double in some preclitellar segments, simple where passing septa	Simple throughout the whole body
Thickened septa	Septa four to five thickened, with obligatorily thickened septum 6/7	Septum 6/7 not thickened	Septum 6/7 not thickened	Septum 6/7 not thickened	Septum 6/7 not thickened
Setae	Minute, in peculiar arrangement, often not noticeable, *cd* sometimes absent	Noticeable, closely or somewhat distantly paired, in four rows	Noticeable, closely or somewhat distantly paired, in four rows	Noticeable, closely or somewhat distantly paired, in four rows	Noticeable, closely or somewhat distantly paired, in four rows
Body size	Small to medium (not exceeding 160 mm)	May reach 1 m; some species more than 2 m	Small to medium, a few species large	Small to medium	Medium-sized
Number of segments	Average 80–100, rarely a few segments more than 100	More than a few hundred; there may be up to 1000	100–400	>100, not exceeding 500	100–500
Body shape	Compact, short	Elongated	Elongated	Elongated	Elongated

The characteristics investigated are as follows: the location of male funnels; the excretory system; the oesophageal gizzards, their appearance and location; features of the dorsal blood vessel; the level of the thickening of the anterior septa; the setae; body shape; dimensions; and the total number of segments. The characters that distinguish genera in the composite family Microchaetidae (s.l.) are shown in Table 1.

Terminology used in this article follows that used in my previous publications. However, it is admitted that in some of my earlier papers, the male funnels were erroneously termed the 'spermiductal funnels', sometimes corrected to 'spermiducal funnels'. Nephridial bladders were previously termed 'caeca' by me, following Brinkhurst and

Jamieson (1971: 57–60). Cited texts in foreign languages were translated into English by Dr R. Schmelz from the University of A Coruña, Spain.

Other acronyms and abbreviations used in this paper: KZN – KwaZulu-Natal Province, South Africa; NMSA/Olig. – NMSA Oligochaeta collection, Pietermaritzburg, South Africa; RSA – Republic of the South Africa.

TAXONOMY

Family **Tritogeniidae** fam. n.

Type genus: *Tritogenia* Kinberg, 1867.

Diagnosis: Body compact, shorter than 160 mm. Number of segments around 80, rarely over 100. Holandric (male funnels in segments 10 and 11), enclosed or free, posterior pair usually smaller than anterior. Two seminal vesicles attributed to segments 10 and 11, the posterior vesicle often smaller than the anterior vesicle. Excretory system meroic; two or more small nephridia per segment (except in some anterior segments, sometimes also absent from a few posterior segments). Oesophageal gizzards: one in 6–7 (*Tritogenia*), or two in 6–7 and 9 (*Michalakus*), the second much smaller and soft. Dorsal blood vessel double in segments 4–10, 11, 12, including when crossing septa; simple posteriad of segment 12. Four or five septa: 4/5–8/9 variably thickened, with septa 6/7 always attached to gizzard at various parts along its length. Setae difficult to see, being minute; on preclitellar segments noticeable only as a few pairs of *cd*, sometimes *ab* on various segments; on 9 and a few following, *ab* setae usually associated with papillae, occasionally extending on a few segments beyond clitellum; on post-clitellar segments eight per segment in four rows located ventrolaterally, although sometimes only *ab* may be noticeable, with *cd* difficult to trace; convergence of *ab* may occur on a few preclitellar segments, divergence postclitellarly.

Description: Unpigmented; live specimens (Fig. 3) whitish or pinkish grey, body plump and compact; when preserved slightly extended, usually 25–100 mm, rarely reaching 150 mm; 3–15 mm wide at segment 10, much wider at tubercula pubertatis. Average number of segments 60–100, seldom exceeding 120. Annulation of pre-clitellar segments present: 1–3 usually simple, 4–9, 10 ringleted, with 2–4 ringlets annulated or not, with an external segmental subdivision characteristic for species. Female pores in 14. Male pores occur variably in clitellar area, although difficult to detect externally.

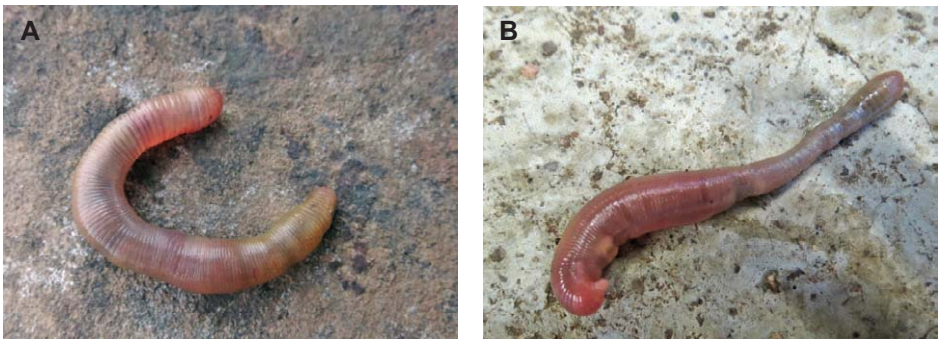
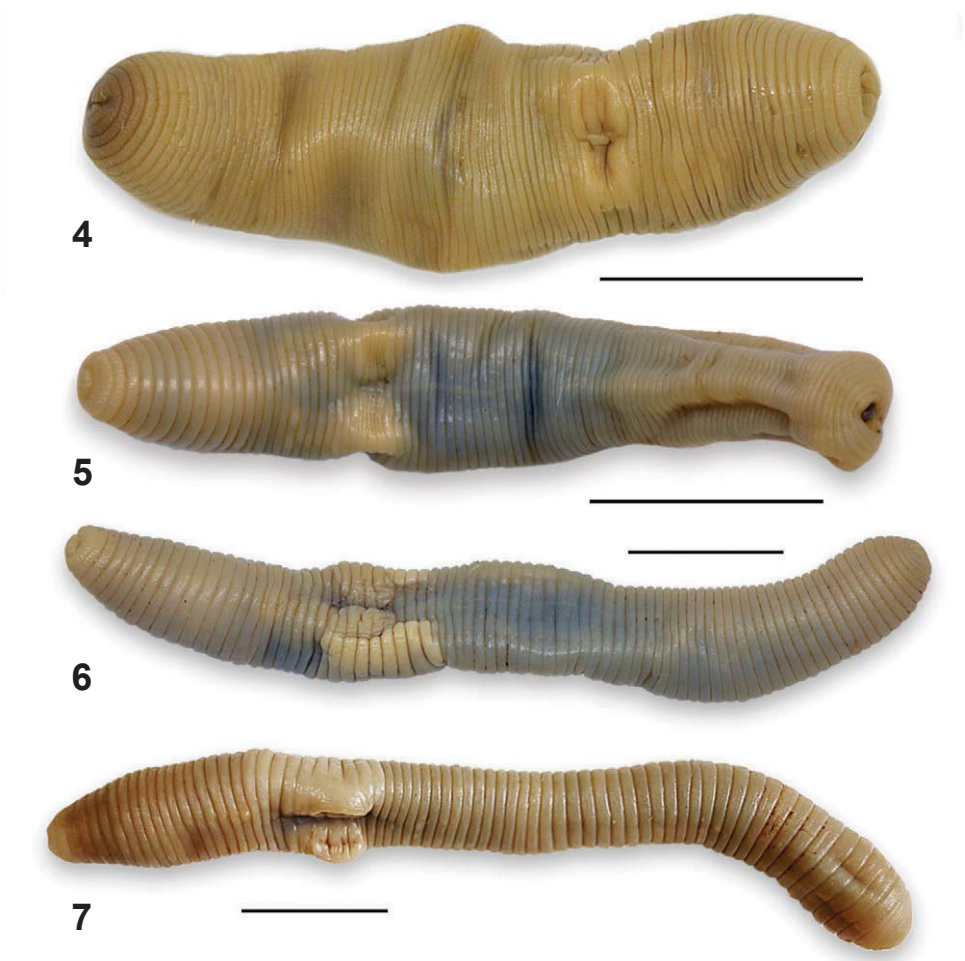


Fig. 3. *Tritogenia* sp., live specimens: (A) juvenile; (B) specimen developing tubercula pubertatis. (Photo by H. Grobler)

Clitellum is saddle-shaped. Tubercula pubertatis variable in shape. Spermathecae small, variably shaped, ampullae elongated, paired or multiple, with pores pretestical, testical, or post-testical; in one to six intersegmental furrows: 9/10–15/16, 16/17. Calciferous glands stalked or not, in segments 9, 10, 9–10. Genital glands variably shaped, either present or not.

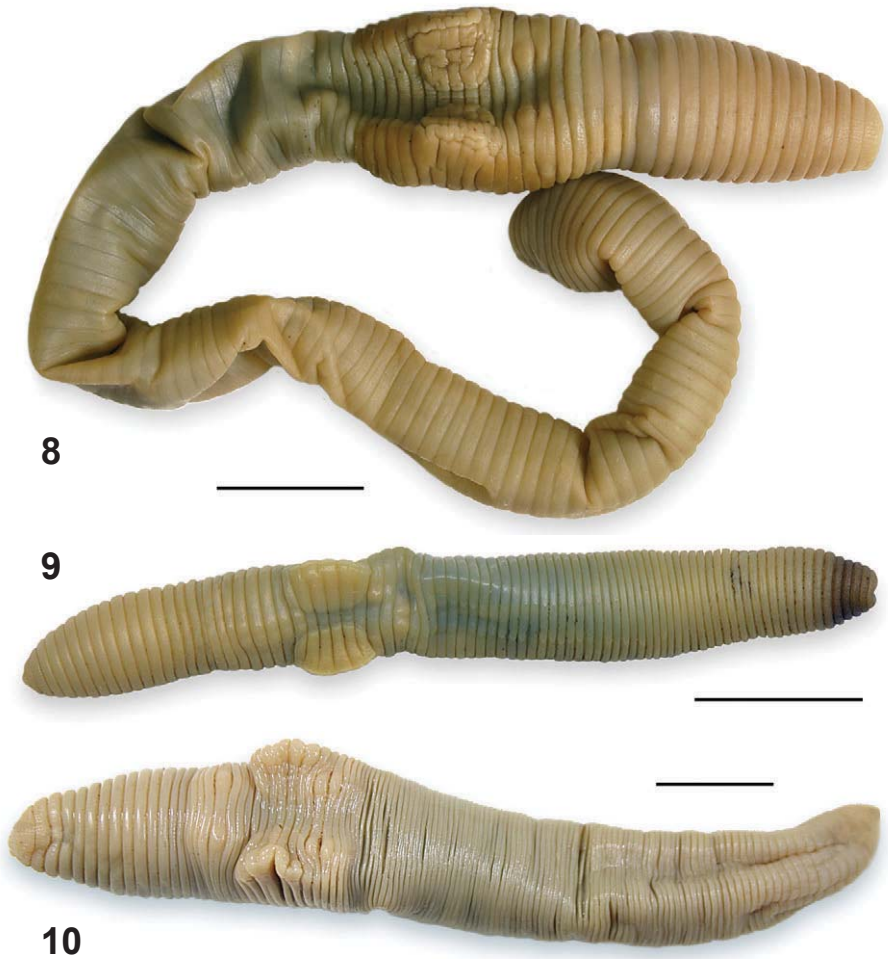
Notes: Although no specific histological study on the musculature of Tritogeniidae species was conducted, it was noted that the external muscle bundles observed under microscopic magnification (usually 150–250×) differ in structure from those in Microchaetidae (s. str.). Future histological examination may shed more light on muscle differences, perhaps also providing an indication of evolutionary lineages for these two families.

Composition: There are two genera in this new family. The genus *Tritogenia* Kinberg, 1867 comprises the following 35 species: *T. alveata* Plisko, 1997; *T. annetteae* Plisko,



Figs 4–7. Paratypes of (4) *Tritogenia curta* Plisko & Zicsi, 1991; (5) *T. hiltonia* Plisko, 2003; (6) *T. insolita* Plisko, 1997; and (7) *T. koilia* Plisko, 1997. Scale bars = 1 cm.

1997; *T. ataxia* Plisko, 1997; *T. curiosa* Plisko, 1997; *T. curta* Plisko & Zicsi, 1991 (Fig. 4); *T. debbieae* Plisko, 2003; *T. diversa* Plisko, 1997; *T. douglasi* Plisko, 1997; *T. grisea* (Michaelsen, 1902); *T. herbana* Plisko, 1997; *T. hiltonia* Plisko, 2003 (Fig. 5); *T. howickiana* (Michaelsen, 1913); *T. insolita* Plisko, 1997 (Fig. 6); *T. karkloofia* Plisko & Zicsi, 1991; *T. koilia* Plisko, 1997 (Fig. 7); *T. kruegeri* Plisko & Zicsi, 1991; *T. liversagei* Plisko, 1997; *T. lunata* Plisko, 1997; *T. melmothana* (Michaelsen, 1928); *T. miniseta* Plisko, 1997; *T. monosticha* Plisko, 1997; *T. morosa* Cognetti de Martiis, 1906; *T. mucosa* Plisko, 1997; *T. ngelensis* Plisko, 1997; *T. ngomensis* Plisko, 1992; *T. palusicola* Plisko, 1997; *T. phinda* Plisko, 2005; *T. qudeni* Plisko, 2003; *T. shawi* Plisko & Zicsi, 1991 (Fig. 8); *T. silvicola* Plisko, 1997; *T. soleata* Plisko, 1997; *T. sulcata* Kinberg, 1867 (Fig. 1); *T. tetrata* Plisko, 2003 (Fig. 9); *T. turneri* Plisko, 1997; *T. zuluensis* (Beddard, 1907) (Fig. 10).



Figs 8–10. *Tritogenia* species: (8) *T. shawi* Plisko & Zicsi, 1991, material from the area adjacent to the type locality; (9) *T. tetrata* Plisko, 2003, paratype; (10) *T. zuluensis* (Beddard, 1907), syntype. Scale bars = 1 cm.

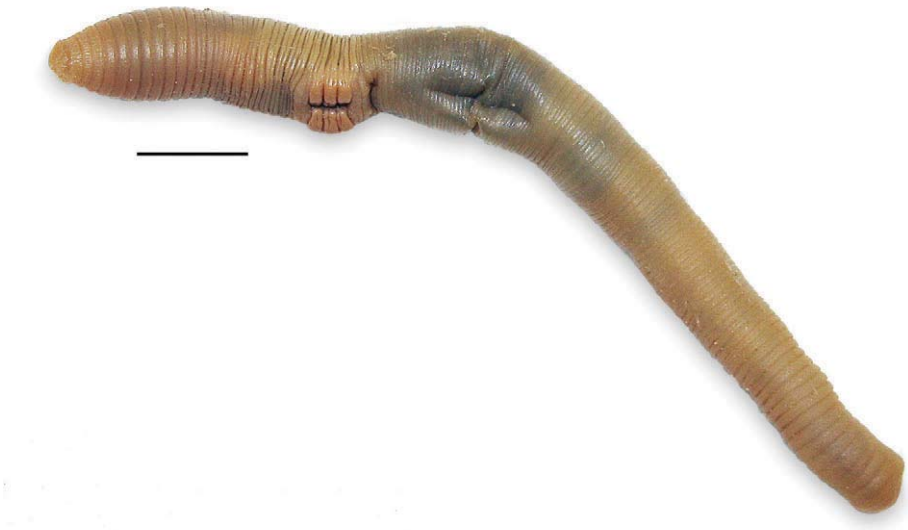


Fig. 11. *Michalakus initus* Plisko, 1996, holotype.

The genus *Michalakus* Plisko, 1996 contains only one species, *M. initus* Plisko, 1996 (Fig. 11).

Species *incertae sedis*: *T. benhami* (Michaelsen, 1900) and *T. crassa* Michaelsen, 1918.

Distribution: Tritogeniidae species are known from a limited area of the north-eastern part of the RSA. *Tritogenia* species have been found at the northern border of the Eastern Cape province, extending through KZN, Mpumalanga and Limpopo, to the Limpopo River as the northern boundary of their diestribution range. However, their occurrence may be expected in neighbouring Botswana, Zimbabwe, Swaziland, and Mozambique. They are distributed from the sea level up to higher altitudes in the Drakensberg escarpments and eastern Soutpansberg range. Although mostly recorded from unpolluted grassland, indigenous bush, and river bank biotopes, some of the species (*zuluensis* and *douglasi*) are to be found in fairly disturbed, contaminated places.

The monotypic genus *Michalakus* has been recorded in a more restricted area in the KZN midlands in the vicinity of the Umgeni River valley, where species of *Tritogenia* have also been encountered. Although *initus*, the sole species of *Michalakus*, has been collected in only a few localities, it could also occur in neighbouring sites.

Discussion: In respect of the majority of the species, evidence of speciation, species endemism and marked restriction to certain ecological conditions are of particular note. At present, with knowledge of the evolutionary history of Oligochaeta still being limited, the idea that the Tritogeniidae have undergone separate evolutionary development during various geological periods is a speculative concept. The characters noted in *Tritogenia* and *Michalakus* differ notably from these observed in species of the Microchaetidae (s. str.). The meroic excretory system, which has been viewed primarily as a generic character for *Tritogenia*, may be considered as homoplasy, being frequently seen in other Oligochaeta. However, its occurrence together with the complex of instantly recognizable characters (Table 2), supports its unambiguous value. Extended study of these

TABLE 2
Diagnostic characters for Tritogeniidae and Microchaetidae (s. str.).

Tritogeniidae fam. n.	Microchaetidae (s. str.)
Male funnels in holandric arrangement	Male funnels in holandric, proandric, or metandric arrangement
Excretory system meroic	Excretory system holoic
Oesophageal gizzard in two segments (6–7) (*Tritogenia*); two gizzards, one in 6–7 and the second in 9 (*Michalakus*)	Oesophageal gizzard always in one segment (7)
Dorsal blood vessel in some preclitellar segments double, including where passing septa	Dorsal blood vessel simple throughout the whole body, or when double in some preclitellar segments, simple where passing septa
Four to five septa enlarged, with obligatorily thickened septum 6/7	Only two, three or four septa variably thickened; septum 6/7 not thickened
Setae minute, in peculiar arrangement, often not noticeable, *cd* absent sometimes	Setae noticeable, closely or somewhat distantly paired, in four rows
Body small to medium (not exceeding 160 mm)	Medium to very large; may reach 1 m, some species over 2 m
Number of segments: 80, rarely a few segments more than 100	Number of segments: usually over 100; may exceed 1000
Body shape compact in life; slightly extended when preserved, although still contracted	Body shape elongated

characters may shed more light on the evolutionary situation as regards the indigenous South African megadriles. Recent data based on selected gene sequences observed in *T. lunata* (James & Davidson 2012) indicate a basal sister-group relationship with the microchaetid species. A follow-up molecular study on the indigenous South African megadriles may elucidate the evolutionary position of the Tritogeniidae.

Key to genera of Tritogeniidae

1 One oesophageal gizzard in segment 6–7 ..... **Tritogenia**
– Two oesophageal gizzards, one in segment 7 extending to 6, large; second gizzard small, soft, in segment 9 ..... **Michalakus**

Genus *Tritogenia* Kinberg, 1867

Figs 1–10

Brachydrilus: Benham 1888: 72 (sp.); Michaelsen 1900: 462 (for *benhami*, with type locality unknown); Michaelsen 1918: 332; Stephenson 1930: 900; Reynolds & Cook 1976: 77 (for *benhami*, with a note 'Typus amissus').

Microchaetus: Michaelsen 1902: 33 (for *griseus*); Michaelsen 1907: 6 (for *zulu* that later became a junior synonym of *T. zuluensis* Beddard, 1907); Michaelsen 1913: 431 (for *T. sulcata* and *T. howickiana*); Reynolds & Cook 1976: 77, 192 (with a note for *griseus* 'Typus amissus', incorrect attribution of Michaelsen's authorship to *zuluensis*.

Type species: *Tritogenia sulcata* Kinberg, 1867. Type material NHRS 157 (Fig. 1). Type locality: [RSA, KZN] 'Port Natal' [= Durban, RSA] (Kinberg 1867: 97).

Diagnosis: Two or more small nephridia per segment (except for three anterior segments, sometimes also missing in a few posterior segments). One oesophageal gizzard in 6–7. Dorsal blood vessel double in segments 4–10, 11, 12; double when crossing septa;

single after segment 10, 11 or 12. Four or five septa variably thickened, with septa 6/7 attached externally and anteriorly to various parts of the gizzard.

Description: Annulation of pre-clitellar segments present; 1–3 usually simple, 4–9, 10 ringleted, with 2–4 ringlets annulated or not, with an external segmental subdivision; first ringlet usually longer than second. Post-clitellar segments may or may not be externally subdivided. Setae: extremely small and irregularly placed; on preclitellar segments, may be recognizable under high magnification (120–250×) and only as a few pairs of *ab* or *cd*; sometimes *ab* seen only on a few segments. As from segment 9, *ab* may be associated with papillae, which occasionally extend on a few segments beyond clitellum. On post-clitellar segments, setae easier to notice, although variably placed; might be in four pairs located mostly ventrally, with *ab* and *cd* paired very closely, or distantly, with *aa* 2–3 times as *bc*; *dd* nearly 0.60–0.70 of U. In some species, *ab* on a few preclitellar segments may slightly converge, diverging postclitellarly. Occasionally *cd* not noticeable, when *ab* easily noted. Papillae and genital glands variably shaped, with segments on/in which they occur varying, occasionally associated with genital setae. Male pores occur variably in the area of tubercula pubertatis, although the pores are difficult to detect externally and are species-specific. Spermathecae small, often deeply embedded in body tissue; variably shaped, paired or multiple; in the majority of species they are close to septa 11/12 and 12/13, although in some species may be located in more segments, sometimes up to six.

Distribution: The genus is known only from a restricted area of the north-eastern part of the RSA, extending from the northern border of the Eastern Cape province through KZN and Mpumalanga and reaching Limpopo province. Occurrence in one or more of the neighbouring countries (Lesotho, Botswana, Zimbabwe, and/or Swaziland) is possible or, in fact, likely.

Genus *Michalakus* Plisko, 1996

Fig. 11

Type species: *Michalakus initus* Plisko, 1996. Holotype NMSA/Olig.00868 (Fig. 11). Type locality: RSA, KZN, Albert Falls (29°28'S 30°27'E), near small stream, grassland, moderately wet soil.

Diagnosis: Two gizzards: one in segment 6–7, large, muscular, with septa attached at ⅓ of its length; second in 9, much smaller than the first, anteriorly muscular, soft posteriorly. Dorsal blood vessel double in 4–11, 12 and when crossing septa 4/5–11/12; single, although thick, in 13 and the following segments. Two pairs of nephridia per segment, noticeable in posterior segments; dorsal pairs with long thin tubes; ventral pairs close to median body line, with shorter tubes. Five variably thickened septa: 4/5–8/9.

Description: Secondary annulation exists in some anterior segments: 1–3 short, simple, with irregular longitudinal grooves; 4–6 with 2 simple ringlets similar in size and appearance; 7–9 with two ringlets, randomly annulated; 10–12 superficially divided into two annuli; clitellar segments dorsally simple, ventrally irregularly annulated; post-clitellar segment simple, randomly annulated. Setae minute, closely paired; first pairs of *ab* visible only under 250× magnification on segment 7; post-clitellar setae larger, easier to observe. Nephridial pores not seen. Female pores in 14, minute openings in front of *ab*. Male pores not detected externally, possibly present in 16, where vasa deferentia

abruptly insert into the body tissues. Clitellum saddle-shaped, segmented, whitish grey, extended dorsally between *ab* setal lines. Tubercula pubertatis below clitellar edges; in live specimen, manifest as glandular swellings; when preserved as three glandular swellings, clearly divided by intersegmental furrows, ventrally separated by distinct field. Papillae present, paired or single, small swellings in *ab* setal lines on some preclitellar and postclitellar segments. Septa: 4/5, 5/6 and 6/7 thickened most, 7/8 and 8/9 thickened less than anterior septa. Spermathecae minuscule with no diverticula, various shapes: ampullae are elongated tubes, bent or serpentine, close to septa 10/11, 11/12 and 12/13, spermathecae paired, or occasionally only two of them at one side.

Distribution: At present, the only known species occurs in the KZN Midlands, although more species may eventually be found in nearby areas.

Family Microchaetidae Beddard, 1895 (s. str.)

Figs 12–14

Type genus: *Microchaetus* Rapp, 1849.

Diagnosis: Body elongated, mature earthworms usually longer than 100 mm (few species slightly shorter, 60–100 mm), often much longer. Number of segments usually more than 100. Holandric (male funnels in 10 and 11) or proandric (male funnels in 10) or metandric (male funnels in 11), enclosed or free. Excretory system holoic; one pair of nephridia per segment (except for three anterior segments); large or medium-sized, tightly coiled loops with elongated nephridial bladders, V-shaped or J-shaped at the ectal end. One oesophageal gizzard in segment 7. Dorsal blood vessel undivided, simple along the whole length, or double anteriorly in 4–9 but simple when crossing septa, and simple posterior to segment 10. Two, three or four anterior septa: 4/5, 5/6, 7/8 and 8/9,

Fig. 12. *Microchaetus papillatus* Benham, 1892, live juvenile specimen. (Photo by A. Armstrong)

Fig. 13. *Kazimierzus* sp., live specimen. Scale bar = 1 cm. (Photo by S. James)

which may be variably thickened. One or two seminal vesicles located in one or two segments: 9, or 9 and 10, or 10 and 11, or extended posteriorly through a variable number of segments, sometimes twisting forwards. Spermathecae variably shaped: ampulae, elongated tubes, bent, serpentine or tightly coiled loops; small or much enlarged; paired or multiple; with pores pretestical, testical, or post-testical; in one to six intersegmental furrows: 9/10–15/16, 16/17. Setae: eight per segment, paired, variably sized; in some species convergent in a few preclitellar segments, diverging postclitellarly.

Description: Live elongated (Figs 12, 13), usually firm; preserved (Fig. 14) slightly stretched or contracted, although not compact. Pigmented or not, variably coloured (with violetish, greyish, greenish, whitish or pinkish grey tint). Body length 60–2600 mm. Number of segments 80–1200. Preclitellar segments variably annulated: 1–3 usually simple, 4–9 ringleted and annulated with 2–4 annuli; external segmental subdivision (annulation) characteristic for species. Female pores on 14, variable in position. Male pores occur variably (species character): pre-clitellarly as from 14/15 intersegmental furrow, clitellarly at tubercula pubertatis. Clitellum saddle-shaped or slightly extended ventrally. Papillae present; variably sized and shaped, usually in line with the ventral setae on some of the preclitellar segments, occasionally extending beyond clitellum on a few segments. Calciferous glands variably shaped, stalked or not, in segment 9, or 9–10, or 10. Genital glands variably shaped and sized, found in various segments.

Composition: *Microchaetus* Rapp, 1849; *Geogenia* Kinberg, 1867; *Proandricus* Plisko, 1992 and *Kazimierzus* Plisko, 2006.

Distribution: Although the southern part of the African continent has been poorly investigated in that a large part of it has not yet been searched for earthworms, it can nevertheless be stated that representatives of this family occur widely, wherever ecological and climatic conditions permit. They are known from the northern part of the RSA, including the vicinity of the Limpopo River, extending to the southern edge of the continent and appearing in all provinces. Microchaetidae are also present in Lesotho and Swaziland, and are likewise expected to occur in the neighboring countries of Botswana, Zimbabwe, and Mozambique. The majority of species have been found at sea level alongside the Indian and Atlantic oceans, and in the Drakensberg mountains, some-

Fig. 14. *Microchaetus vernoni* Plisko, 1992, paratype, entire length 2.6 m.

times at high altitudes. The earthworms live in various biotopes, but their occurrence depends on the soil characteristics, water content, and the climatic conditions. It may, furthermore, be concluded that presently known genera occur in separate territories which, however, overlap slightly (see the generic distributional information published in Plisko 2012). *Kazimierzus* appears in the western part of South Africa along the Atlantic border, although overlapping with *Microchaetus* in the south-eastern part of the Western Cape. *Geogenia* occurs along the Indian Ocean coast, extending to the Drakensberg range; in the south of the RSA, it overlaps with *Microchaetus*, and in the northern areas it co-occurs with *Proandricus*. The genus *Proandricus* has species that are evidently undergoing morphological changes. In a number of localities, it occurs together with *Geogenia*, which often demonstrates some similarity to proandric species. It should be said that species of Tritogeniidae, although occurring partly in the *Geogenia*/*Proandricus* distributional area, usually inhabit environmentally different sites.

Key to genera of Microchaetidae (s. str.)

1 Proandric (male funnels in 10). Holoic, with V-shaped nephridial bladders. Variably sized, from small to large (60–500 mm). Segment number 80–450 .. **Proandricus**

– Holandric or metandric (male funnels in 10 and 11, or only in 11) 2

2 Holandric or metandric (male funnels in 10 and 11, or only in 11); dorsal blood vessel simple throughout the whole body length; excretory system holoic with J-shaped nephridial bladders. Medium-sized (60–250 mm). Segment number 180–450 ..... **Kazimierzus**

– Holandric (male funnels in 10 and 11); dorsal blood vessel double in certain preclitellar segments, simple when crossing septa; excretory system holoic, with large or medium-sized, tightly coiled loops and elongated, V-shaped nephridial bladders .. 3

3 Coiled nephridial loops bushy, very large, V-shaped nephridial bladders widely open. Spermathecae always located posterior to testis, multiple in all or in some of the segments. Very large (550–2600 mm). Segment number usually over 500, may exceed 1200 ..... **Microchaetus**

– Small, bushy loops of holoic nephridia, with V-shaped nephridial bladders. Spermathecae located anterior or posterior to testis, or in testicular segments. Mature individuals small or medium-sized, not reaching 500 mm, with the segment number between 100 and 500.....**Geogenia**

DISCUSSION

After analysis of data obtained from the literature and subsequent evaluation of diagnostic generic/species features, the taxonomic position of the genus *Tritogenia* together with its sister genus *Michalakus* was seen in a new light. It was found that the genus *Tritogenia* has for many years been incorrectly evaluated, despite the fact that the first descriptions of its type species, *Tritogenia sulcata*, even though they were limited to only a few external characters, clearly indicated differences from the other microchaetid species known at that time. Few subsequent inspections of the type material did not result in accurate generic and species portrayal; moreover, particular features attracted attention and there were proposals for its placement in some non-microchaetid taxonomic unit. Nonetheless, an initial suggestion that this species should be included in the Eudrilinae ('Megachaeta') was not considered further, not even by the authors of the proposal. Subsequent, unfortunate placement of *sulcata* in *Microchaetus* and incorrect character evaluation by Beddard (1895) and Michaelsen (1900) added uncertainty to the *Tritogenia* generic position, which it prevailed for years. Michaelsen (1913), who transferred *sulcata* and its 'variation' *howickiana* to the genus *Microchaetus* (following his consecutive species revisions and description of *howickiana* on the basis of new material), ignored a suite of characters that clearly differed from those noted in other microchaetids, namely: the meroic excretory system, gizzard location, peculiarity in location of setae, and a particular body shape. It was only later that Michaelsen (1918), when transferring meroic *Brachydrilus* to synonymy with *Tritogenia*, accepted the excretory system as a generic taxonomic character for some of the South African indigenous earthworms; but he ignored the other typical characteristics. Subsequent researchers followed Michaelsen's errors, and although they noted meroic characteristics as a particular *Tritogenia* generic character-trait, did not link it with the other specific features occurring only in species of this genus (i.e. the gizzard location in segments 6–7; thickened septum 6/7; and the nature of the dorsal blood vessel), and ignored their value as distinctive characteristics. Now that the unique assemblage of characters is recognized as being so distinctive, there can be no doubt that *Tritogenia* is a valid genus, representing the new family. Re-evaluation of the diagnostic features (Table 2) allows upgrading of these to the characteristics of the family, and transfer of two genera from the composite Microchaetidae (s. l.) to the new family Tritogeniidae. Distribution and ecological requirements of the *Tritogenia* and *Michalakus* species fully support their separation from the Microchaetidae (s. str.). The assemblage of characteristics occurring in both these genera, which support the establishment of the Tritogeniidae, are:

(1) The meroic excretory system exclusive to *Tritogenia* and *Michalakus*. (The holoic system is constantly noted in the other four genera left in the Microchaetidae (s. str.): *Microchaetus*, *Geogenia*, *Proandricus* and *Kazimierzus*.)

(2) One gizzard occurring in segments 6–7 in *Tritogenia*; two gizzards in *Michalakus*: one in 6–7 and the second in 9. (In the other genera, there is only one gizzard in segment 7.)

(3) The dorsal blood vessel is double in some preclitellar segments, remaining so when passing the septa. (In the other genera, the vessel is usually simple throughout the whole body; or when it is double in a few preclitellar segments, it is simple where it crosses the septa.)
(4) The thickening of the anterior septa includes four to five septa, always including septum 6/7. (Only two, three, or four septa may be variably thickened in the other genera, with constant exclusion of thickening of the septum 6/7.)
(5) The peculiar setae on preclitellar segments, observed as being extremely minute, often inverted under cuticular tissues, and frequently inconspicuous externally. In some *Tritogenia* species, *cd* is indiscernible. (In other genera, all eight setae are visible on preclitellar segments, being either closely or slightly distantly paired.)
(6) The body shape particularly compact, with the capability of strong contraction of the segments, evidently differing in this respect from the other elongated body shapes noted amongst the microchaetid genera.
(7) The body small to medium, rarely extending to 160 mm in *Tritogenia* and *Michalakus*. (The body is medium to very large, often reaching almost one metre, sometimes more than 2 meters, are observed in the other genera.)
(8) The number of segments: average 80, rarely over 100 in *Tritogenia* and *Michalakus*, whereas in Microchaetidae (s. str.), the number of segments is usually higher, and may exceed 1500.

An earlier suggestion for the exclusion *Tritogenia* and *Michalakus* from the family Microchaetidae was made by Plisko (2006*a*, 2012), with a parallel suggestion concerning possible ancestral differences between these and the rest of microchaetids. Plisko (2012) anticipated that the results of the DNA studies of the South African megadrile species will support this decision. According to the recent molecular phylogeny of megadriles, based on 28S, 18S and 16S gene sequences (James & Davidson 2012), the family Microchaetidae is thought to be mostly related to the Lumbricoidea clade and to be a sister-family of other Lumbricoidea families (as defined by James & Davidson 2012). The authors also noted differences between representatives of *Tritogenia* and other microchaetids (James & Davidson 2012: 225): 'Within the Microchaetidae, *Tritogenia* is basal to the other sampled genera, and is morphologically distinct from other Microchaetidae by having multiple nephridia per segment (meroic) and having an unusually short, thick body form'. It is hoped that additional molecular work on other South African earthworms will reveal more about their relationships, and confirm that the decision to separate these species (with their special characteristics) from other earthworms and place them in the family Tritogeniidae was correct. It should, however, be noted that the monophyly of the Tritogeniidae has not yet been researched.

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