

Notes on the status of the family Microchaetidae

(Oligochaeta)

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Abstract. Short historical overview of the variable taxonomic rank of the family Microchaetidae is given. The dispersal of the South African endemic taxa based on paleo-geological evidence is noted. Present familial status and the generic composition are outlined. A correlation between specific features and the species distribution is indicated. Selected familial and generic diagnostic characters and their plesiomorphic and apomorphic conditions are discussed. The possible relationship between Microchaetidae and other families *sensu* various authors is marked out.

Key words. Microchaetidae, *Microchaetus*, *Geogenia*, *Tritogenia*, *Michalakus*, *Proandricus*, *Kazimierzus*, South Africa, endemic, biogeography.

Introduction

This paper incorporates recent knowledge on the origin of the earthworm fauna and the dispersal directions of the southern African megadrile species accredited to the indigenous family Microchaetidae. With the lack of the fossil earthworm material the most hypotheses on the evolutionary process within Oligochaeta rely on the speculative timing of the tectonic movements and the actual earthworm distribution. The major hypothesis on the creation of the phylogenetic earthworm lineages and the geographical distribution of the ancestral megadrile was discussed by MICHAELSEN (1903, 1922) as the parallel process to the continental drift. In the light of the theory of plate tectonics, the possible evolutionary development and area of origin of Oligochaeta might be similar to that proposed by OMODEO (2000), who suspected that the evolutionary steps began from the most primitive taxa among limicolous/terrestrial forms of the Lumbricoidea, what supposedly took place in the middle of Cretaceous. The ancient Lumbricoidea occurrence may be seen in the area corresponding to the northern and eastern territories of Pangaea. According to OMODEO (2000) the most primitive taxa among Lumbricoidea were limicolous forms and their distribution is noted over a broad territory corresponding to the northern and central regions of the Early Triassic Pangaea. The dispersal might took place over a broad territory to the northern and central regions of the Early Triassic Pangaea as it is shown on the map drawn by OMODEO (2000) (see Fig. 1).

The subsequent evolutionary development and dispersal of the southern African megadrile fauna possibly took place in accordance with the other continental changes. The evolution of the Lumbricoidea appears to have a line in specialization of oesophageal and intestinal regions, development of nephridial bladders, and a modification of the reproductive organs.

Southern part of the African continent and its microchaetids

At various occasions southern Africa has been indicated as one of the richest land in terms of invertebrate biodiversity, with many endemics, and thousands of species to be described. During the last decades a progress on the earthworm knowledge in southern Africa has advanced noteworthy, although it is still in developing phase. The information on megadrile biodiversity richness is still limited although the representatives of two families: Acanthodrilidae and Microchaetidae are known to occur in the soils in South Africa, Lesotho and Swaziland. The microchaetids greatly differ anatomically and ecologically from acanthodrilids and are recognized as indigenous for this part of the African continent. Commonly it is accepted that these two families do not have a 'recent common ancestor'.

Since the description of the first microchaetid by RAPP (1849), two species found by KINBERG (1867) and other 36 species added by BENHAM (1886a,b, 1892), BEDDARD (1886a-b, 1907), ROSA (1891, 1897, 1898), COGNETTI DE MARTIIS (1906), MICHAELSEN (1899, 1902, 1907, 1908, 1913a-b, 1918, 1928a, 1933), BROOCK & DICK (1935), SCIACCHITANO (1960), REINECKE & RYKE (1969) and PICKFORD (1975), the species grouping in a taxon of a higher rank have had a confused record. Similarly the microchaetid approval at family level has had a long evidence of its instability indicated by PLISKO (2006a-b). For decades the microchaetid species collected in southern part of Africa, accredited to *Microchaetus*, *Geogenia* and *Tritogenia*, with inclusion or exclusion of several species known from the other parts of the world, placed in *Alma*, *Callidrilus*, *Drilocrius*, *Glyphidrilus*, *Kynotus*, were assembled under the names Lumbricoidea, Lumbricina, Glossoscolecoidea, Glossoscolecidae, Microchaetinae or Microchaetidae. The suspected relationships between Lumbricidae, Glossoscolecidae and Microchaetidae have been under scrutiny. Numerous efforts, with inclusion or exclusion of the number of genera into these families have been undertaken by many researchers, viz. BENHAM (1890), BEDDARD (1895), MICHAELSEN (1900, 1012, 1928b), STEPHENSON (1930), GATES (1959), BRINKHURST & JAMIESON (1971), REYNOLDS & COOK (1976, 1993), SIMS (1978, 1980, 1982), JAMIESON (1978, 1988), OMODEO (1956, 1998, 2000), and many others. The genera *Kynotus*, *Alma*, *Callidrilus*, *Glyphidrilus*, *Drilocrius*, *Biwardrilus*, *Microchaetus*, *Tritogenia*, *Geogenia* and the recently added *Proandricus*, *Michalakus* and *Kazimierzus* were added, withdrawn, raised to a family level, or transferred to other families, confirming uncertainty of microchaetids at the family level.

During the last two decades, following the earlier discussions, inclusions or exclusions, the Microchaetidae have incorporated only southern African taxa. PLISKO (1992) has withdrawn the proandric species from the composite genera, establishing a new genus *Proandricus* for them. Consecutively numerous new species were added (PLISKO 1991, 1992, 1993a,b, 1994, 1996a,b, 1997, 1998, 2000, 2002a,b, 2003, 2005, PLISKO & ZICSI 1991, ZICSI & PAJOR 1992) and a family was presented (PLISKO 2006a) with four genera, the holandric *Microchaetus*, *Tritogenia* and *Michalakus*, and proandric *Proandricus*. A composite status of the *Microchaetus* and the specific characters observed in *Tritogenia* and *Michalakus* were noted. Considering a correlation between specific characters and species geographical distribution, this revision of the most composite holandric genus *Microchaetus* allows to separate it in three genera: *Microchaetus* (*s. str.*), *Geogenia* and *Kazimierzus*. These, together with the other two holandric genera, the *Tritogenia* and *Michalakus*, and proandric *Proandricus* presently constitute Microchaetidae family with total of 142 species.

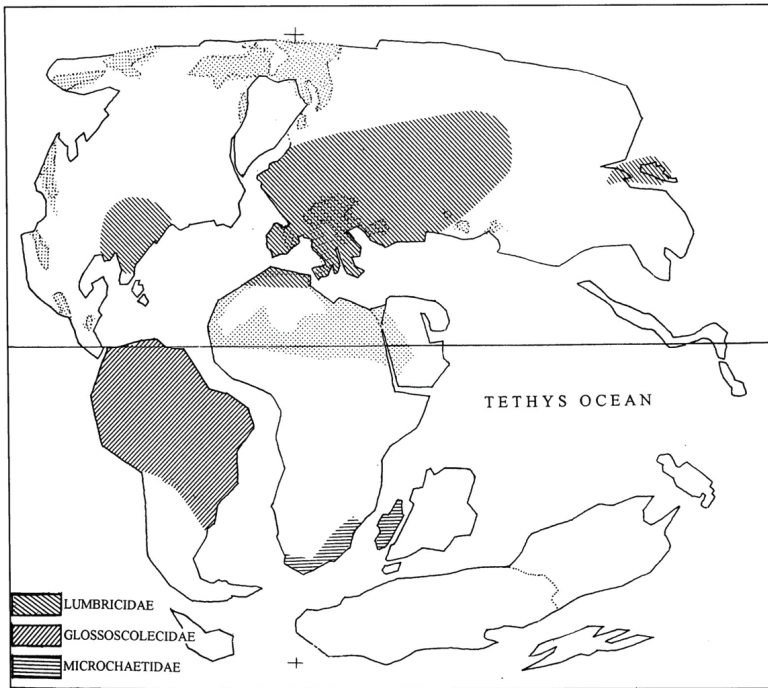


Fig. 1. Distribution of the terrestrial Lumbricoidea projected on the map of the middle Cretaceous of Pangaea (after OMODEO 2000).

Microchaetidae Beddard, 1895 emend.

Reproductive organs: Testes and male funnels in holandric condition (in 10 and 11), or proandric (in 10), or metandric (in 11). Vasa differentia commencing at lateral sides of male funnels, clearly visible or embedded in wall tissue. Seminal vesicles paired or fused dorsally, confined to one or two segments, or stretching posterior to one or more segments. Male pores paired, post-testicular. Ovaria paired in segment 13. Spermathecae with no diverticula, one or two pairs, or multiple at each side of segment, in one or more segments. Spermathecal pores in one or more intersegmental furrows, pretestical, testical and post-testical. Excretory system: Holonephric (holoic), with V-shaped or J-shaped nephridial bladders; or meronephric (meroic), enteronephric (enteroic). Oesophageal gizzard: One in segment 7, or in 6–7; or two in 6–7 and 9. Dorsal blood vessel: Simple in the whole length of the body; or double in preclitellar segments – (crossing septa may be single or double) and simple post-clitellarly. Paired dorsoventral vessels in 4, 5–11, enlarged and contractile in 9–11, slightly resembling a string of beads. Calciferous glands oesophageal, moderately developed, variable in size, shape – (stalked or not stalked), located variably (species condition). Typhlosole occupying nearly 70% of intestinal segments, variably developed, V- or U-shaped (species condition). Genital glands: Variable in shape, size, number and location, poorly known organs.

Body shape: Cylindrical, occasionally flattened at clitellar area. Body length highly variable, ranging from 25 to 2600 mm. Segment number variable at species level although might be a generic feature. Secondary annulation of preclitellar segments occurs as the external, transverse furrows, or grooves, demarcating segments externally into shorter portions. Prostomium: Prolobous. Setae: Eight per segment, in four pairs along the body (with some discrepancy occurring in some species). Clitellum: Present in sexually mature individuals, although in some adults the clitellar area can be consist of a tin layer of vestigial clitellar tissues, marked by dark-brown coloration; a range of occupied segments highly variable between species, usually, with small deviations, constant specific; saddle shaped or slightly encircling the body, although the clitellar tissues are not covering the medial part of the body. Tubercula pubertatis appearing in an earlier state of sexual maturity, preceding formation of clitellum; paired, glandular, variably shaped, although their shape and location are constant within species. Papillae: Glandular swellings variable in size, shape and position, usually associated with setal pairs, or genital glands.

Distribution: Representatives of this family are known from the southernmost part of the African continent, being accepted as indigenous to South Africa, Lesotho and Swaziland. More microchaetid species might be expected in adjacent countries. Six genera are selected with indication on their specificities. The generic features, ecological preferences and the appearance in separated geographically areas is clearly noticeable indicating on their separated evolutionary development.

***Microchaetus* Rapp, 1849**

After a revision of the composite *Microchaetus* (*s. lato*) by PLISKO (2006b), in the *Microchaetus* (*s. str.*) eight species remained: *microchaetus*, *papillatus*, *rappi*, *decipiens*, *braunsi*, *kloperi*, *stuckenbergi* and *vernoni*. These species are characterized by large body size (extending over one meter in length, sometimes over 2 meters, and number of segments may exceed one thousand). Characteristic external subdivision of preclitellar segments present. Holandric (testes and their funnels in segment 10 and 11). Holoic, with nephridial bladders V- shaped. Dorsal blood vessel double. Gizzard in 7. Spermathecae multiple per segment, with pores located always in post-testicular segments. Two pairs of seminal vesicles, in two segments. Clitellum and tubercula pubertatis exceptionally extended on numerous segments (from 10 to 34, or on some of these segments).

The species live deep in soil, supposedly at the water level, coming near to the surface after heavy rain when soil is well saturated. Being robust they need deep environment for protection and space for living, as well the moving-digging conditions. They can be found close to the surface in muddy, permanently waterlogged sites. The species of this genus occur in the south-eastern part of the South Africa (Fig. 2). The area from which the species were collected is located in the southern part of the Eastern Cape, although some not confirmed information refers also to the north of Cape Peninsula. Only two species were found in southern KwaZulu-Natal (not marked in Fig. 2).

***Kazimierzus* Plisko, 2006**

Genus *Kazimierzus* assembles 21 species initially described in the *Microchaetus* or *Proandricus*. This genus includes medium-sized (60–330 mm long, with number of segments 200–500). Characteristic external subdivision of preclitellar segments is present. Holandric (10 and 11) or metandric (11). Excretory system holoic with nephridial bladders J-shaped.

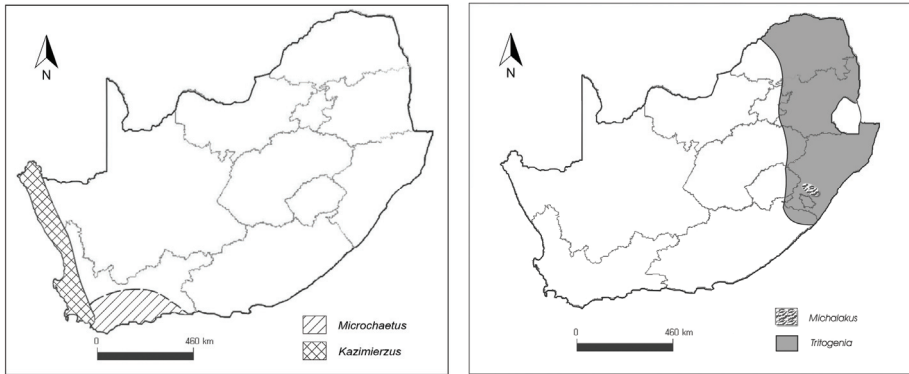


Fig. 2 (left). Distribution of *Kazimierzus* and *Microchaetus* species. – Fig. 3 (right). Distribution of *Tritogenia* and *Michalakus* species.

Dorsal blood vessel simple through the whole body. Spermathecae post-testicular. Two pairs of seminal vesicle often extended backwards.

Majority of the species were found in the waterlogged, soggy-sipping cold-water biotopes, often at high altitudes in mountains. Some of the species were detected by large casts discarded between rocks in very hard soil, suggesting that they may live at the water level, coming to the surface occasionally. The species of this genus differing morphologically (dorsal blood vessel simple; nephridial holoic bladders J-shaped; holandric and metandric) from the other geographically distanced genera *Tritogenia*, *Michalakus*, *Geogenia* and *Proandricus*, appearing in the south-western part of South Africa (Fig. 2), confirm evidently their specific identities. The environmental/ecological preferences observed in the numerous species of the *Kazimierzus* preferring soggy biotopes, muddy soil, sipping cold water at mountain high altitudes may reflect their ancient habitats.

***Tritogenia* Kinberg, 1867 and *Michalakus* Plisko, 1996**

The 37 holandric species constitute the genus *Tritogenia*. One monotypic species is in sister genus *Michalakus*. The particular body shape (plump and compact), small body size (25–145 mm long), and a number of segments rarely exceeding 100 characterize the species. Characteristic external subdivision of the preclitellar segments present and specific, differing slightly from the other genera. Holandric (10 and 11). Excretory system meronephric (meroic) in both genera. Oesophageal gizzard: in *Tritogenia* in 6–7; in *Michalakus* in 6–7 and 9. Dorsal blood vessel: Double in anterior part of the body with inclusion of the crossed septa, in both genera. Spermathecae: Small, multiple in segments, and their pores occurring variable in one to six intersegmental furrows pretestical testical, or post-testical intersegmental furrows, in 9/10–15/16, 16/17. Two seminal vesicles attributed to two segments.

The particular features, the meronephric excretory system, presence of one or two oesophageal gizzards located in 6–7 (*Tritogenia*), or 6–7 and 9 (*Michalakus*), the dorsal blood vessel double in anterior part of the body (with inclusion of the crossed septa) specific for both genera, distinctly separate them from the other microchaetids. Both genera appear in

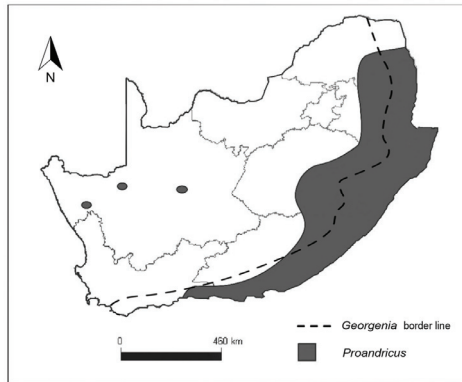


Fig. 4. Overlapping distributions of *Geogenia* and *Proandricus* species.

limited areas of the north-eastern part of South Africa (Fig. 3), spreading out through Limpopo and Mpumalanga, extending through KwaZulu-Natal and terminating occurrence at the northern border at the Eastern Cape province. The species were found at the sea level and higher altitudes, mostly in unpolluted areas, in grassland, indigenous bushes, river banks. Species endemism, speciation and excessive restriction to ecological conditions are highly noted (PLISKO 2009, 2010).

At this state of the general knowledge on evolutionary development of microchaetids it may be only speculation that *Tritogenia* might have undergone separate evolutionary development during various geological periods. Although direct relationship of the characters observed in *Tritogenia* and *Michalakus* and in the species accredited to Hormogastridae is not obvious, some of the affiliations may be suspected.

***Geogenia* Kinberg, 1867**

The genus *Geogenia* Kinberg, 1867 was resurrected by PLISKO (2006b) for the 21 species initially described in this genus or accounted to *Microchaetus* (*s. lato*). The species accredited to this genus are quite diverse, sharing only few characters. Characteristic external subdivision of preclitellar segments present. The majority of species are 40 mm to 300 mm in length, few species extending to 400 mm, and one to 800 mm. Number of segments 100–500. Holandric (10 and 11). Holonephric (holoic) with V-shaped bladders. Gizzard in segment 7. Dorsal blood vessel double in certain anterior segments. Spermathecae and their pores might be in pre-testicular, testis, or post-testicular furrows. Location of spermathecal pores is inconsistent and occurs in one to six intersegmental furrows (10/11–15/16). It is worthy to note that when they appear in the 11/12 and 12/13 furrows (feature characteristic for species of the genus *Proandricus*) the proandric reduction of male features may occur, suggesting a transverse state from a holandric to proandric stage. These apomorphic variations evolving in some otherwise morphologically very different species may suggest convergent adaptations. However, occurrence of some of the species sympatrically with or close to proandric species, in which reduction of the posterior pair of testes already took place, suggests that *Geogenia* species are undergoing apomorphic evolutionary steps.

The taxonomic position of this genus and also its distribution are of high interest. Possibly the assembled species are undergoing adaptations at the evolutionary steps, as suggested by PLISKO (2006b). At this state of the knowledge it might be only a speculation. Molecular investigation should be employed to clarify the generic assignment of species.

Geographical distribution of species is also of interest, partially overlapping the area of the *Proandricus* species. The majority of species occur mainly in the eastern part of South Africa (Fig. 4) ranging from Limpopo province, extending through Mpumalanga, KwaZulu-Natal, and terminating its distribution in the south-eastern part of the Western Cape. *G. natalensis* appears commonly in Kruger National Park (Limpopo province), KwaZulu-Natal (numerous sites) and also in Swaziland (REYNOLDS 1993). *G. namaensis* was reported (MICHAELSEN 1908) from the only locality in the Northern Cape (Namaqualand). Two species *benhami* and *mkuzi*, anatomically similar, occur in two distant areas: *benhami* in the Western Cape, *mkuzi* in the northern part of KwaZulu-Natal, what is suggesting that investigation on their identity and relationship is required.

***Proandricus* Plisko, 1992**

To this genus are accounted 54 species uniformly characterized by location of testes and their funnels in segment 10 (proandric character). Characteristic external division of the preclitellar segments is present. Excretory system holonephric (holoic) with nephridial bladders V-shaped. One oesophageal gizzard in 7. Dorsal blood vessel double in preclitellar segments, simple when crossing septa and posterior to segment 10. Seminal vesicles one pair confined to one segment, rarely two pairs in two segments, in *bergvillensis* extended backwards in three to five segments. Spermathecae and their pores post-testicular, in the majority of species reduced to two pairs located in intersegmental furrows 11/12 and 12/13. In a small group of species the pores occur in the pre-testicular position, or behind testes segment (or in 9 intrasegmental, not functional).

These peculiarities are usually occurring together with irregular placement of the seta in the clitellar area where some of the pairs of of *ab* are shifted up between *bc*, forming an irregular arrangement. Occasionally on some clitellar segments a pair of additional setae may occur, giving six pair of setae per segment. This unique, seldom noted event has been elaborated by PLISKO (2009). The species characterized by the atypical for microchaetid characters, noted sometimes in the glossoscolecids, occur in the central Drakensberg mountain region, extend through the northern part of Lesotho, stretch to foothills in KwaZulu-Natal and to the eastern part of the Free State.

Species of this genus were found in Lesotho and South Africa, ranging from the north through the part of Mpumalanga, KwaZulu-Natal, and terminating its distribution in the south-eastern part of the Eastern Cape (Fig. 4). Nearly a half of species are endemic to KwaZulu-Natal. The Eastern Cape species are also not spreading widely, centred on their original areas. Most of the species are confined to natural biotopes, indigenous grasslands, bushes and bushveld habitats, forests and open savannah, although they can also be found in less disturbed biotopes on the banks of rivers and road verges. Only *P. modestus* has been found in and outside of the distributional generic borders, in the numerous agricultural fields and in some other biotopes of the North West province. *P. londti* was probably transported from the Lesotho mountain area to a garden in Pretoria (Gauteng province). Distribution of *Proandricus* partly overlaps the occurrence of *Geogenia* species, sometimes sharing the same sites.

Table 1. The main generic characters observed within South African microchaetids. Character states are coded as plesiomorphic (= P) or apomorphic (= A).

	<i>Tritogenia/ Michalakus</i>	<i>Kazimierzus</i>	<i>Microchaetus</i>	<i>Geogenia</i>	<i>Proandricus</i>
Dorsal blood vessel	Double in 4-9, 10, 12 = A	Simple = P	Anteriorly doubled = A	Variably doubled: 4-7 = A	Variably doubled anteriorly = A
Oesophageal gizzard	6, 6-7 / 6-7 and 9 = A	7 = A	7 = A	7 = A	7 = A
Excretory system	Meronephric = P? or A?	Holonephric J-shaped = P? & = A	Holonephric V-shaped = P & = A	Holonephric V-shaped = P & = A	Holonephric V-shaped = P & = A
Testes	Holandric = P	Holandric = P, Metandric = A	Holandric = P	Holandric = P	Proandric = A
Seminal vesicles	Two pairs; not extending backwards = P	Two pairs; extending backwards = A 80%	Two pairs; not extending = P	One or two pairs; not extending = A	One or two pairs; rarely extending backwards = A
Spermathecae	Multiple, paired or absent = A	Paired or multiple = A	Multiple = A	Paired or multiple = A	Paired or multiple = A
Shape/size	Small to medium = P	Medium = A	Very large = A	Small to medium = P & = A	Small to large = A
Environmental preferences	Terrestrial/ litter = A	Soggy/water-sipping = P	Living at water level, coming at surface = P & = A	Terrestrial/ litter = A	Terrestrial/moist/ soggy/water-level = A
Geographical distribution	North-eastern part of the country	South-western area along Atlantic	South-eastern inland area, with some species in midland	Eastern part, not extending behind Drakensberg and south areas (few exceptions)	Occurs with <i>Geogenia</i> , centering at Midland, specific at Drakensberg, not extending behind mountain range

Conclusion

The southern part of the South African continent holds a rich and characteristic megadrile fauna. Currently 142 microchaetid species, and over a hundred of acanthodrilids, are known from the South Africa, Lesotho and Swaziland. This area was not extensively investigated so far, and more species are expected to be discovered. A high number of species endemics in the earthworm fauna is therefore of high taxonomic and ecological concern. Proandry (apomorphic) against holandry (plesiomorphic) allowed establish the genus *Proandricus*, and the other holandric genera, subsequently divided according to differences in dorsal blood vessel and a shape of nephridial bladders into *Microchaetus*, *Kazimierzus*, and *Geogenia*, and meronephric *Tritogenia* and *Michalakus*.

The species grouped in six genera differ from each other morphologically (Table 1) and geographically (Figs 1-4). The meronephric excretory system indicates species separation in *Tritogenia* and *Michalakus*, and the other, holoic species, in other genera. Morphological characters and distribution of species accounted to *Tritogenia* and *Michalakus* indicate their specific identities, underlining their separation from the other genera. Their close morphological similarities and their similar ecological requirements may suggest that they have undergone isolated evolutionary development in a small area, due to isolation during various

geological phases. It may be also speculated that before their territorial isolation, their possible ancestor separated from the other microchaetids presently known from southern Africa.

It may be concluded that the transformation observed in *Proandricus* species with the second pair of testes absent, may lead to variable apomorphic changes in other features (location of spermathecae, position of clitellum, tubercula pubertatis). The atypical location of the setae and spermathecae found in some species occurring in the isolated areas may be other apomorphic alterations, although a reflection to evolutionary steps may be not excluded. Being holandric, the *Geogenia* species are going through transformations similar to proandric species, creating at present a generic group, which is poorly-supported morphologically. Ongoing apomorphic transformations observed in *Proandricus* and *Geogenia*, which distribution overlaps, may suggest their evolutionary relations. The morphological differences noted in *Kazmierzus* and notably its distant geographical occurrence suggests isolated evolutionary steps, possibly with some linkage to other original roots.

In the light of the present study, the family Microchaetidae has a complex structure and may eventually be split into two or more taxa of the familial rank. Studies of the mitochondrial and nuclear DNA, which are underway, may shed light on the validity of this assumption as well as on presumed divergence times of different clades constituting the family in its present volume.

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