

An overview of stygobiontic invertebrates of Poland based on published data

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Abstract

Based on published literature, at least eighty species of stygobiontic invertebrates are confirmed in Poland. The highest number of these species is found in interstitial waters and wells, while a lower number was discovered in caves and springs. Hydrachnidia is represented by 45 species living mainly in interstitial waters, Crustacea by 24, Annelida by eleven species, while Turbellaria and Gastropoda are each represented by one species. As many as 14 endemic species were described from Poland but the taxonomical status of some of them is unclear. The highest number of stygobionts was stated in southern part of Poland, an area onto which most of the studies were focused on.

Keywords

subterranean fauna, checklist, caves, wells, springs, interstitial waters

Introduction

Various classifications of subterranean aquatic habitats were made over the years (e.g., Thienemann 1926, Botosaneanu 1986) and occasionally some have been evaluated (Culver and Pipan 2011, Gutjahr et al. 2014). Stygobiontic invertebrates inhabit shallow underground waters, access to which is possible through caves, springs, and wells (Gibert et al. 1994, Gunn 2004) as well as through other man-made subterranean habitats such as adits, shafts or mines. Moreover, obligate subterranean fauna living in interstitial waters beneath streams and rivers (the hyporheic zone) and in the spaces among alluvial sediments deposited along the banks also is recognized as stygobiontic.

Literature reviews of subterranean invertebrates have been published from different perspectives, including a focus on obligate subterranean fauna in one country (Reboleira et al. 2012), for the whole cave fauna in one country (Strouhal and Vornatscher 1975, Kováč et al. 2014) or for particular taxonomic groups in selected geographic regions, such as shrimps (Anker 2008) or annelids (Martínez-Ansemil et al. 2016, Artheau and Giani 2006).

In Poland, the southern part of the country has been the focus area for studies involving aquatic subterranean fauna and, to a lesser degree, the central parts of the country; unfortunately, there is little to no information from the northern regions. Moreover, for some taxonomic groups with stygobionts there are no detailed studies – i.e. there is almost a complete lack of information concerning Turbellaria and Copepoda. Even in the case of the Amphipoda, intensively investigated by Skalski (Table 1; entry no. 73–79, Hydrachnidia studied by Biesiadka (Table 1; entry no. 2–7, 9) and Ostracoda studied by Sywula and Namiotko (Table 1; entry no. 1, 64, 85–88, 90, 91) there have been no publications in recent years. Only Oligochaeta (Table 1; no 14–24, 28, 30–33, 35, 42–44, 46–48, 63) have been studied by Dumnicka and co-workers up to now. The only checklist of Polish trogllobionts and stygobionts was compiled by Skalski (1981) as an appendix in a local journal. He stated the presence of 54 species. Thus, there is a need, after more than 35 years, to compile and update the list of stygobionts.

Methods

Species found on the present territory of Poland were taken into consideration. Papers with data concerning Polish aquatic subterranean fauna are scattered. We reviewed journal literature, conference abstracts, and monographs, but did not include synopses, reviews and syntheses based on previously published original papers.

Species names follow Fauna Europea (<http://www.faunaeur.org>). When the species is not included in Fauna Europea or incorrect information was published in it (as in the case of *Crangonyx paxi* – see Table 1) “Fauna of Poland” (Bogdanowicz et al., 2004, 2008) was referred to.

Results

Source publications and analysis of species taxonomical status

The literature concerning Polish invertebrate fauna from subterranean waters (including stygophiles and stygoxenes) is limited. Since the end of the 19th century, when the description of *Niphargus tatrensis* was published (Table 1; entry no 95), around 100 papers have contributed to the stygobiontic fauna of Poland. Relatively few studies reported on the fauna of subterranean waters prior to the 1960s, with most publications occurring from 1960 to 1999 (Fig. 1).

Table 1. List of stygobiontic species known of Poland and their association with the geographic regions and habitats. Abbreviations of geographic names: B. – Beskid Mts; K.-Cz. – Kraków–Częstochowa; Depr. – Depression; Lakel. – Lakeland; Up. – Upland; Val. – Valley. Abbreviations of habitat names: AS – artificial subterranean habitats; C – caves; HR – hypotelminorheic habitat; I – interstitial waters; SP – springs; SW – surface waters; W – wells.

Group/ Species	Region	Habitat	References
Tricladida			
<i>Dendrocoelum</i> cf. <i>carpaticum</i> Komarek, 1919	Małopolska Gap	W	79
Annelida			
<i>Troglochaetus beranecki</i> Delachaux, 1921	Kłodzko Basin	C	84
<i>Cernosvitoviella parviseta</i> Gadzińska, 1974	Łask Up., Kłodzko Basin, B. Śląski Mts, Tatra Mts	C, W	20, 23, 30, 35
<i>Enchytraeus dominicae</i> Dumnicka, 1976 E	K.-Cz. Up., Tatra Mts, Świętokrzyskie Mts, Kłodzko Basin, Łask Up.	C, W, I	14, 16, 20, 33
<i>Enchytraeus polonicus</i> Dumnicka, 1977 E	K.-Cz. Up.	C	15, 17
<i>Gianius aquaedulcis</i> (Hrabě, 1960)	K.-Cz. Up.	SP	24
<i>Haber speciosus</i> (Hrabě, 1931)	B. Śląski Mts	W	42
<i>Rhyacodrilus subterraneus</i> Hrabě, 1963	K.-Cz. Up., Elk Lakel.	W, I	28, 29
<i>Trichodrilus cernosvitovi</i> Hrabě, 1937	Tatra Mts, Pieniny Mts, K.-Cz. Up.	I, SP, SW	20, 22, 47, 48
<i>Trichodrilus moravicus</i> Hrabě, 1937	Tatra, B. Śląski Mts, Pieniny Mts, K.-Cz. Up., Kłodzko Basin	C, I, SW, W	18, 20, 23, 28, 47
<i>Trichodrilus pragensis</i> Vejdovský, 1876	Kłodzko Basin	C	20
<i>Trichodrilus spelaeus</i> Moszyński, 1936 E	Kłodzko Basin	AS	63
<i>Trichodrilus</i> sp. juv. Claparède, 1862	Małopolska Gap	W	X
Amphipoda			
<i>Crangonyx paxi</i> § Schellenberg, 1935 E	Kłodzko Basin	AS, SP	71, 82
<i>Gammarus pulex polonensis</i> Karaman & Pinkster, 1977 E	Poznań Lakel.	I	41
<i>Niphargus</i> ? <i>aquilex</i> Schiödt, 1856	Central Oder Val.	W	37
<i>Niphargus casimiriensis</i> Skalski, 1980 E	Małopolska Gap	W, SP	79
<i>Niphargus inopinatus</i> Schellenberg, 1932	Tatra Mts	SP	73
<i>Niphargus leopoliensis</i> Jaworowski, 1893	Bieszczady Mts, K.-Cz. Up. Jędrzejów Plateau	SW, W	73, 76
<i>Niphargus puteanus</i> † Koch, 1836	Wałbrzych Mts, Central Oder Val.	C, SW, I	65
<i>Niphargus tatrensis</i> Wrześniowski, 1888	K.-Cz. Up., Orava-Podhale Depr., Tatra, B. Żywiecki, B. Śląski, B. Mały, B. Wyspowy, B. Niski, Gorce, Bieszczady Mts, Kłodzko Basin, Małopolska Gap	I, W, SP, C, SW	10, 11, 18, 22, 28, 31, 36, 59, 60, 69, 72, 74, 75, 76, 77, 79, 80, 84, 96, 97
<i>Niphargellus arndti</i> (Schellenberg, 1933)	Wałbrzych Mts, Kłodzko Basin	C, AS	38, 58, 70
<i>Synurella tenebrarum</i> (Wrześniowski, 1888)	Orava-Podhale Depr.	W	95
<i>Synurella coeca</i> Dobreaun & Manolache, 1951	Małopolska Gap	W	79
Bathynellacea			
<i>Bathynella natans</i> Vejdovský, 1882	Kłodzko Basin, Orava-Podhale Depr.	I	89
Isopoda			
<i>Proasellus slavus</i> (Remy, 1948)	Orava-Podhale Depr.	I, W	89
Copepoda			
<i>Acanthocyclops rhenanus</i> Kiefer, 1936	Łask Up.	SW	92

Group/ Species	Region	Habitat	References
<i>Diacyclops clandestinus</i> (Kiefer, 1926)	Tatra Mts, Oświęcim Basin	C, W	11, 57
<i>Graeteriella unisetigera</i> (Graeter, 1908)	Central Oder Val.	W	94
Ostracoda			
<i>Cryptocandona matris</i> (Sywula, 1976)	Małopolska Gap, Silesian Foothill, B. Wschodni Mts, Pieniny Mts	W, I	1, 79, 87, 90, 91
<i>Cyclocypris</i> sp. Brady & Norman, 1889	B. Wyspowy Mts	I	85
<i>Fabaeformiscandona latens</i> (Klic, 1940)	Gorce Mts	SP	86
<i>Fabaeformiscandona wegelini</i> (Petkovski, 1962)	Vistula catch. down to Kazimierz Dolny town, Gorce Mts, Oder catch. down to outlet of Warta	W, I, SW	79, 85
<i>Nannocandona stygia</i> Sywula, 1976 E	Sudety Mts, B. Śląski Mts	W, I	87
<i>Pseudocandona eremita</i> (Vejdovský 1882)	Małopolska Gap, Vistula Fen Country, Central Oder Val., Bóbr R. catchment	W, SW, I	64, 79, 88
<i>Pseudocandona mira</i> (Sywula, 1976) E	B. Żywiecki Mts, Orava-Podhale Depr.	W	87
<i>Pseudocandona szoeci</i> Farkas, 1958	Małopolska Gap, Orava-Podhale Depr.	W	79, 88
Hydrachnidia			
<i>Albaxona elegans</i> Walter, 1947	Bieszczady Mts	I	7
<i>Albaxona lundbladi</i> Motas & Tanasachi, 1947 = <i>A. gracilis</i> Schwoerbel, 1962 (sensu Bogdanowicz et al. 2008)	Bieszczady Mts	I	7
<i>Albaxona minuta</i> Szalay, 1944	Bieszczady Mts	I	83
<i>Arrenurus corsicus</i> Angelier, 1951	Central Oder Val.	W	5
<i>Atractides barbarae</i> Biesiadka, 1972 E	B. Wyspowy Mts	I	4
<i>Atractides gorcensis</i> Biesiadka, 1972	Gorce Mts	I	2
<i>Atractides latipalpis</i> Motas & Tanasachi, 1946	Tatra Mts	I	5
<i>Atractides latipes</i> (Szalay, 1935)	B. Wyspowy, Bieszczady Mts, Wieliczka Foothills	I	3, 83
<i>Atractides phreaticus</i> (Motas & Tanasachi, 1948)	Pieniny Mts, B. Wyspowy Mts, Bieszczady Mts, Range of Babia Góra	I, SW	3, 6, 83, 96
<i>Atractides pilosus</i> Schwoerbel, 1961 = <i>A. tener</i> ? sensu Gerecke, 2003	Orava-Podhale Depr.	I	5
<i>Atractides pumilus</i> (Szalay, 1946) = <i>A. primitivus</i> (Walter, 1947) sensu Gerecke, 2003	Orava-Podhale Depr., Pieniny Mts, Bieszczady Mts	I	5, 6, 83
<i>Atractides sokolowi</i> (Motas & Tanasachi, 1948)	Pieniny Mts, Bieszczady Mts	I	6, 9
<i>Aturus karamani</i> Viets, 1936	Tatra Mts	I	5
<i>Aturus paucisetus</i> Motas & Tanasachi, 1946	Gorce Mts, Pieniny Mts, Bieszczady Mts	I	3, 6, 83
<i>Aturus petrophilus</i> Biesiadka, 1979‡ E	Pieniny Mts	I	6
<i>Aturus pulchellus</i> Biesiadka, 1975 E	Tatra Mts	I	5
<i>Axonopsis cogitatus</i> Biesiadka, 1975	Orava-Podhale Depr.	I	5
<i>Axonopsis inferorum</i> Motas & Tanasachi, 1947	B. Wschodni Mts	I	5
<i>Axonopsis vietsi</i> Motas & Tanasachi, 1947	Bieszczady Mts	I	83
<i>Barbaxonella angulata</i> (Viets, 1955)	Bieszczady Mts	I	7
<i>Erebaxonopsis brevipes</i> Motas & Tanasachi, 1947	B. Wschodni Mts	I	5, 83
<i>Feltria mira</i> (Motas & Tanasachi, 1948)	Orava-Podhale Depr., Tatra, B. Wyspowy Mts	I	3, 5
<i>Feltria subterranea</i> Viets, 1937	Bieszczady Mts	I	7
<i>Frontipodopsis reticulatifrons</i> Szalay, 1945	Bieszczady, Pieniny Mts	I, SW	5, 6, 83

Group/ Species	Region	Habitat	References
<i>Hungarohydracarus subterraneus</i> Szalay, 1943	B. Żywiecki Mts, Bieszczady Mts	I	5, 83
<i>Kawamuracarus chappuisi</i> Motas & Tanasachi, 1946	Orava-Podhale Depr.	I, W	5
<i>Kongsbergia alata</i> Szalay, 1954	Central Oder Val.	I	5
<i>Kongsbergia arenaria</i> Angelier, 1951	Orava-Podhale Depr., Bieszczady Mts	I	7
<i>Kongsbergia clypeata</i> Szalay, 1945	Bieszczady Mts	I	7
<i>Kongsbergia dentata</i> Walter, 1947	Tatra Mts, Pieniny Mts	I	5, 6
<i>Kongsbergia d-motasi</i> Motas & Tanasachi, 1958	Bieszczady Mts	I	7
<i>Kongsbergia lundbladi</i> Szalay, 1956	Bieszczady Mts	I	Biesiadka pers. com.
<i>Kongsbergia pectinata</i> Walter, 1947	Bieszczady Mts, Gorce Mts	I, SW	3, 83
<i>Kongsbergia rutneri</i> Walter, 1930	Pieniny Mts	I	6
<i>Kongsbergia wroblewskii</i> ‡ Biesiadka, 1997 E	Bieszczady Mts	I	7
<i>Lethaxona cavifrons</i> Szalay, 1943	Orava-Podhale Depr., B. Wschodni Mts, Pieniny Mts, Gorce Mts	I	3, 4, 5, 6
<i>Lethaxona pygmaea</i> Viets, 1932	Bieszczady Mts, Gorce Mts	I	7, 83
<i>Neocarus hibernicus</i> Halbert, 1944	Orava-Podhale Depr. B. Wschodni Mts, B. Wyspovy Mts, Pieniny Mts	I	3, 5, 6
<i>Neumania phreaticola</i> Motas & Tanasachi, 1948	Bieszczady Mts	I	7
<i>Sperchonopsis phreaticus</i> Biesiadka, 1975 E	Tatra Mts, Bieszczady Mts	I	5, 83
<i>Stygomononia latipes</i> Szalay, 1943	Bieszczady, Pieniny, Tatra, B. Żywiecki, B. Wyspovy Mts, Kłodzko Basin	I	3, 5, 6, 83, 96
<i>Wandesia thori</i> Schechtel, 1912	Tatra Mts, Gorce Mts	SW	67, 68
<i>Wandesia stygophila</i> Szalay, 1944	Bieszczady Mts	I	83
Halacaroida			
<i>Loboharacarus weberi quadriporus</i> Walter, 1947	B. Żywiecki, Pieniny, B. Wschodni Mts, Tatra Mts, Orava- Podhale Depr.	I	5, 6
<i>Parasoldanellonyx parviscutatus</i> (Walter, 1917)	Orava-Podhale Depr.	W	5
Gastropoda			
<i>Falniowska neglectissima</i> Falniowski & Steffek, 1989 E	K-Cz. Up.	HR	34

† – misidentification, ‡ – nomen nudum; § – species known from Kłodzko Basin only, localization in Germany is false (Fauna Europaea); | – described as *S. coeca rafalskii* by Skalski (1981); E – species endemic to Poland; x – leg. A. Skalski 14.07.1977, det. E. Dumnicka.

Several factors make it difficult to come up with an exact number of Polish stygobionts. First, among species found only once many years ago, a few probably were not correctly determined (e.g., *Niphargus puteanus*) or exactly determined (*N. cf. inopinatus* and *Dendrocoelum cf. carphaticum*) (Table 1). Second, the taxonomic position of some species from various groups is not clear due to numerous subsequent taxonomic revisions. For example *Enchytraeus polonicus* (Oligochaeta) is treated by Schmelz and Collado (2010) as a cave population (with an additional pair of spermathecae) of a very common species *E. buchholzi*. Two forms of *Synurella ambulans* (*S. ambulans* f. *subterranea* and *S. ambulans* f. *tenebrarum*) were considered in Polish literature as stygobionts. Now, these forms are not listed in Fauna Europea, while in WoRMS (<http://>

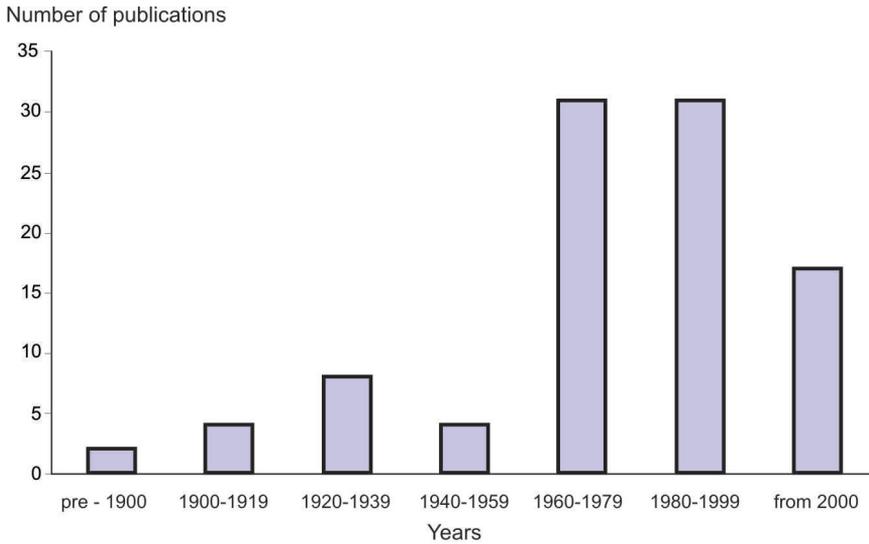


Figure 1. Number of publications concerning subterranean aquatic fauna of Poland through time.

www.marinespecies.org/) *S. ambulans* f. *tenebrarum* is elevated to the species level (as *S. tenebrarum*). This species is listed in the Table 1. Moreover, two species of Hydrachnidia (*Aturus petrophilus* Biesiadka 1979 and *Kongsbergia wroblewskii* Biesiadka 1997) are *nomen nudum* (Biesiadka pers. com.), though the first species is included in the list of Hydrachnidia in Fauna Europea.

In some cases, so-called local stygobionts were included in the checklist (Table 1). For example, *Rhyacodrilus subterraneus* is found exclusively in subterranean waters in Poland, it is known from surface waters in northern Europe (Dumnicka 2014). Three species of Hydrachnidia known exclusively from interstitial waters in Poland are considered stygobionts (Bogdanowicz et al. 2008).

Stygobiotic species in particular taxonomic groups

Approximately eighty stygobiotic species (Table 1) are known from aquatic subterranean environments in Poland, documented in various regions of the country (Fig. 2). The detailed localities of many stygobiotic species are given in publications but for some species only the range of their occurrence was published, with no specific localities.

Turbellaria seems to be the most poorly known group of invertebrates in Poland, due in part to a lack of researchers specializing in this group. There is a record of stygobiotic *Dendrocoelum* that has not yet been verified.

The phylum Annelida is represented by only one stygobiotic species of Polychaeta (*Troglochaetus beranecki*). It is known only from Radochowska and Rogózka caves (Table 1; entry no. 84), but has not been found since the original report, despite intensive sampling in the Radochowska cave and in interstitial waters of nearby streams and

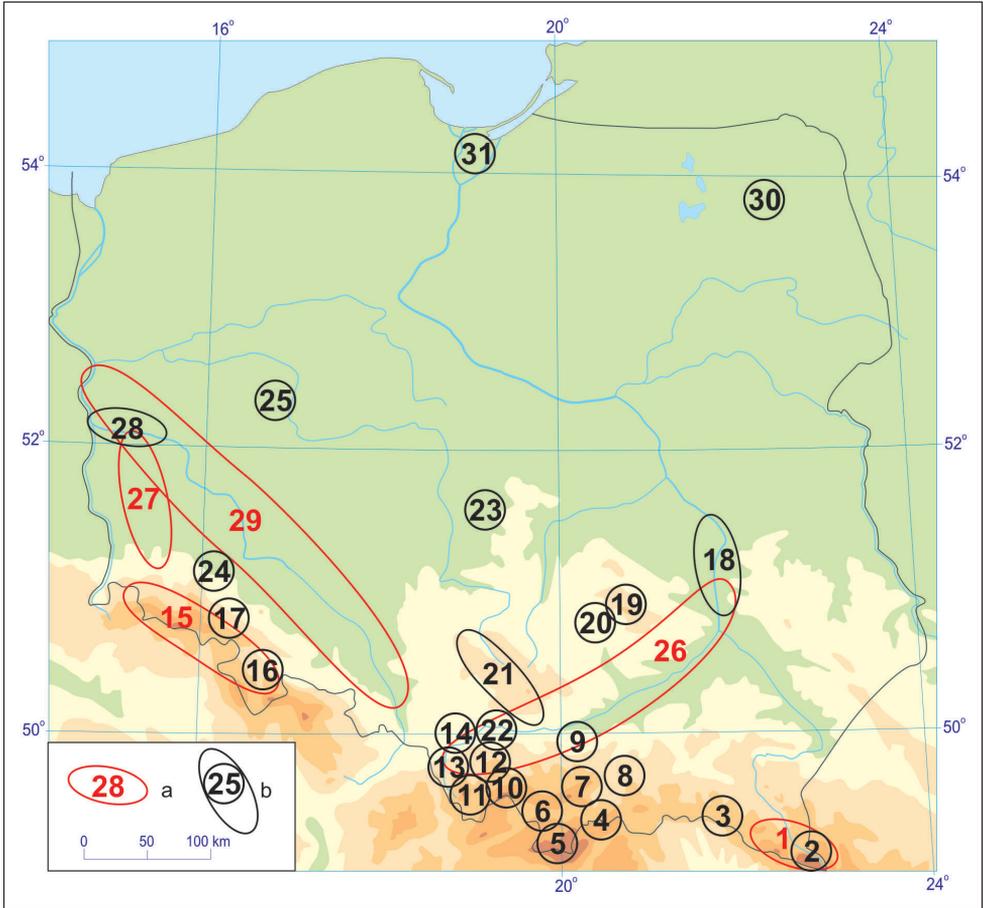


Figure 2. Regions of Poland studied by various authors: **1** Beskid Wschodni Mts. **2** Bieszczady Mts. **3** Beskid Niski Mts. **4** Pieniny Mts. **5** Tatra Mts. **6** Orava-Podhale Depression **7** Gorce Mts. **8** Beskid Wyspowsy Mts. **9** Wieliczka Foothill **10** Range of Babia Góra **11** Beskid Żywiecki Mts. **12** Beskid Mały Mts. **13** Beskid Śląski Mts. **14** Silesian Foothill **15** Sudety Mts. **16** Kłodzko Basin **17** Wałbrzych Mts. **18** Małopolska Gap of the Vistula **19** Świętokrzyskie Mts. **20** Jędrzejów Plateau **21** Kraków- Częstochowa Upland **22** Oświęcim Basin **23** Łask Upland **24** Legnica Plain **25** Poznań Lakeland **26** Vistula catchment up to Kazimierz Dolny town **27** Bóbr River catchment **28** Central Oder Valley **29** Oder catchment up to the outlet of the Warta River **30** Elk Lakeland **31** Vistula Fen Country. **a** area of species occurrence without exact localization given **b** geographical regions with detailed localization of species provided.

springs (Table 1; entry no. 20, 38, 89). At least ten stygobiotic Oligochaeta species occur in Poland, with representatives in habitats of all types. Their list and detailed distribution was recently provided (Dumnicka 2014). Moreover, juvenile specimens of *Trichodrilus* were found in materials collected by Skalski (Table 1).

Crustacea, which usually dominate in subterranean waters of south-western Europe (Danielopol et al. 2000, Deharveng et al. 2009, Sket 1999), are represented in Poland by only 24 species (Fig. 3).

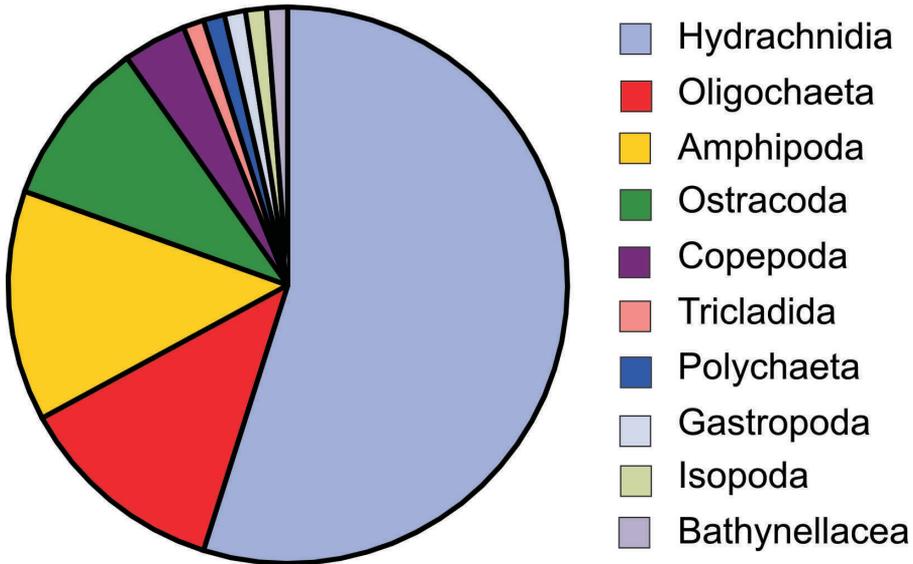


Figure 3. Percentage share of stygobiontic species from particular taxonomic groups.

Among the Amphipoda, eleven stygobiontic species have been reported, six of them belong to genus *Niphargus*. Of these, identification of *N. puteanus* (Table 1; entry no. 65) was contested by Skalski (Table 1; entry no. 77). The occurrence of two other *Niphargus* species (*Niphargus*? *aquilex* and *N. inopinatus*) in Poland has not been confirmed in the last 100 years. For *N. inopinatus*, it is possible that the species occurs in the Polish part of the Tatra Mountains, because it was confirmed in the southern part of this mountain range, in Slovakia (http://www.zoo.sav.sk/voda_pdf/voda_pdf.htm). The most common *Niphargus* in all studied habitats is *N. tatrensis*, which is sporadically found in surface waters also (Fig. 4). This species has been repeatedly observed in some caves, especially in Tatra Mountains. Additionally, it has been recorded from piezometer samples taken in Carpathic effluents of the Vistula. However, *Niphargus tatrensis* has patchy distribution because it has not been recorded from the many sampled wells in a large area in south-eastern Poland (Table 1; entry no. 76). The only stygobiontic subspecies from genus *Gammarus* shows morphological features typical for stygobiontic species such as the absence of eyes and slender antenna and pereopods (Table 1; entry no. 41).

The remaining orders of Malacostraca: Bathynellacea and Isopoda are each represented by one species (*Bathynella natans* and *Proasellus slavus*, respectively) (Table 1), and are rarely found in interstitial waters. Both species have also been recorded from wells.

None of the eight stygobiontic species of ostracods known from Poland have been recorded from cave waters. Instead, stygobiontic Ostracoda have been collected most frequently from wells and interstitial waters (Table 1). Two species have wide distribution (*Fabaeformiscandona wegelini*, *Pseudocandona eremita*) while the remaining have been stated only in southern Poland. Stygobiontic Copepoda have been poorly studied

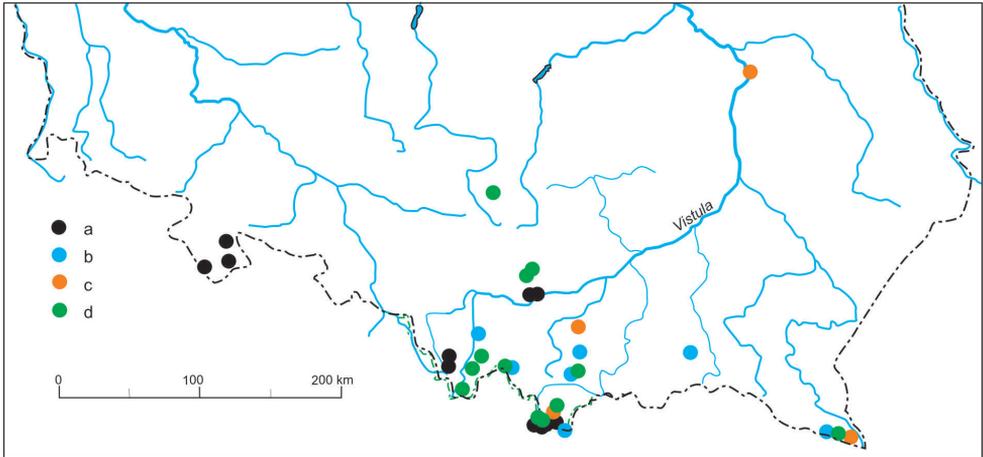


Figure 4. Distribution of *Niphargus tatrensis* in various habitats in Poland; **a** caves **b** surface waters **c** wells **d** springs.

in Poland, with only three species reported in subterranean waters. There is no published data on Harpacticoida, which is likely due to their occurrence predominantly in interstitial and epikarstic waters.

Mites, represented by Hydrachnidia (43 species) and Halacaroidea (two species) constitute over 50% of all stygobiotic species in Poland (Fig. 3). They inhabit almost exclusively (42 species) interstitial waters, but a few species have been reported from wells and surface waters. *Wandesia thori*, considered a stygobiotic species (Bogdanowicz et al. 2008, Botosaneanu 1986) was described from bottom samples collected in streams from the Tatra Mountains (Table 1; entry no. 67) and yet it has also been reported in a spring and two spring brooks in Gorce Mountains (Table 1; entry no. 68).

A species of Hydrobiidae (Gastropoda), *Falniowskaia neglectissima*, has been described from wet litter covering the ground (Table 1; entry no. 34) and it is treated as a stygobiont living in the hypothelminorheic habitat (Culver and Pipan 2011).

Our review indicates that 14 endemic species (including two *nomen nudum*) have been described from Poland: three Oligochaeta, five Crustacea, five Hydrachnidia and one Gastropoda. Some of these have broad distributions, such as *Enchytraeus dominicae* (Table 1), while most of the 14 endemics described from the country are known from only one region.

Species richness in particular habitats

Of all the groundwater habitats, cave waters have been the most intensively investigated in Poland, yet the number of records of stygobiotic species from Polish caves is relatively low (Fig. 5), a pattern also observed in Slovakia (Kováč et al. 2014). In many caves of Poland, no stygobiotic species have been found (Table 1; entry no.

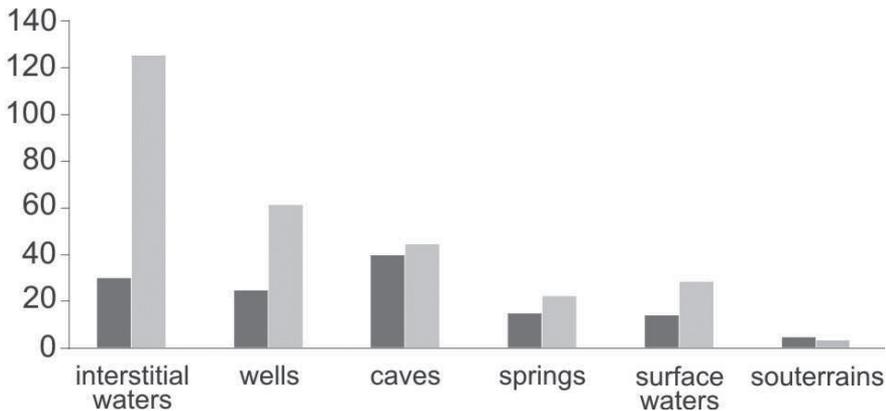


Figure 5. Number of studies performed in particular habitats (dark bar) and number of records of stygobiontic species found in them (light bar).

32), and in some cases aquatic fauna appeared to be totally absent (Kur et al. 2016). In contrast, interstitial waters of Poland contain numerous stygobiontic species, especially Hydrachnidia. Records of subterranean fauna collected from wells are relatively numerous, although this habitat seldom has been studied.

Conclusions

1. In Poland, the stygobiontic fauna proved to be unexpectedly rich in comparison to that of Belgium (Martin et al. 2009), while the more intensively studied subterranean waters of Germany have revealed a greater number of species (Hahn and Fuchs 2009). The comparison of richness of stygobiontic fauna with that stated in other neighboring countries is difficult. In Slovakia some invertebrate groups have barely been investigated in the subterranean habitat e.g. Hydrachnidia, whereas other groups such as Copepoda have been studied in more detail (Košel 2009, Juberthie et al. 2001, http://www.zoo.sav.sk/voda_pdf/voda_pdf.htm). The situation is similar in the Czech Republic, where Harpacticoida were intensively studied by Štěrba (1964, 1965, 1968) and a list of stygobionts was prepared by Bosák et al. (2001). In adjacent countries across the eastern border of Poland such studies are limited.
2. More intensive studies of stygobiontic species in Poland's interstitial waters and wells are needed because these habitats are threatened by river regulations and abandonment of wells use. In addition, some regions of Poland have been poorly studied with regard to the stygobiontic fauna, especially in northern part of the country (see Fig. 2), and more effort should be dedicated to investigating these understudied regions.
3. Due to the decline in the number of active taxonomists in recent years, the status of some stygobiontic species remains unclear. Additional societal support for taxonomic research is needed so that various groups in need of revision can be studied.

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The troglomorphic adaptations of Namanereidinae (Annelida, Nereididae) revisited, including a redescription of *Namanereis cavernicola* (Solís-Weiss & Espinasa, 1991), and a new Caribbean species of *Namanereis* Chamberlin, 1919

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Abstract

Most species belonging to *Namanereis* Chamberlin, 1919 live in freshwater and subterranean waters, even in water bodies several meters above sea level. A new species belonging to the stygobiont *Namanereis* group is described here; it shares the common morphological characters of absence of eyes and pigmentation, bifid jaws, elongation of chaetae and cirri, which have been recently regarded as troglomorphies. Because these features are used in evaluations of phylogenetic affinity in *Namanereis*, a review of these features was made for all known namanereidins, and it was extended to include species in *Namalycastis* Hartman, 1959. It is shown that elongation of tentacular and dorsal cirri, or elongation of upper sub-acicular falcigers in pre- or post-acicular fascicles, are not exclusive or restricted to species living in subterranean habitats or to *Namanereis*, because these features are also present in several *Namalycastis* species. However, the presence of bifid jaws, and the absence of eyes are exclusively found in namanereidins living in subterranean habitats. A hypothetical evolutionary derivation of bifid jaws is proposed, based upon observations of jaw morphology of several species. These exclusive troglomorphic characters (bifid jaws, eyeless) are regarded as convergent features to aphotic environments, and they should be discouraged as indicators of common ancestry. The new species, herein described as *Namanereis christopheri* **sp. n.**, was collected in a cave 435 m above sea level in Saint Vincent, Caribbean Sea. The species resembles *N. cavernicola* but it differs because it has shorter tentacular cirri, margin of prostomium entire, rounded neuropodial lobes and broader dorsal cirri throughout body. A key to identify all known *Namanereis* species is included.

Keywords

Troglophic features, convergence, elongation of appendages, evolution of jaws

Introduction

Troglophism comprises a set of convergent features found in organisms living in subterranean, aphotic environments, presumably resulting from similar selective pressures (Christiansen 1962, Culver and Pipan 2009b); such features are called troglomorphies, while the species showing them are called troglomorphs (Culver and Pipan 2009b). The troglomorphies often include a mixture of reductions and gains; the former includes loss of eyes and body pigmentation, and the latter relate to over-development of non-optic sensory structures, and elongation of appendages (Culver and Pipan 2009b). During many years, the troglomorphism was considered as resulting from selective factors operating in caves linked to modified patterns of nutrient availability and type of habitat. However, because the absence of light is the only common factor in all cases (Culver et al. 2010), these modifications might not be related exclusively with cave environments.

In an ecological classification, obligate residents of subterranean habitats are called troglobionts, and specifically stygobionts if they live in aquatic systems; interestingly, not all organisms living in subterranean environments are troglomorphs, nor are all organisms showing troglomorphic features are troglobionts (Sket 2008, Culver and Pipan 2009b, Pipan and Culver 2012, Konec et al. 2015). The fact that troglomorphic features are present in species living in non-cave environments indicates that their evolution is more complex than supposed (Heads 2010); therefore, the assumption of features as troglomorphic just because some morphologically modified species have current subterranean distributions deserves critical attention.

Oligochaetes are the most common annelid troglobionts, but polychaetes can also be so, especially those species belonging to the family Nereididae de Blainville, 1818 and specifically the subfamily Namanereidinae Hartman, 1959 (Glasby and Timm 2008, Glasby et al. 2009). This subfamily includes two genera, *Namanereis* Chamberlin, 1919 and *Namalycastis* Hartman, 1959, including a *incertae sedis* species and genus *Lycastoides alticola* Johnston, 1903 (Glasby 1999, Alves and Santos 2016). While most nereidids are estuarine or marine, namanereidins typically occur in freshwater and groundwater habitats, while a few can even thrive in semi-terrestrial ones. In contrast with other nereidids with complex parapodial morphology, the parapodia of namanereidins are reduced, possessing one main chaetal lobe carrying both noto- and neuroaciculae and a few chaetae, with a consequent reduction of taxonomically useful characters (Glasby 1999). Nevertheless, 43 namanereidin species have been described, and the usual diagnostic features are the shape of antennae and jaws, presence of a cleft in anterior margin of prostomium, presence of eyes, relative length of dorsal cirri along body, and arrangement and shape of chaetae (Glasby 1999).

A group of at least 12 stygobiont *Namanereis* (from a total of 18 in the genus) have interestingly shared morphological features, such as the absence of body pigmentation and eyes and the elongation of appendages (cirri and chaetae), including some other

features not present in all species as the presence of distally bifid and edentate jaws, and heterogomph falcigers in sub-preacicular fascicles increasing their length posteriorly, even being replaced with spinigers (Glasby et al. 2014). Glasby et al. (2014) made an analogy between these features and those present in other hypogean organisms, arguing that those features could be regarded as troglomorphies; also, they detailed several hypotheses about possible origins and colonization of extant *Namanereis* based mainly on jaw morphology and the current distributions of species.

However, the same troglomorphic features are present at least in one other epigeal species from another genus living within mangrove leaves litter, *Namalycastis occulta* Conde-Vela, 2013, as already noted in a previous contribution (Conde-Vela 2013: 481). A recent phylogenetic study challenged the generic placement of this species, suggesting that *N. occulta* is more related to *Namanereis* than to any described *Namalycastis*, forming a strongly supported clade with *Namanereis hummelincki* (Alves and Santos 2016: 509–510). However, the synapomorphies supporting such clade (absence of eyes, presence of bifid jaws and elongated falcigers in preacicular position) are precisely those regarded as troglomorphic features. It means that morphological resemblance could be due to common ancestry but also to convergence, and therefore they must be evaluated cautiously to avoid misleading interpretations (Wiens et al. 2003). Because the supposedly troglomorphic features are not restricted to stygobitic *Namanereis* group, a re-assessment of these features, as a result of living in subterranean habitats is required.

On the other hand, in the *Namanereis* stygobitic group, three species were found in groundwater at several meters above sea level (asl): *N. beroni* (Hartmann-Schröder & Marinov, 1977) from Papua New Guinea, 1700 m asl, *N. cavernicola* (Solís-Weiss & Espinasa, 1991) from Mexico, 1650 m asl and *N. gesae* Fiege & Van Damme, 2002 from Yemen, 700 m asl, while the top record of altitude is for *Lycastoides alticola*, found at 2150 m asl in Mexico (Johnson 1903, Glasby et al. 2014). Glasby (1999: 83) extended the distribution of *N. cavernicola* after based on morphological similarities of specimens from Saint Vincent, Hispaniola and Cuba, Caribbean Sea, and comparison with type material. Subsequently, Glasby et al. (2014: 34) suggested that the current distribution of *N. cavernicola* in Mexico could be explained from a littoral species subsequently becoming ‘trapped’ in water bodies during orogenic uplifting, a hypothesis that matches well with the tectonic history of the Mexican region (Padilla y Sánchez 2007), but that it could not explain the current disjunct distribution of a single putative species across Caribbean islands with distinct geologic histories (Bouysson 1984, Bouysson et al. 1990). Even restricted distribution is expected in *N. cavernicola* due to the very exclusive environment it inhabits, the altitude and the limited or non-existent connection with the sea, but it currently has amphiamerican status. A preliminary examination of material from the Caribbean Sea and type material of *N. cavernicola*, some morphological differences were observed, suggesting the present study: a reassessment of the amphiamerican status of *N. cavernicola*.

The main goal of this contribution is the re-assessment of troglomorphic morphology in namanereidins. As an introduction to the troglomorphic morphology in stygobitic namanereidins, the systematic section is presented first, addressing the description

of a new species of *Namanereis* and the redescription of *N. cavernicola*, and including a key to identify all known species of the genus. After, the discussion of troglomorphic features is presented, focused on the elongation of cirri and chaetae, the arrangement of chaetae and the morphology of the jaws.

Materials and methods

For the morphology re-assessment, specimens of 7 species were examined and are deposited in the National Museum of Natural History, Smithsonian Institution (USNM), the Natural History Museum of Los Angeles County (LACM-AHF), and in the Reference Collection of El Colegio de la Frontera Sur, Chetumal (ECOSUR). They include paratypes of *Namanereis cavernicola* from Mexico (USNM 136559), topotypes of *Namanereis hummelincki* from Bonaire (USNM 29715, 29716), holotype (USNM 178870) and paratypes (USNM 31011) of *Namalycastis intermedia* from the Gulf of Mexico, and topotypes of *Namalycastis occulta* (ECOSUR P-2649), and non-type specimens of *Namanereis* cf. *amboinensis* (ECOSUR P-2902) and *Namalycastis borealis* (ECOSUR P-2651) from Chetumal Bay.

Specimens were examined under stereomicroscope (Olympus SZ40) and compound microscope with differential interference contrast (Olympus BX51). The photographs were made with a digital camera (Canon T5i) with adaptor for both microscopes. Plates and images were made with Adobe Photoshop® and Illustrator®. If not everted, pharynx was dissected to examine interior structures and, in some specimens, jaws were removed, mounted and observed in compound microscope. Parapodia from anterior, middle and posterior chaetigers were removed and mounted in semi-permanent slides, and examined under compound microscope. Some specimens were whole-mounted for examination of chaetal changes along body.

For descriptions, parapodial and chaetal terminology provided by Glasby (1999) and Conde-Vela (2013) were followed. In addition to the examined specimens, and in order to achieve an almost exhaustive discussion of the namanereidin morphology, all pertinent literature including original descriptions, revisions, notes about ecology and distribution, were taken into account. Morphological ratios and measurements used in some sections were obtained mainly from descriptions by Glasby (1999), and only from original descriptions for species described in other publications (Glasby 1997, Fiege and Van Damme 2002, Glasby et al. 2007, Magesh et al. 2012, Conde-Vela 2013, Glasby et al. 2014, Magesh et al. 2014, Alves and Santos 2016). Only ratios of type material were included and, if a range was declared, the average was used; if not clearly stated in descriptions, measures for ratios were obtained from illustrations. Histograms were made with the ratios obtained, sorted from highest to lowest ratio; in all histograms, *Namalycastis* species were highlighted in boldface and *Namanereis* species in lightface, while stygobiont species were labeled with an asterisk.

For the relative length of parapodial cirri, the ratios between the length of dorsal cirri (**Ld**) and length of neuroacicular lobe (**Ln**), for anterior ($A_{Ld/Ln}$) and posterior

($P_{Ld/Ln}$) chaetigers were used. The subtraction of $P_{Ld/Ln}$ and $A_{Ld/Ln}$ (D_{p-a}) is less than or equal to zero if anterior cirri are equal or longer than posterior ones, indicating elongation of anterior cirri; and greater than zero if posterior cirri are longer than anterior ones, indicating elongation of posterior cirri. With $A_{Ld/Ln}$ and $P_{Ld/Ln}$, two histograms were made, the first explores the distribution of elongation of dorsal cirri in both anterior and posterior chaetigers, whilst the second shows the same distribution but based on anterior chaetigers only.

For the relative length of tentacular cirri, the ratio between length of posterodorsal tentacular cirri (**Lpt**) and wide of prostomium (**Wp**) was used. **Lpt/Wp** was obtained from illustrations directly (excepting *Namalycastis geayi*, *N. longicirris* and *N. siolii*). This measure was preferred over the number of chaetigers reached when posterodorsal tentacular cirri are placed backwards (Glasby 1999), because differences in preparation of specimens and contraction of body during fixation can cause misleading measurements (Oliveira et al. 2010, Bonyadi-Naeini et al. 2016).

For the relative length of blades of chaetae, the ratio between length of blade (**Lb**) and the width of shaft (**Ws**), standardized to chaetiger 10, was used; only the ratio of the dorsalmost (**Dm**) and ventralmost (**Vm**) falcigers in sub-acicular fascicle were considered. The subtraction of **Dm** and **Vm** (D_{d-v}) is zero or nearly so if both falcigers have subequal length, and greater than zero if **Dm** is greater than **Vm**, indicating elongation in **Dm**.

Results

Systematics

Family Nereididae de Blainville, 1818

Subfamily Namanereidinae Hartman, 1959

Genus *Namanereis* Chamberlin, 1919

Namanereis cavernicola (Solís-Weiss & Espinasa, 1991)

Fig. 1

Lycastilla cavernicola Solís-Weiss & Espinasa, 1991: 632–635, figs 1a–e, 2a–f.

Namanereis cavernicola Glasby, 1999: 83–86 (*partim*).

Type locality. Izote Cavern, Guerrero, Mexico, 1650 m above sea level.

Material examined. Paratypes USNM 136559 (2), Izote Cavern, (18°36'40"N, 99°33'25"W), Guerrero, Mexico 1650 m above sea level, 20 November 1988, Coll. L. Espinasa.

Description. Paratypes in excellent condition, one complete; 29 mm long, 1.1 mm wide at chaetiger 10, 69 chaetigers. Body pale, without pigmentation (Fig. 1A, C). Prostomium wider than long, anterior margin incised, groove present

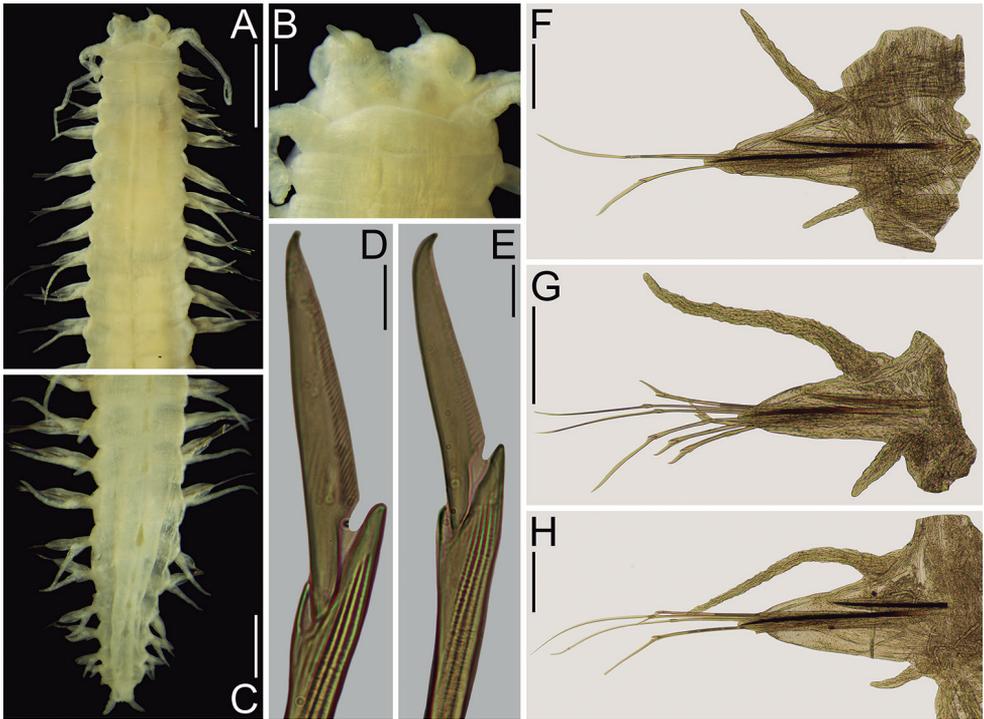


Figure 1. *Namanereis cavernicola* (Solís-Weiss & Espinasa, 1991). **A–H** Paratype USNM 136559 **A** Anterior end, dorsal view **B** Close-up of prostomium **C** Posterior end, dorsal view **D** Supra-acicular falciger, chaetiger 62 **E** Sub-acicular falciger, chaetiger 62 **F** Chaetiger 5, right parapodium **G** Chaetiger 20, right parapodium **H** Chaetiger 62, right parapodium. Scale bars: 1 mm (**A**); 0.2 mm (**B, F–H**); 0.5 mm (**C**); 10 μ m (**D, E**).

(Fig. 1A–B); antennae cirriform, as long as prostomium; eyes absent (Fig. 1B). Tentacular ring as long as first chaetiger; three pairs of tentacular cirri, superficially annulated, longest one reaches chaetiger 4 (Fig. 1A); cirrophores 1.5–2.0 times longer than wide.

Parapodial cirri pattern: Dorsal cirri sub-equal to neuroacicular lobes in anterior chaetigers, becoming longer than neuroacicular lobes toward posterior end, basally inserted throughout body. Ventral cirri shorter than neuropodial lobes, basally inserted throughout body.

In anterior chaetigers (Fig. 1F), dorsal cirri subequal to neuropodial lobes; neuropodial lobes subconical, twice longer than wide, twice longer than ventral cirri; ventral cirri half as long as dorsal ones. In middle chaetigers (Fig. 1G), dorsal cirri twice longer than neuropodial lobes; neuroacicular lobes subconical, twice longer than wide, twice longer than ventral cirri; ventral cirri one-third to one-half as long as dorsal ones. In posterior chaetigers (Fig. 1H), dorsal cirri 1.2 to 1.5 times longer than neuropodial lobes; neuropodial lobes subconical, 1.5 times longer than wide, 3 times longer than ventral cirri; ventral cirri one-third to one-half as long as dorsal ones.

Notochaetae absent. Neurochaetae in type D arrangement, i.e. supra-acicular chaetae heterogomph falcigers (Fig. 1D) and sesquigomph spinigers in pre- and post-acicular fascicles respectively; sub-acicular chaetae heterogomph falcigers with short (Fig. 1E) or long blades and spinigers in pre-acicular fascicles. Supra-acicular sesquigomph spinigers pectinated, teeth minute, decreasing in size towards tip; sub-acicular heterogomph falcigers pectinated, teeth minute, tip falcate, decreasing in length towards tip (Fig. 1D–E).

Pygidium tripartite; a pair of anal cirri cirriform, short, as long as pygidium (Fig. 1C).

Remarks. Solís-Weiss and Espinasa (1991) proposed *Lycastilla* with this species based on the presence of jointed antennae, cleft prostomium and notoacaculae with recurved tips. Posteriorly, Glasby (1999) regarded such features as insufficient and synonymized *Lycastilla* with *Namanereis* Chamberlin, 1919. The original description matches well with the species examined. Glasby (1999) redescribed the species with paratypes and non-type material from the Caribbean; however, part of his Caribbean material is herein regarded as a distinct undescribed species (see below).

***Namanereis christopheri* sp. n.**

<http://zoobank.org/FFA8CE1A-AF4A-48F7-96D7-CB2392E8F2ED>

Fig. 2

Namanereis cavernicola Glasby, 1999: 83–86, figs 8c, 35a–g (*partim, non* Solís-Weiss and Espinasa 1991).

Type locality. Saint Vincent, Lesser Antilles.

Etymology. The specific name is after Christopher J. Glasby, in recognition of his numerous contributions in polychaete taxonomy, especially about nereidid taxonomy, and because he identified this species as new after his first evaluation (see below).

Type material. Holotype LACM-AHF 1227 and paratypes LACM-AHF 1228 (1), and LACM-AHF 1229 (10), Golden Grove, near Chateaubelair Bay (13°17'18"N, 61°14'25"W), Saint Vincent, Saint Vincent and the Grenadines, 31 July 1972, 435 m above sea level, spring pool in *Colocasia* (Araceae) swamp, Coll. J.J. Rankin.

Description. Holotype complete, 32 mm long, 1 mm wide at chaetiger 10, 95 chaetigers; body with several parapodia removed in middle region, otherwise in good condition. Paratypes complete, in good conditions, 10–30 mm long, 1–2 mm wide, 62–95 chaetigers. Body pale, without pigmentation (Fig. 2A, B).

Prostomium wider than long, anterior margin entire, groove present; antennae cirriform, as long as prostomium; eyes absent (Fig. 2A, C). Tentacular ring as long as first chaetiger; three pairs of tentacular cirri, longest one reach chaetiger 3 (Fig. 2A, C); cirrophores 1.5–2.0 times longer than wide. Pharynx dissected; jaws with layer running throughout cutting edge, two distal teeth, with bifid appearance (Fig. 2E). Pharynx with cushion-shaped papillae on area VI (Fig. 2D), papillae rounded, laterally fused; other areas smooth.

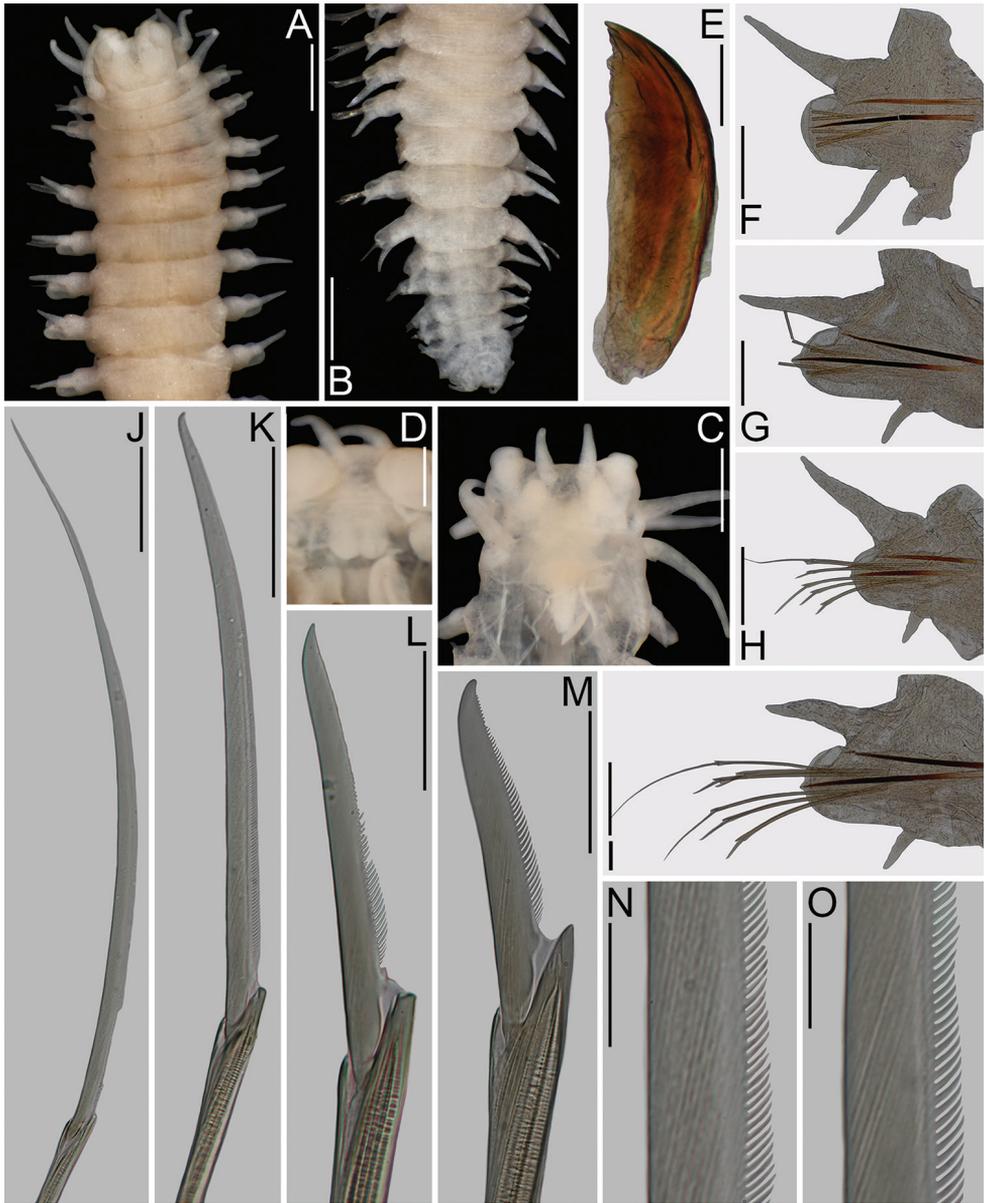


Figure 2. *Namanereis christopheri* sp. n. **A, B, F–O** Holotype LACM-AHF 1227 **C–E** paratype LACM-AHF 1229 **A** Anterior end, dorsal view **B** Posterior end, dorsal view **C** Close-up of prostomium **D** Areas V and VI, pharynx dissected **E** Right jaw, dorsal view **F** Chaetiger 5, right parapodium **G** Chaetiger 21, right parapodium **H** Chaetiger 49, right parapodium **I** Chaetiger 90, right parapodium **J** Supra-acicular sesquigomph spiniger, chaetiger 49 **K** Sub-acicular heterogomph falciger, chaetiger 49 **L** Supra-acicular heterogomph falciger, chaetiger 49 **M** Sub-acicular heterogomph falciger, chaetiger 49 **N** Close-up of blade, supra-acicular sesquigomph spiniger, chaetiger 49 **O** Close-up of blade, supra-acicular heterogomph falciger, chaetiger 49. Scale bars: 0.5 mm (**A–D**); 0.1 mm (**E**); 0.1 mm (**F–I**); 50 μ m (**J, K**); 30 μ m (**L, M**); 10 μ m (**N, O**).

Parapodial cirri pattern: Dorsal cirri longer than neuropodial lobes, basally inserted throughout body. Ventral cirri shorter than neuropodial lobes, basally inserted throughout body.

In anterior chaetigers (Fig. 2F), dorsal cirri 3 times longer than neuropodial lobes; neuropodial lobes rounded, as long as wide, as long as ventral cirri; ventral cirri half as long as dorsal ones. In middle chaetigers (Fig. 2G–H), dorsal cirri twice longer than neuropodial lobes; neuropodial lobes rounded, slightly longer than wide, twice longer than ventral cirri; ventral cirri one-third to one-half as long as dorsal ones. In posterior chaetigers (Fig. 2I), dorsal cirri twice longer than neuropodial lobes; neuropodial lobes rounded, as long as wide, 3 times longer than ventral cirri; ventral cirri half as long as dorsal ones.

Notochaetae absent. Neurochaetae in type D arrangement, i.e. supra-acicular chaetae heterogomph falcigers and sesquigomph spinigers in pre- and post-acicular fascicles respectively; sub-acicular chaetae heterogomph falcigers with short and long blades in pre-acicular fascicles.

Supra-acicular sesquigomph spiniger pectinated, teeth minute, decreasing slightly in size towards tip (Fig. 2J, N); supra-acicular heterogomph falcigers pectinated, teeth minute, decreasing slightly in length towards tip (Fig. 2L). Sub-acicular falcigers pectinated, teeth minute, tip falcate, decreasing slightly in size towards tip; upper heterogomph falcigers long bladed, blades 2–3 times longer than lower ones (Fig. 2K, O), lower falcigers stouter than upper ones (Fig. 2L–M).

Pygidium tripartite; anal cirri cirriform, short, as long as last chaetiger (Fig. 2B).

Remarks. The material of this species was previously examined by Glasby (1999) and identified as *N. cavernicola*. The three vials from the Los Angeles Museum include two labels. One label has the name “*Lycastopsis F*”, identified in 1988, and includes the designation of holotypes and paratypes. The other label has another unpublished manuscript name, dated 1990. Likely, Glasby initially regarded it as a new species, but later he changed his mind and included them with *N. cavernicola* (Glasby 1999) resulting in an amphiamerican distribution. The incised anterior margin of prostomium and other features were compared with *Lycastoides alticola* but not with *N. cavernicola*, arguing that the only difference among Caribbean and Pacific materials were the longer dorsal cirri in *N. cavernicola* (Glasby 1999: 85). The result was a description of *N. cavernicola* with mixed features and encompassing high ranges of variation.

On the other hand, *N. christopheri* sp. n. and *N. cavernicola* share some features as having falcigers with relative long blades and blades with several minute teeth. However, they have some important differences. First, *N. christopheri* sp. n. has an anterior margin of prostomium entire and antennae are shorter than prostomium, while in *N. cavernicola* the anterior margin is incised and antennae are longer than prostomium. Further, tentacular cirri in *N. christopheri* sp. n. are smooth and reach chaetiger 3, while in *N. cavernicola* they are annulated and reach chaetiger 5–6. In addition, *N. christopheri* sp. has jaws much broader than *N. cavernicola*. *N. cavernicola* has neuropodial lobes tapered, subconical with pointed tips, two or three times longer than wide, while in *N. christopheri* sp. n. they are rounded and as long as wide; and parapodial cirri in *N. cavernicola* are thinner than in *N. christopheri* sp. n.

As indicated in the key below, *N. christopheri* sp. n. is also closely related to *N. hummelincki*, differing mainly in chaetal features as Glasby (1999: 85) previously noted. In *N. christopheri* the blades of sub-acicular falcigers and spinigers have several, minute teeth and they have a similar size along the cutting edge, while in *N. hummelincki* they have fewer teeth, and the basal ones are notably longer than medial and distal ones.

Glasby (1999: 85) noted, after the revision of parapodia of *N. cavernicola*, several grades of curvature in notoaciculae and even in neuroaciculae, which are absent in *N. christopheri* sp. n., and considered them as artifacts of preservation. However, since all notoaciculae observed had recurved tips, this feature is regarded here as specific one. Glasby (1999: 74) thought that these features, together with the presence of articulated antennae and tentacular cirri were not sufficient to recognize *Lycastilla* as distinct, and this decision is herein corroborated. Finally, all specimens of *N. christopheri* sp. n. were whole-mounted and examined under microscope, no spinigers were found in sub-acicular fascicles; the long-bladed, uppermost sub-acicular chaetae in Fig. 2H–I have falcate tips, i.e., they are falcigers. The species does not replace upper long-bladed falcigers by spinigers toward posterior chaetigers, sharing this peculiarity with *N. gesae*.

Key for *Namanereis* species from the world

(Modified after Glasby 1999)

1	Four pairs of tentacular cirri.....	2
–	Three pairs of tentacular cirri	4
2	Prostomium with entire anterior margin.....	
	... <i>N. quadraticeps</i> (Blanchard in Gay, 1849) (Strait of Magellanes, Chile) ¹	
–	Prostomium with cleft anterior margin	3
3	Dorsal cirri shorter than neuroacicular ligule on posterior chaetigers	
 <i>N. minuta</i> Glasby, 1999 (Grand'Anse, Haiti)	
–	Dorsal cirri longer than neuroacicular ligule on posterior chaetigers.....	
 <i>N. stocki</i> Glasby, 1999 (St. Ann's Bay, Jamaica)	
4	With antennae.....	5
–	Without antennae.....	
 <i>N. malaitae</i> (Gibbs, 1971) (Malaita, Solomon Islands)	
5	Eyes present	6
–	Eyes absent	11
6	Eyes conspicuous, separate	7
–	Eyes barely visible, coalesced	
 <i>N. sublittoralis</i> Glasby, 1999 (Smoke Alley Well, Sint Eustatius)	
7	Supra-acicular spinigers present	8
–	Supra-acicular spinigers absent.....	
 <i>N. pontica</i> (Bobretzky, 1872) (Bay of Sevastopol, Black Sea)	

8	Falcigers with long, strongly falcate tips, one half to one third of cutting edge of blade without teeth.....	9
–	Falcigers with short, weakly falcate tips, teeth on almost all length of cutting edge of blade.....	10
9	Falcigers with blades longer than boss of the joint (i.e. long blades)	
 <i>N. amboinensis</i> (Pflugfelder, 1933) (Ambon Island, Indonesia)	
–	Falcigers with blades as long as boss of the joint (i.e. short blades)	
 <i>N. riojai</i> (Bastida-Zavala, 1990) (La Paz Bay, Mexico)	
10	Jaws with 9 subterminal teeth (6–14).....	
 <i>N. catarractarum</i> (Feuerborn, 1931) (Bedali, Java)	
–	Jaws with 5 subterminal teeth (5–8).....	
	<i>N. littoralis</i> (Müller & Grube in Grube, 1872) (Santa Catarina Island, Brazil) ¹	
11	Jaws with terminal and subterminal teeth	12
–	Jaws with two bifid distal teeth and smooth cutting edge.....	15
12	Prostomium with anterior margin entire.....	13
–	Prostomium with anterior margin cleft.....	
	<i>N. tiriteae</i> (Winterbourn, 1969) (Turitea Stream, North Island, New Zealand)	
13	Dorsal cirri shorter or subequal than neuropodial lobes throughout body....	14
–	Dorsal cirri longer than neuropodial lobes throughout body.....	
	<i>N. beroni</i> Hartmann-Schröder & Marinov, 1977 (Bem Tem, Papua New Guinea)	
14	Supra-acicular falcigers with several, minute teeth (ca. 30)	
	<i>N. gesae</i> Fiege & Van Damme, 2002 (Abd al-Kuri Island, Socotra Archipelago, Yemen)	
–	Supra-acicular falcigers with few, minute teeth (7–11)	
	.. <i>N. pilbarensis</i> Glasby, Fiege & Van Damme, 2014 (Pilbara Region, Australia)	
15	Prostomium with anterior margin cleft	16
–	Prostomium with anterior margin entire.....	17
16	Dorsal cirri longer than neuropodial lobes in first chaetigers.....	
 <i>N. araps</i> Glasby, 1997 (Nakhal, Oman)	
–	Dorsal cirri shorter than to subequal than neuropodial lobes in first chaetigers	
	<i>N. cavernicola</i> (Solís-Weiss & Espinasa, 1991) (Izote Cavern, Mexico)	
17	Supra-acicular falcigers with pectinate, minute teeth.....	18
–	Supra-acicular falcigers with serrated, coarse teeth.....	
 <i>N. serratis</i> Glasby, 1999 (Étang Saumâtre, Haiti)	
18	Upper sub-acicular falcigers with blades two or more times longer than lower falcigers.....	19
–	Upper and lower sub-acicular falcigers with subequal blades	
 <i>N. socotrensis</i> Glasby, Fiege & Van Damme, 2014 (Socotra Island, Yemen)	
19	Supra-acicular falcigers with teeth increasing their length greatly basally	
 <i>N. hummelincki</i> (Augener, 1933) (Fontein, Bonaire)	
–	Supra-acicular falcigers with teeth increasing their length slightly medially ...	
 <i>N. christopheri</i> sp. n. (Saint Vincent)	

¹Species groups of these species were not considered, but only information of type materials.

Ratios of elongation

Elongation of parapodial cirri. The results of elongation ratios of parapodial cirri are depicted in Fig. 3. Most *Namalycastis* species had high difference between anterior and posterior ratios ($D_{p-a} > 1$), whilst five had slight or no difference ($D_{p-a} \leq 1$) (Fig. 3A). On the other hand, eight *Namanereis* had posterior dorsal cirri slightly longer than anterior ones, ($1 \geq D_{p-a} > 0$) while in 11 they were subequal or shorter ($D_{p-a} \leq 0$) (Fig. 3A). In regard to elongation of dorsal cirri towards posterior segments, stygobiont *Namanereis* were not show evident differences in comparison to epigean *Namanereis* (Fig. 3A), excepting *N. cavernicola* having high difference ($4 \geq D_{p-a} > 2$).

Based on ratios of anterior chaetigers only (Fig. 3B), most species of both genera had dorsal cirri longer than neuroacicular lobes ($A_{Ld/Ln} > 1$). Indeed, *Namanereis araps*, *N. christopheri* sp. n. and *N. serratis* had the greatest $A_{Ld/Ln}$ among stygobiont species ($A_{Ld/Ln} > 2$), but the epigean species *N. amboinensis* had similar ratios as well. Next, eight stygobiont and three epigean *Namanereis* shared the second range with dorsal cirri slightly longer than neuroacicular lobes ($2 \geq A_{Ld/Ln} > 1$), while in three stygobiont and three epigean *Namanereis* they were shorter, occupying the third range ($A_{Ld/Ln} \leq 1$). *Namalycastis* species were present in all ranges, with more representatives in the second one ($2 \geq A_{Ld/Ln} > 1$).

Elongation of tentacular cirri. The resultant histogram of Lpt/Wp ratios is shown in Fig. 4A. Most stygobiont *Namanereis* had high ratios and four occupy the first places with the highest ones ($2 \geq Lpt/Wp > 1$), but other four species had tentacular cirri subequal or shorter than prostomium ($Lpt/Wp \leq 1$); moreover, some *Namalycastis* and epigean *Namanereis* had similar ratios than some stygobiont *Namanereis* in both ranges (Fig. 4A). Excepting *N. pontica*, most epigean *Namanereis* had tentacular cirri subequal or shorter than prostomium.

Elongation of chaetae. The results of D_{d-v} for most species is shown in Fig. 4B. Eight stygobiont *Namanereis* species had high distances between Dm and Vm ($D_{d-v} > 1$), occupying the first places (Fig. 4B). At the same range, and between the stygobiont *Namanereis* with the highest difference (-11.3), *N. christopheri* sp. n., and the lowest one (-2.7), *N. stocki*, there are six *Namalycastis* species, four reported with elongated falcigers, excepting *N. hawaiiensis* and *N. fauveli* (Glasby 1999) (Fig. 4B). Following this group, there are four *Namalycastis* species with moderate differences ($3 > D_{d-v} > 1$) and ten with lower ones ($D_{d-v} \leq 1$), while all epigean *Namanereis* species have low differences ($D_{d-v} \leq 1$) (Fig. 4B).

Discussion

Re-assessment of morphological adaptations of Namanereidinae

Typical morphology of stygobiont *Namanereis* are depicted in figures of *N. cavernicola* Solís-Weiss & Espinasa, 1990 and *N. christopheri* sp. n. (Figs 1 and 2, respectively). In

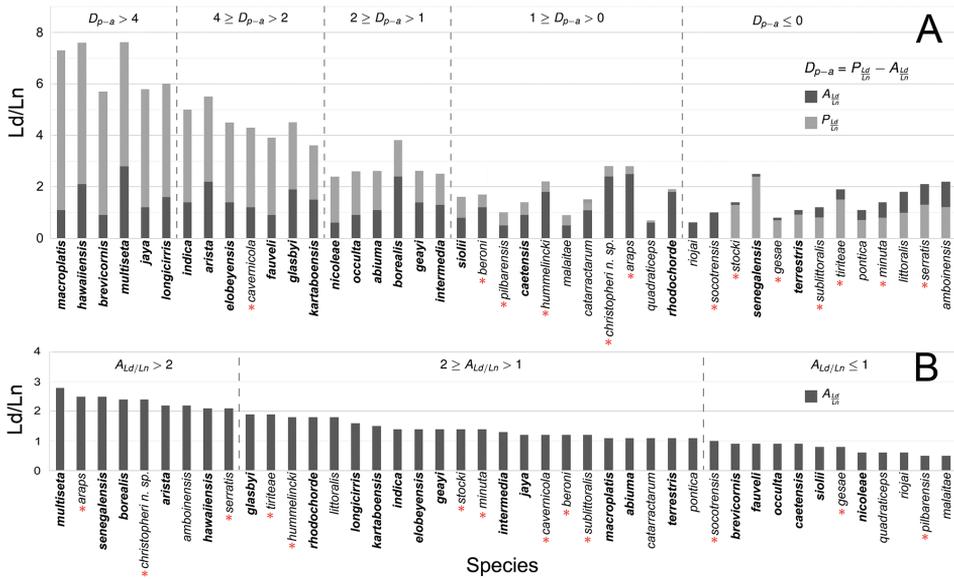


Figure 3. Histograms showing length ratios of parapodial cirri among *Namalycastis* (boldface) and *Namanereis* (lightface) species. **A** Ratios between length of dorsal cirri (Ld) and length of neuroacicular lobe (Ln) at anterior ($A_{Ld/Ln}$) and posterior chaetigers ($P_{Ld/Ln}$), and difference among them (D_{p-a}). **B** Ratios between length of dorsal cirri (Ld) and length of neuroacicular lobe (Ln) at anterior chaetigers ($A_{Ld/Ln}$) only. Sorted from highest to lowest ratios; asterisks highlight stygobiont *Namanereis*.

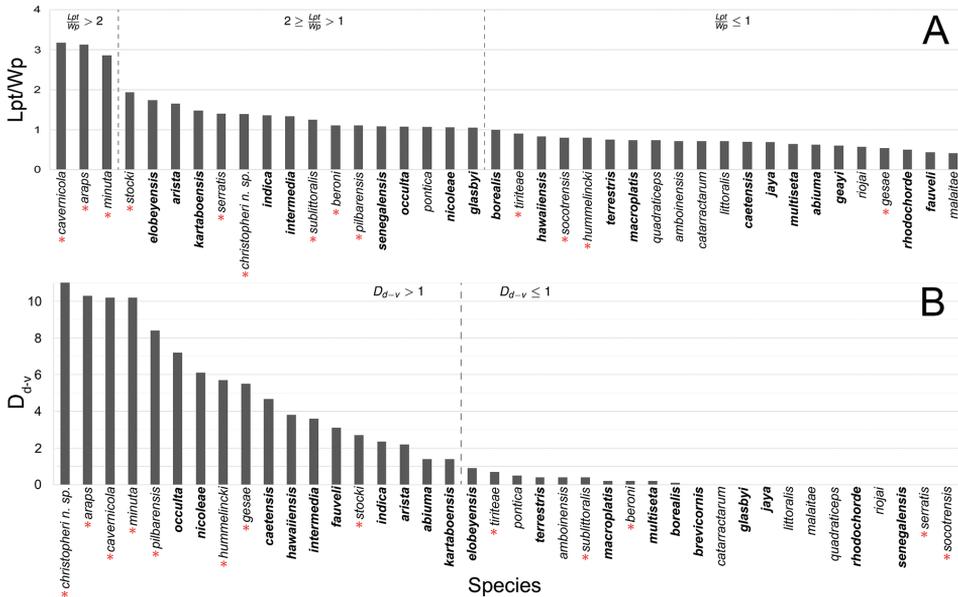


Figure 4. Histograms showing length ratios of some troglomorphic features among *Namalycastis* (boldface) and *Namanereis* (lightface) species. **A** Ratios between length of tentacular cirri (Lpt) and wide of prostomium (Wp). **B** Difference (D_{d-v}) between ratios of dorsalmost (Dm) and ventralmost (Vm) falcigers at chaetiger 10. Sorted from highest to lowest ratios; asterisks highlight stygobiont *Namanereis*.

order to illustrate troglomorphic features in other namanereidins and facilitate comparison, a species from Bonaire, *Namanereis hummelincki* (Augener, 1933), and three other namanereidins from Chetumal Bay, Mexican Caribbean, *Namalycastis occulta* Conde-Vela, 2013, *N. borealis* Glasby, 1999 and *Namanereis* cf. *amboinensis*, were examined (Fig. 5). None of the specimens of the last four species were found in caves but in aphotic environments: Bonaire specimens were found in a cement gutter from a spring with mud and decayed leaves (Wesenberg-Lund 1958: 4–5), whereas Chetumal Bay specimens were found in muddy and sandy bottoms under red mangrove decayed leaves, and in sheltered, shaded places by dense mangrove patches.

Notably, *N. hummelincki*, *N. occulta*, *N. cavernicola*, and *N. christopheri* sp. n. share loss of both eyes and body pigmentation (Figs 5A, C, 1A and 2A, respectively), the presence of bifid jaws (Figs 2E, 5J, 7D–F) and clear elongation of blades in sub-acicular falcigers from the dorsalmost position regard to ventralmost ones (Figs 2J–M, 5M). On the other hand, *Namanereis* cf. *amboinensis* shares the loss of pigmentation with species above mentioned, but its parapodial morphology (Fig. 5F) is quite similar to *N. hummelincki* and *N. christopheri* sp. n. regarding the relative length and shape of dorsal cirri along body (Figs 5E and 2F–I, respectively). In contrast, *N. occulta* is more similar to *N. borealis* in regard to those features (Fig. 5G, H, respectively). Furthermore, *N. cf. amboinensis* and *N. borealis* share presence of eyes, serrated jaws and sub-acicular falcigers with subequal blades (Fig. 5B, I, L and 5D, K, N, respectively). Finally, length and shape of both tentacular and parapodial cirri of *N. cavernicola* (Fig. 1A, F–H) do not resemble to any of the last species.

Glasby et al. (2014: 31) used *Namanereis araps* as example of the elongation of appendages observed in subterranean *Namanereis* species and absent in their “marine surface-dwelling counterparts”: the tentacular cirri are long and annulated and its posterodorsal pair extends beyond chaetiger 4; dorsal cirri generally are slender and subequal to, or longer than, respective neuroacicular lobes; and all have neuropodial heterogomph falcigers increasing in blade’s length toward posterior chaetigers (Glasby 1997). If elongation was restricted to stygobiont *Namanereis* species, a clear clustering of these ones in the histograms is expected, having the highest ratios. Indeed, *N. araps* and three or four stygobiont *Namanereis* had the highest ratios of elongation of tentacular cirri and chaetae, but not for elongation of dorsal cirri in anterior chaetigers, and even most stygobiont *Namanereis* were ranked along with epigeic *Namanereis* and *Namalycastis* in all ranges (Figs 3A–B, 4A–B). Therefore, not all stygobiont *Namanereis* have evident elongation of dorsal cirri in anterior segments, but even they have similar ratios than epigeic *Namanereis*.

A possible explanation of the similar $A_{Ld/Ln}$ in stygobiont *Namanereis* and epigeic *Namanereis* and *Namalycastis* species is related to the shape of neuroacicular lobes. In some species, neuroacicular lobes are subconical, i.e., longer than wide with pointed tips, while in other they are rounded, i.e., as long as wide with rounded tips; then, species with relatively short dorsal cirri and rounded neuroacicular lobes have high ratios because rounded lobes are shorter respect to subconical ones. The effect of this difference is appreciable in *N. araps*, *N. amboinensis* and *N. christopheri* sp. n.: they have similar $A_{Ld/Ln}$ but with evident subconical neuroacicular lobes in the former spe-

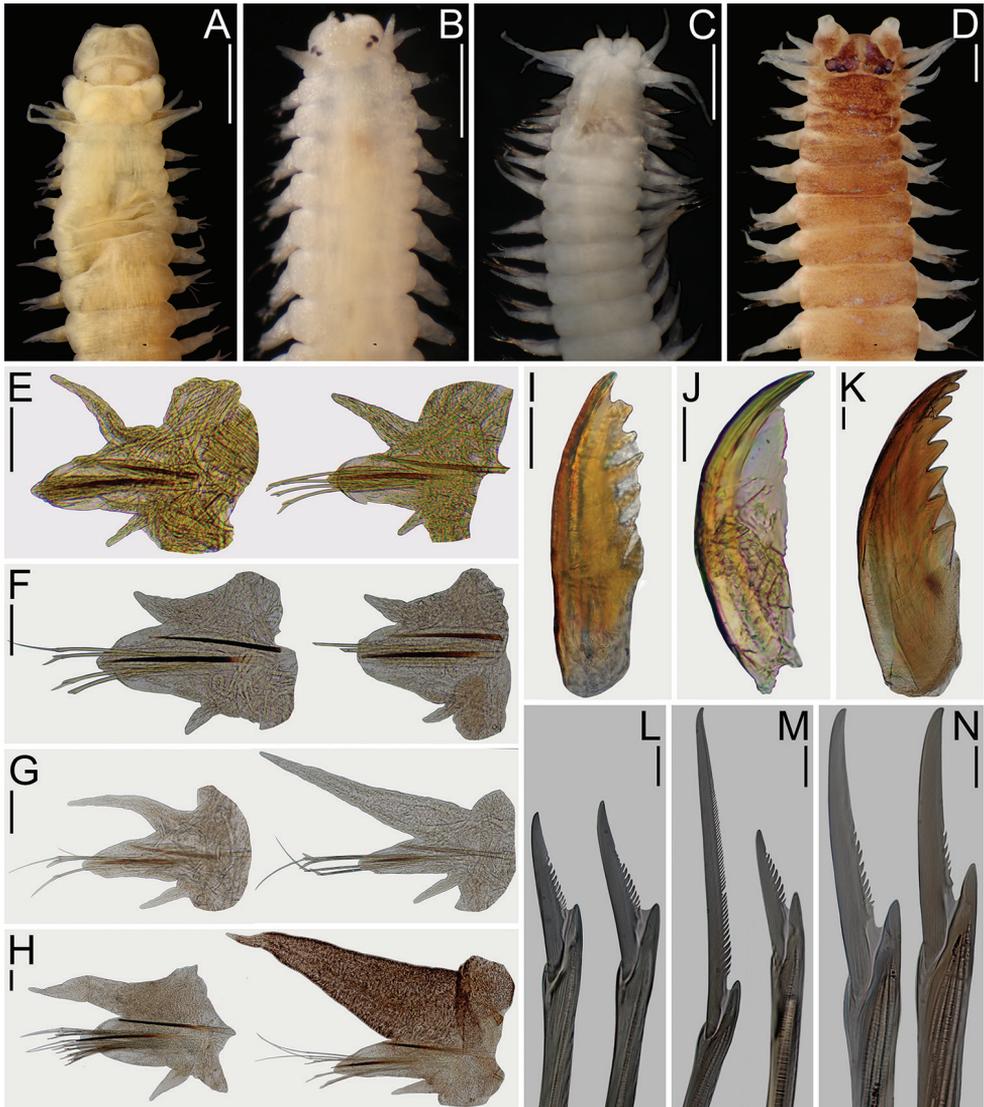


Figure 5. Morphological comparison among namanereidins. *Namanereis hummelincki* (**A, E**) (USNM 29715, 29716); *N. cf. amboinensis* (**B, F, I, L**) (ECOSUR P-2902); *Namalycastis occulta* (**C, G, J, M**) (ECOSUR P-2649); *N. borealis* **D, H, K, N. A-D** (ECOSUR P-2651). Anterior ends, dorsal view **E-H** Right parapodia from anterior (10, left) and posterior (right) chaetigers **I-K** Left jaws, dorsal view **L-M** Dorsalmost (left) and ventralmost (right) sub-acicular, heterogomph falcigers from chaetiger 10. Scale bars: 0.5 mm (**A-D**); 0.1 mm (**E-H**); 50 μ m (**I-K**); 10 μ m (**L-N**).

cies and rounded ones in the last two (Glasby 1997; 1999; this paper). However, most *Namalycastis* species have subconical neuroacicular lobes and dorsal cirri longer than lobes, while only *N. araps*, *N. minuta* and *N. tiriteae* have remarkable subconical lobes (Glasby 1997, 1999).

As expected, most *Namalycastis* had high values of D_{p-a} since elongation of dorsal cirri toward posterior chaetigers is usual of that genus (Glasby 1999), but in *N. caetensis*, *N. rhodochorde*, *N. senegalensis*, *N. siolii* and *N. terrestris* there is no evident elongation of dorsal cirri in posterior chaetigers ($D_{p-a} \leq 1$). Although, they have a notable basal widening and flattening in comparison to anterior chaetigers (Glasby 1999), being a remarkable morphological change used as diagnostic for the genus (Glasby 1999). In other species such as *N. nicoleae* Glasby 1999, *N. occulta* and in *N. intermedia* Glasby, 1999, this feature is weakly developed, and the three had similar D_{p-a} (Fig. 3A). On the other hand, eight *Namanereis* have posterior dorsal cirri slightly longer than anterior ones, while in 11 they are subequal or shorter. Notably, *N. cavernicola* is the only species ranked together with *Namalycastis* species with high differences, however dorsal cirri do not become foliose as in the latter ones. In regard to elongation of dorsal cirri towards posterior segments, stygobiont *Namanereis* do not show evident differences in comparison to epigean *Namanereis* (Fig. 3A).

Based on the results of the analysis performed (Fig. 4A, B), the elongation of both sub-acicular, dorsalmost falcigers and tentacular cirri are not restricted to stygobiont *Namanereis*. As expected, the eight *Namanereis* species with $D_{d-v} > 1$ are those ones previously described as bearing elongated neuropodial falcigers. Only four *Namalycastis* have been described with elongated falcigers (*N. caetensis*, *N. intermedia*, *N. occulta* and *N. nicoleae*), but six more had similar ratios as well (Fig. 4B). Similarly, most stygobiont *Namanereis* had elongated tentacular cirri (Fig. 4A), and even the first four species (including *N. araps*) have jointed tentacular cirri (Glasby 1997, 1999), but this feature cannot be regarded exclusively as an adaptation to subterranean habitats, because it is also present in epigean species such as *Namalycastis elobeyensis*, *N. indica* and *N. kartaboensis* (Glasby 1999), and even outside namanereidins. All *Namalycastis* and epigean *Namanereis* with clear elongation of upper neuropodial falcigers occur in freshwater or brackish environments as ponds, streams and estuaries, and in muddy to sandy sediments (Glasby 1999, Conde-Vela 2013, Alves and Santos 2016), but not in subterranean habitats.

As shown above, the elongation and articulation of appendages are not restricted neither to *Namanereis* species nor stygobiont ones, but are rather present in several species occurring in different habitats. Some confusion can be led by evaluating the elongation of appendages *a priori* as troglomorphic features. For example, Heads (2010) described a new fossil spider cricket (Insecta: Orthoptera), *Araneogrillus dylani*, embedded into amber, showing troglomorphic features as the elongation of structures, as in other closely related troglobitic genera. Given its inclusion in amber, *A. dylani* presumably lived in plant litter, so such troglomorphies were not obtained the result of troglobitic habits. His phylogenetic analysis of subtribe Amphicustina showed that the troglomorphic features are not restricted to troglobitic species, and that those troglomorphies evolved at least twice (Heads 2010). Therefore, the presence of elongated structures resulted from exaptation and were later conserved in recent troglobitic species, and not the result of adaptation to current cave habitats. So, at least the elongation of appendages in namanereidins seems to respond to independent selective pressures

and not exclusively generated in cave environments. Furthermore, since most species showing elongation do not have a close phylogenetic relationship (Glasby 1999, Alves and Santos 2016), and the diversity of habitats they currently occur, it suggests that this feature evolved at least twice, asynchronously and in distinct scenarios.

While the factors driving the elongation of appendages in namanereidins are elusive, the evidence in other groups is weak or inconclusive. For example, the elongation of some segments of legs seems to be unique among stygobiont millipedes, but not the elongation of antennae (Liu et al. 2017). On the other hand, Delić et al. (2016: 46) found for the stygobiont amphipod *Niphargus croaticus* (Jurinac, 1887) that elongation in legs is more related with local factors as low of absent water flow and interspecific competition, rather than food availability or time of colonization; moreover, they found a high differentiation among closely related populations, suggesting a fast morphological change regarding this feature (p. 46). It is unknown the function of evident elongation of specific sub-acicular falcigers, especially after relationships among length and shape of chaetae and type of substrate or movement abilities are uncertain (Merz and Edwards 1998, Hesselberg and Vincent 2006a, 2006b). Being that most namanereidins (especially *Namanereis* species) have small body size and distinct parapodial morphology when compared with other nereidids, a further experimental evaluation is needed to discard possible relationships with both biotic and abiotic factors.

Neurochaetal arrangement. The arrangement of neurochaetae deserves additional comments. Glasby (1999: 7–8) proposed a classification based on the neurochaetae arrangement respect to the neuroacacula, along discrete bundles or fascicles, depicted in Fig. 5. Four main neuropodial fascicles (Fig. 6A) can be discerned, and six distinct arrangements were observed depending on the type of chaetae in each fascicle; *Namalycastis* has type A or B arrangements, while *Namanereis* has C, D, E or F (Glasby 1999: 7). Some problems with types C and D are herein addressed, and “pre-” or “postacicular” fascicles in the remaining section must be assumed that they are referred as sub-acicular ones, unless otherwise indicated.

By definition, types C and D do not have chaetae in postacicular fascicles (Fig. 6D and 6E, respectively). The main difference between them is that type D has heterogomph spinigers and heterogomph falcigers with elongated blades in preacicular positions (Fig. 6B), whereas type C presents heterogomph falcigers without elongated blades only. These falcigers with elongated blades are commonly called “pseudospinigers” and, if parapodium is mounted laterally, they are the dorsalmost falcigers, occupying this position in all cases, notably longer than remaining falcigers but shorter than spinigers (Figs 5M, 6B), and having a terminal hook or falcate tip, as is the case for falcigers (Glasby 1997: 160). However, they are just long-bladed falcigers as indicated by their falcate tips, such that the dismissal of the term had been proposed (Conde-Vela 2013, Alves and Santos 2016). Some inconsistencies were highlighted by Glasby (1999: 87) about the type D present in some *Namanereis* species; he found that it is difficult to state if “pseudospinigers” are in pre- or postacicular position, and he regarded them as preacicular for cladistics analysis; moreover, Fiege and Van Damme (2002: 241) and Conde-Vela (2013: 481) found the same problem for *Namanereis gesae* and *Namalycas-*

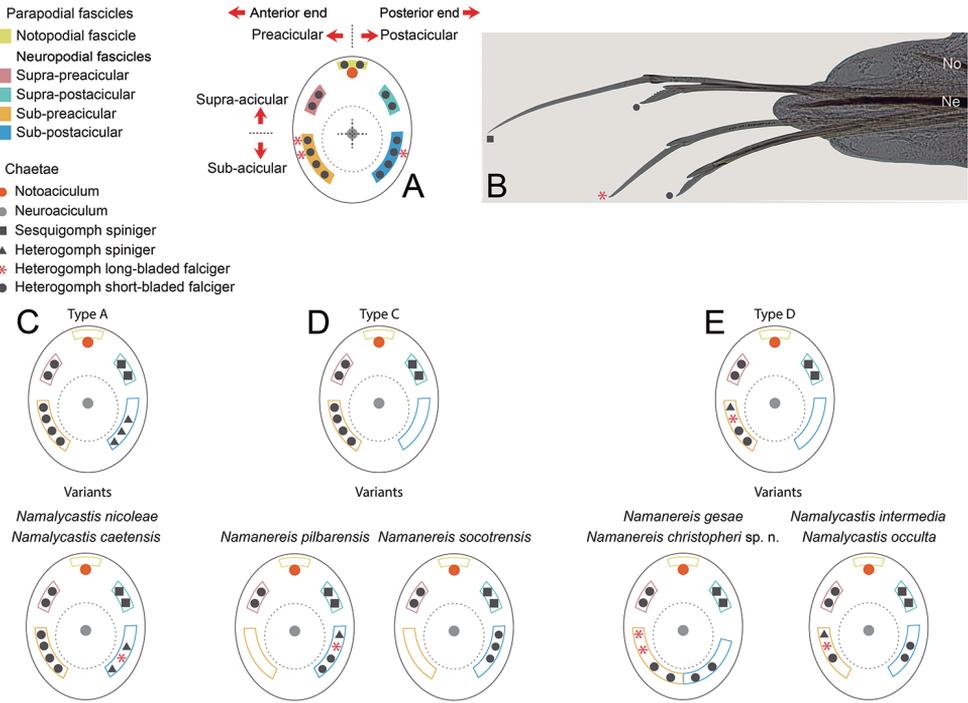


Figure 6. Chaetal arrangement of some namanereidins referred in this study. **A** Scheme showing the parapodial fascicles and their positions in relation to neuroaciculum **B** Neuropodial lobe of right parapodium from chaetiger 10 of *Namalycastis occulta*, showing the position of chaetae in type D species when mounted **C–E** Chaetal arrangement of types A, C and E, and their variants found in literature (modified from Glasby 1999, Fig. 1).

is occulta, respectively. A possible variant of type D is found in *N. gesae* and *N. christopheri* sp. n. (Fig. 6E), where sub-preacicular heterogomph spinigers were not found.

On the other hand, type A arrangement, typical of *Namalycastis* species, is characterized by having only falcigers in both supra- and sub-preacicular fascicles, and only spinigers in both supra- and sub-postacicular ones (Fig. 6C). Before *N. occulta*, the only *Namalycastis* species described with “pseudospinigers” was *N. nicoleae* Glasby, 1999 that has them in postacicular fascicles, together with spinigers, but considered as a type A arrangement without further explanation (Glasby 1999: 65). Later, Glasby et al. (2014: 31) stated that the position of these “pseudospinigers” is not homologous with those found in *Namanereis* species in preacicular fascicles. In the same work (p. 25), the new species *Namanereis pilbarens* was described as having falcigers and “bifid pseudospinigers” in postacicular fascicles and type C arrangement without further explanation; the other new species, *N. socotrensis*, was described as having type C arrangement but with falcigers in postacicular fascicles instead of preacicular ones (p. 29), requiring a reassessment in both species. In order to avoid confusion, a term should not be used for two structures with likely distinct

origin or function. Since “pseudospinigers” might not be homologous structures, this is another indication that such term must be dismissed (Conde-Vela 2013, Alves and Santos 2016).

Another species from the Gulf of Mexico, *Namalycastis intermedia*, was described as having a type A arrangement, but heterogomph falcigers in both supra- and sub-preacicular fascicles are replaced by heterogomph spinigers toward posterior chaetigers (Glasby 1999: 55); also, elongated falcigers (“pseudospinigers-like”) were described in upper, sub-acicular position (Glasby 1999, fig. 22g) and since it has a type A arrangement, these elongated falcigers must be present in preacicular fascicles, as corroborated after the revision of type material. The replacement of falcigers (short blades) by spinigers (long blades) in posterior chaetigers in both supra- and sub-preacicular fascicles is also shown by *Namalycastis arista*, *N. macroplatis* and *N. senegalensis* (Glasby 1999: 57). In a recent contribution, Alves and Santos (2016: 504) pointed out the presence of “elongated falcigers” in postacicular fascicles in their new species *Namalycastis caetensis*, regarded it as a relevant feature (p. 505) and included in the diagnosis of the genus (p. 502); the type of arrangement in this species was not stated, but based on the description it corresponds to a modified type A.

Summarizing, *Namalycastis caetensis*, *N. intermedia* and *N. nicoleae* are species with type A arrangements but also with elongated falcigers or “pseudospinigers” in pre- or postacicular fascicles, resembling the type D arrangement. However, in type A species, typically the chaetae are clearly positioned in their fascicles and are abundant (e.g. Glasby 1999: 124–125), whereas in type D their position sometimes is ambiguous and they are in low number (pp. 126–127). Based on revision of type material, here *Namalycastis intermedia* is stated as having type D arrangement instead of type A (Glasby 1999: 55). A similar analysis is required for *Namanereis pilbarensis* and *N. socotrensis*, both described with type C neurochaetae, although it can be advanced that *N. pilbarensis* has type D neurochaetae after the presence of “pseudospinigers” and that *N. socotrensis* has sub-acicular falcigers in preacicular fascicles; if not, additional new types or arrangement might be needed.

Jaws. The jaws of nereidids are formed by a cross-linked matrix of proteins, where the hardness and stiffness properties are due to the presence of high levels of glycine and histidine, halogens (especially chlorine) and zinc; the distribution of these elements is not homogeneous throughout jaw, but is more concentrated at the tip (Lichtenegger et al. 2003, Birkedal et al. 2006, Broomell et al. 2006, 2008), and this unequal distribution is presumably related to the pigmentation gradient from tip (darker) to base (lighter) (Khan et al. 2006). This tendency in distribution of elements is observed in other polychaetes and even in fossils, suggesting a functional significance (Eriksson and Elfman 2000), although direct corroboration in nereidids could not be possible due to their easy degradation (Colbath 1988). On the other hand, the jaws grow throughout worm’s life, and this growth seems to be restricted to the basal section (Paxton 1980). This agrees with the ontogenetic development, where the terminal or ‘primary’ tooth is formed first, with subsequent addition of basal teeth (Bass and Brafield 1972, Tzetlin and Purschke 2005, Fischer et al. 2010).

It has been suggested that bifid jaws in stygobiont *Namanereis* are a derived condition from the typically serrated jaws in nereidids, implying that species with bifid jaws arise from other *Namanereis* or *Namalycastis* ancestor with serrated jaws (Glasby 1999: 23, Glasby et al. 2014: 32–33). There are some evidences supporting this hypothesis. All namanereidins have ‘ensheathed’ teeth, i.e., basal and most subterminal teeth are surrounded by a layer, always lighter than remaining jaw (e.g. Fig. 5I–K); this layer can be observed in other nereidids but it has been less frequently recorded (pers. obs.). In most cases, terminal and some subterminal teeth are not covered by the layer, and since the terminal teeth are formed first, it follows that the layer appears in later stages. Further, because this layer is lighter than remaining jaw, the ensheathed teeth can be seen when jaws are mounted for observation under light microscope, but from the surface teeth cannot not be seen. This clearly occurs in *N. tiriteae* (Winterbourn, 1969) that has several teeth observed by transparency, but show up as a smooth cutting edge on SEM photographs (Gray et al. 2009, Fig. 3), and in *N. stocki* Glasby, 1999 (Glasby 1999, Fig. 48b). Furthermore, some species as *N. socotrensensis* Glasby, Fiege & Van Damme, 2014 have remnants of teeth, now fully covered and fused with the layer (Glasby et al. 2014, Fig. 6E).

Glasby et al. (2014: 32) proposed that bifid jaws are formed by sclerotization of subterminal teeth, leading to some likely scenarios of formation. Initially, the spaces among original teeth would be “filled” by growth of new layers of proteins, forming a continuous plate. This means that jaws with deeply incised, but ensheathed teeth, as *N. tiriteae* and *N. stocki* arise from another one with that kind of teeth, however there are no records about neither namanereidin nor even nereidid species with so sharp teeth. Also, it means that remnants of original teeth must be clearly visible in the plate as in the last two species, but this does not occur in most cases. Conversely, in the second scenario, the original teeth had an overgrowth and filled the spaces among them. If true, the resulting plate must have a similar pigmentation (and consistence) than the remnant jaw, but in fact, this plate is always lighter. Moreover, this scenario cannot explain the observed jaws in *N. tiriteae* and *N. stocki* with remnant ensheathed teeth.

Based upon these previous ideas, another plausible scenario leading to bifid jaws is a hypothetical reduction or loss of teeth (Fig. 7). In the first stage (Fig. 7A), the jaws have a fully dentate cutting edge, with an incipient, barely visible layer running along a few of the most-basal teeth; tips of teeth are rounded or near so, and barely separated from other adjacent teeth or having shallow incisions along the cutting edge. In subsequent stages, the layer continues developing by extending itself along other teeth, and by growing towards tips of teeth; first the layer becomes a slight cover between basal, adjacent teeth (Fig. 7B), and then the layer completely covers basal teeth (Fig. 7C). Simultaneously, during these two latter stages, the teeth start to reduce and become narrower, resulting in incisions along the cutting edge becoming deeper. Further growth of the layer would increase its extension, covering all teeth except the two distal ones, such that the jaw has a smooth cutting edge but with visible remnant teeth (Fig. 7D). The layer does not grow between the two most-distal teeth, perhaps due to the distance with the basal section and their hardness, or because of a more intense erosion. Either case, in the

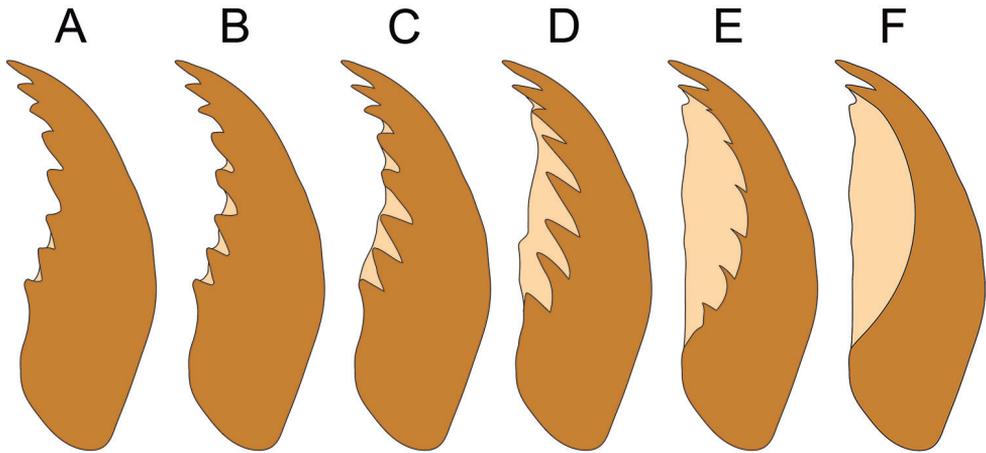


Figure 7. Proposed evolution of jaws in *Namanereidinae*. **A** Jaws with fully dentate cutting edge, layer almost inconspicuous in basal teeth **B** Layer increases their extension among basal teeth and reaches medial ones **C** Layer covers completely basal and medial teeth, and reaches subterminal ones **D** Teeth recede and become narrow, layer covers subterminal teeth excepting the last two **E** Just remnants of teeth are visible if any, layer increases its extension **F** Teeth fully replaced by the layer. Stages B and C in most *Namalycastis* species and *Namanereis* with serrated cutting edge; stage D as in *Namanereis stocki* and *N. tiriteae*; stage E as in *Namanereis socotrensis*; stage F as in *Namanereis* with bifid jaws and *Namalycastis occulta*.

final stages (Fig. 7E–F) most teeth progressively become into smaller, sharper structures, and then completely disappear, such that only the two distal teeth remain uncovered, giving a bifid appearance. The nature of the layer is uncertain, but it is expected to have a lower hardness compared with the tip and outer edge because both are darker.

Based on the literature already cited, *Namanereis* and *Namalycastis* include species in various stages along these hypothetical evolutionary stages. This pattern in jaw morphology has been explained as a shift towards deposit-feeding habits for shovelling (Glasby et al. 2014: 33), but an alternative hypothesis might be related to the scarcity of trace elements needed for hardening of the jaw, or the energetic cost expended in formation of jaws.

Glasby et al. (2014: 33) also proposed how namanereidins colonized brackish and freshwater habitats based on the jaws morphology. The marine ancestor of serrated-jaw *Namanereis* group reached epigeal environments in the late Jurassic in a single event with subsequent speciation by vicariance, whereas the widely distributed, marine ancestor of bifid-jawed *Namanereis* group colonized semiterrestrial and groundwater environments in the Cretaceous in a second, independent event, implying that this last ancestor had serrated jaws as well (Glasby et al. 2014: 34). The hypothesis here proposed of jaws evolution is in full agreement with the proposed shift of jaws morphology, and more important, it does not restrict formation of bifid jaws to *Namanereis* species, so that any ancestral namanereid with serrated jaws might derive into that type of jaw. Consequently, it is likely that some *Namalycastis* ventured into subterranean habitats and their jaws derived to bifid jaws, as in *N. occulta*.

Additional considerations. Although elongation of appendages is not restricted to stygobitic namanereidins, the bifid jaws and absence of eyes are the only features present in namanereidin species living in aphotic environments. Up to date, all bifid-jawed species are blind, whereas some blind species have serrated jaws. A possible explanation to the distribution of troglomorphic features among extant namanereidins is that such features appeared in their ancestors before reaching subterranean habitats, in intermediate habitats called superficial subterranean habitats (SSHs) (Culver and Pipan 2009a). Specifically, elongation of parapodial and chaetal appendages, even loss of body pigmentation, evolved in SSHs, whereas loss of eyes and bifid jaws evolved once species reached deeper caves. This reasoning fits well with the hypotheses by Glasby et al. (2014: 34) about colonization of subterranean realm, and also suggested for troglobitic opilions by Derkarabetian et al. (2010: 11).

However, the current epigeal distribution of *Namalycastis occulta* in Yucatan Peninsula likely is due to a secondary invasion of those habitats. Most land of Yucatan Peninsula uplifted from Jurassic, but it was submerged from Upper Cretaceous through Eocene, and progressively emerged since Oligocene (López-Ramos 1975). During these events, shoreline changed along Cenozoic as well as the distribution of organisms occupying coastal environments, allowing them to reach the vast subterranean realm along Yucatan Peninsula. In this way, the hypothetical ancestor of *N. occulta* colonized coastal habitats such as mangroves, where likely it developed elongated appendages. After, during uplifting events, this ancestor was trapped and obligated to colonize the subterranean realm (Glasby et al. 2014). Once it reached caves, ancestor lost eyes and developed bifid jaws, and after reached coastal environments again by dispersion through subterranean flows seawards as it currently occurs (e.g. Gondwe et al. 2010). In this manner, epigeal species such as *Namalycastis occulta* could gain elongation of appendages without living in caves but in aphotic environments, nor by being closely related to other *Namanereis* species with similar troglomorphies. What is more interesting here is to wonder why the other two species cohabiting with *N. occulta* in mangrove litter leaf, *Namanereis* cf. *amboinensis* and *Namalycastis borealis*, do not show these features. This could indicate a longer time of association to this aphotic environment by *N. occulta*, and a recent colonization by the other species.

Moreover, this also means that the use of troglomorphic features as evidence of phylogenetic affinity must be avoided since they could be convergent features, in disagreement with previous studies (Glasby 1999: 87, Alves and Santos 2016: 510). In his phylogenetic analysis including most namanereidins, Glasby (1999) obtained a clade that groups all eyeless namanereidins, that although the large number of trees obtained in the analysis, is was formed 94 (Nelson consensus) to 95 (50% majority rule consensus) percent of the times (Glasby 1999: 21–22). *Namanereis tiriteae* was the most basal species, having serrated jaws and cleft prostomium, followed by *N. beroni*, a species with serrated jaws as well but with entire prostomium. The group formed by Caribbean species was always recovered and supported by the character bifid jaws (Glasby 1999: 23); *N. serratis*, followed by *N. hummelincki*, both species with entire prostomium, were the sister of the most-derived, sister species in this clade, *N. stocki*

and *N. minuta*, both species with four pairs of tentacular cirri and cleft prostomium. *N. cavernicola* had uncertain relationship with the later species, perhaps by their polymorphic character of cleft and entire prostomium associated to this species (Glasby 1999: 16, 83).

The use of some disregarded morphological features, as the number of tentacular cirri, could help to find better delimited groups. Chamberlin (1919: 196) proposed the genus *Namanereis* for *Lycastis quadraticeps* Blanchard in Gay, 1849, a namanereid with four pairs of tentacular cirri. After, Augener (1922: 42) proposed the genus *Lycastopsis* for species with three pairs, a decision followed by other authors (Glasby 1999: 74). Hartman (1959: 162) suggested the synonymy of *Lycastopsis* with *Namanereis*; perhaps she thought *N. quadraticeps* had three pairs instead of four ones (Glasby 1999: 102). Further, Glasby (1999) obtained a clade containing species with four and three pairs, and therefore validating the suggestion by Hartman. In the same analysis, four pairs of tentacular cirri was regarded as a plesiomorphic character, that combined with the plesiomorphy presence of notochaetae, positioned *N. quadraticeps* as the most-basal species of *Namanereis* (Glasby 1999: 103). Interestingly, character four pairs of tentacular cirri appears again in *Namanereis stocki* and *N. minuta*, but they are positioned in the clade containing the most-derived *Namanereis* (Glasby 1999: 20). The number of tentacular cirri was not considered in the phylogenetic analysis by Alves and Santos (2016).

Among all nereidids, only some *Namanereis* species and *Lycastonereis indica* Rao, 1981 have three pairs of tentacular cirri (Rao 1981, Misra 1999). However, *Namanereis* and *Lycastonereis* are very different genera, just similar in the tendency to simplify their morphology (pers. obs.). We must wonder why the posteroventral pair of tentacular cirri has disappeared. The formation of tentacular cirri occurs in larval stages and following developmental programs distinct to postlarval stage, where the posteroventral pair is the last one to be developed (Kulakova et al. 2007, Fischer et al. 2010, Bakalenko et al. 2013). Consequently, a scenario where this later pair of cirri can appear and disappear selectively among congeneric species becomes very difficult to explain, even if it is supported by a phylogenetic analysis (Glasby 1999). As the number of tentacular cirri seems to be highly conservative among nereidids, its use as a diagnostic generic feature deserves a new evaluation.

Namalycastis occulta clearly resembles *Namanereis minuta* and *N. stocki* by having four pairs of tentacular cirri. Their main difference is the evident elongation of dorsal cirri toward posterior chaetigers and that it becomes flattened in the former species, whereas in the last species they are subequal and cirriform throughout body. Conde-Vela (2013: 481) argued about the elongation of dorsal cirri as part of diagnostic features of *Namalycastis*, but after the comparison made above, neither elongation is restricted to *Namalycastis* nor subequal dorsal cirri are distinctive for *Namanereis*. Based on this feature only, it is possible that 1) *Namanereis minuta* and *N. stocki* be *Namalycastis* as well as *N. occulta*, or 2) the former two species are more related to *Namanereis quadraticeps* than remaining *Namanereis* by having four pairs of tentacular cirri. Since foliose dorsal cirri are absent in both species, the second option is more likely, and if

true, then genus *Lycastopsis* would be reinstated containing species with three pairs of tentacular cirri and *Namanereis* should be restricted for species having four pairs. Since the reinstatement of *Lycastopsis* and restriction of *Namanereis* is beyond the scope of this study, here the current classification was used.

If *Namalycastis occulta* is to be regarded as belonging into *Namanereis*, some problems could arise, as the mixture of current diagnostic features for both genera, exacerbating the problem of delimitation. Indeed, the elongation of appendages, bifid jaws and absence of pigmentation as stygobitic adaptations could explain the observed morphology, but could not account for the elongation and flattening of dorsal cirri towards the posterior body region only, as well as the elongation of sub-acicular, dorsalmost neurochaetae also matches this anterior-posterior gradient, both occurring in *Namalycastis* species as well (see above). It is true that *N. occulta* has not been recorded in cave environments yet, but other *Namanereis* species regarded as having stygobitic adaptations such as *N. hummelincki*, *N. serratis* Glasby, 1999 and *N. tiriteae* are in the same condition.

Of course, the most reliable way to test these and other hypotheses is through new phylogenetic analyses; however, there are some problems preventing it. As Glasby et al. (2014: 35) concluded, the inclusion of molecular evidence could reinforce or refuse several of these issues, mainly about what features are truly troglomorphies and which do not. However, there are no available specimens properly fixed for DNA extraction for most species, and there are few sequences available for a number of species, hindering to test morphology-based hypotheses at specific or generic levels (Alves and Santos 2016: 500). Even, if all appear to be troglomorphic, convergent features, it does not mean that they are not phylogenetically informative, but just that their use as diagnostic features or as signals of common ancestry must be avoided. Finally, an additional difficulty is how to code these features correctly; for example, some troglomorphic features were coded as “absent/present” in previous phylogenetic studies (Glasby 1999, Alves and Santos 2016), as the case for eyes, pigmentation and elongated falcigers, driving to mistaken statements (Fitzhugh 2008).

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A striking new genus and species of troglobitic Campodeidae (Diplura) from Central Asia

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Abstract

A striking new genus and species of Campodeidae (Diplura), *Turkmenocampa mirabilis* Sendra & Stoev, **gen.n.**, **sp.n.**, found in Kaptarhana cave in Eastern Turkmenistan is described. This represents the first record of Diplura from Central Asia and also the first terrestrial troglobiont found in Turkmenistan. The new taxon shows several unique characters such as the lack of crests on the telotarsus, the presence of a side-shoot process and the shape of barbs on the ventral side of the laminar telotarsal processes hitherto unknown in other members of this family. Although *T. mirabilis* is tentatively placed in the subfamily Plusiocampinae, its true affinities remain uncertain. The new finding provides further support to the importance of Kaptarhana as a refuge for a number of endemic invertebrates.

Keywords

Turkmenistan, Koytentag Mountain, *Turkmenocampa mirabilis*, identification key, Plusiocampinae, cave fauna

Introduction

Central Asia is a geographical region which covers an area of approximately 4 million square kilometres stretching from the Caspian Sea in the west to the border of China in the east and from the southern borders of Russia in the north to the northern borders of Iran, Afghanistan and China in the South. This vast geographical area is composed of the territories of five independent countries, the former Soviet republics of Kazakhstan, Uzbekistan, Tajikistan, Kyrgyzstan and Turkmenistan. It is also occasionally referred to as Middle Asia, with other mainly dry and ecologically similar parts of Afghanistan, Pakistan, Mongolia, and at times Xinjiang and Tibet in western China and southern Siberia in eastern Russia are also included in this definition. The complex political history and highly diverse geography and diverse landscape, the latter including high mountains (Tian Shan), deserts (Karakum, Kyzylkum, Taklamakan) and steppes, as well as the comparatively low level of economic development and transport networks, significantly hampered the zoological explorations in the area.

Diplura is one of the four classes that comprise the subphylum Hexapoda. According to Koch (2009) and Zhang (2013), at present it includes 976 extant and 1 fossil species. Despite their worldwide distribution, diplurans are virtually unknown from Central Asia. A few species have hitherto been recorded from the adjacent to Central Asian countries, but most records refer to species found distant from the region or even in other zoogeographical realms. The Japygidae genus *Kohjapyx*, with three species, including the troglobiotic species *Kohjapyx lindbergi* Pagés, 1962 from a cave near Kabul have been described from Afghanistan (Pagés 1953, 1962; Paclt 1958). In a recent study on the Campodeidae of North Iran, Azadbakhsh and Nozari (2016) recorded the soil-dwelling species *Campodea (Dicampa) sprovierii* Silvestri, 1932 and *Campodea (Campodea) fragilis* Meinert, 1865 from the provinces Mazandaran and Alburz. Even in other, better explored areas in Asia, the knowledge is rather poor. For instance, the cave fauna of mainland Asia is known to harbour only seven species (Bareth and Condé 1972; Condé 1956b, 1993; Chevrizov 1978; Ferguson 1997). *Simlacampa clayae* Condé, 1956 is known from three caves in Punjab, India (Condé 1956b). *Plusiocampa (Didymocampa) lipsae* Condé, 1993 is recorded from several caves in the south of China (Condé 1993). From caves in the Russian Far East, Primorskij kraj (or Primor'e) Chevrizov (1978) described two genera – *Plutocampa* and *Pacificampa*, with respectively 3 and 2 troglomorphic species. Furthermore, Ferguson (1997) reported a new species of *Pacificampa* (Diplura: Campodeidae) from a cave in China. Given the general shortage of dipluran material and the low rate of sampling in almost all parts of Asia, many new species of subterranean diplurans are expected to be found in the near future, especially when large collections such as that of Dr. Louis Deharverg (MNHN) from Chinese caves have been studied.

In this paper, a remarkable new genus and species of the dipluran family Campodeidae, found from Kaptarhana cave in South East Turkmenistan, is described. This represents the first formal record of the subclass from the entire Central Asia and also the first terrestrial troglobiont found in Turkmenistan.

The true affinities of the new taxon remain uncertain as it departs significantly from all the currently established campodeid genera. It is tentatively placed in subfamily Plusiocampinae but this may change in future when combined morphological and molecular phylogenetic analysis of Diplura has been undertaken.

The exploration of Kaptarhana cave begun at the end of the summer of 1963 when a group of speleologists from Moscow led by V. Andreyev visited the cave and collected some foraminifers, isopods and harpacticoids from the lake. In November 1963, intrigued by these interesting findings, the cave was visited by the leading (at that time) Soviet biospeleologist S. Ljovuschkin (see Birstein and Ljovuschkin 1965). Ljovuschkin later (1969) published short report on the fauna of the cave mentioning the barklice *Psyllipsocus ramburii* Selys-Longchamps, 1872 (Insecta: Psocodea) an undetermined species of Pseudoscorpiones and Oniscoidea. Furthermore, in 1972 Starobogatov (1972) described the cave hydrobiid gastropod *Pseudocaspia ljovuschkini*. Until the study of Pavel Stoev and Boris Sket in 2015, almost no other biospeleological work was carried out in the cave. The new sampling revealed that the cave is also inhabited by spiders, springtails, parasitic flies and cryptophagid beetles. There is also a large colony of horseshoe bats, *Rhinolophus bocharicus*.

Material and methods

Sampling methods

The material was collected by Pavel Stoev and Boris Sket from the cave Kaptarhana (see details below) in the course of a rapid speleobiological assessment of the caves of Koytendag State Nature Reserve of Turkmenistan undertaken in 2015. The mission was carried out under the Memorandum of Understanding between the State Committee on Environment Protection and Land Resources of Turkmenistan and the Royal Society for the Protection of Birds to protect birds and other biodiversity in Turkmenistan. For sampling, pitfall traps, with Ethylene glycol and smelly cheese as bait, were set along the main gallery of the cave, mostly in humid places, in close proximity to large boulders and guano heaps. Pitfall traps were exposed for several days in the last week of May. Subsequently, all the captured animals were transferred to a container with 95% alcohol solution and properly labelled. Despite the fact that both collectors spent 7–8 hours altogether in the cave, no specimens were found by visual observations, all specimens being caught by pitfall trapping. The cave was very spacious, with large boulders and passages at different levels, making the process difficult for the collection and discovery of cryptic animals (such as diplurans) by methods other than pitfall trapping.

Material processing and identification

Specimens were washed in distilled water and inserted between slides and glass coverslips to be examined under a phase-contrast optical microscope (Leica DMLS) us-

ing Marc André II solution. The illustrations were made with a drawing tube and the measurements were taken with an ocular micrometer. For measuring the body length, the specimens were mounted “in toto” and were measured from the base of the frontal process distal macrochaetae to the abdomen’s supra-anal valve. For measurement of the sensilla and for examination of some minute anatomical parts, six specimens were coated with palladium-gold and studied in a Hitachi S-4100 scanning electron microscope.

The morphological descriptions and abbreviations used in this paper follow Condé (1956a). Although its function is still unknown, the term ‘gouge sensilla’ is used for the concavo-convexly shaped sensilla located on the antennae (as described by Bareth and Condé 1981). For the position of macrosetae on the occiput, *ma*, *la* and *lp*, Wygodzinsky (1944) was followed.

Abbreviations

NMNHS National Museum of Natural History, Sofia.

For notal macrosetae: *ma*, medial-anterior, *la*, lateral-anterior and *lp*, lateral-posterior; for urotergal macrosetae: *post*: posterior.

Results

Taxonomy

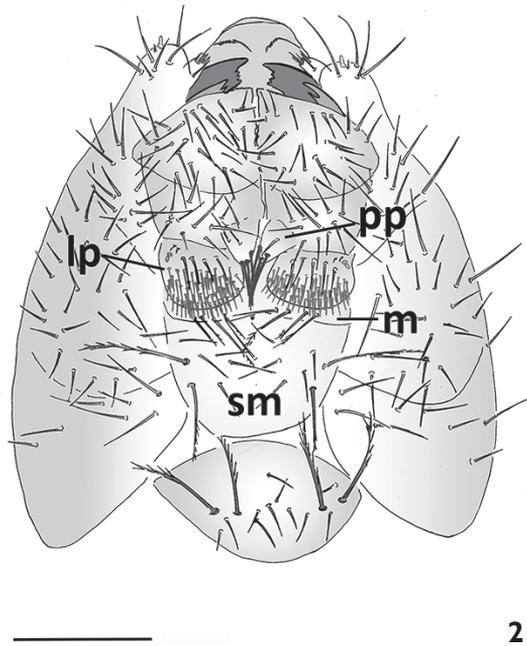
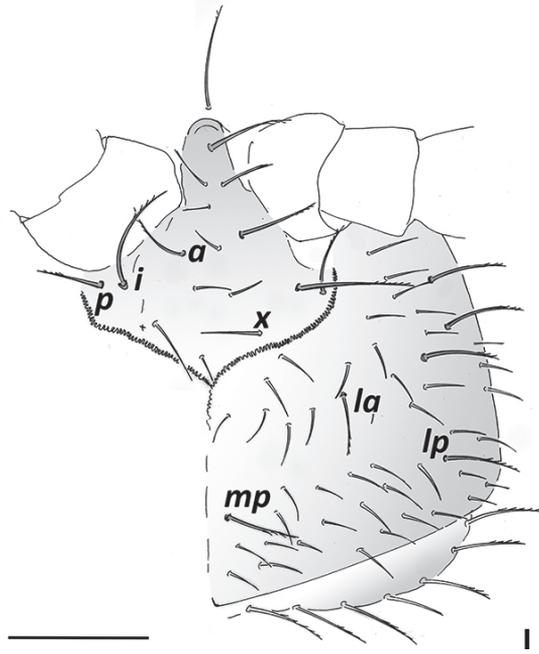
Turkmenocampa Sendra & Stoev, gen. n.

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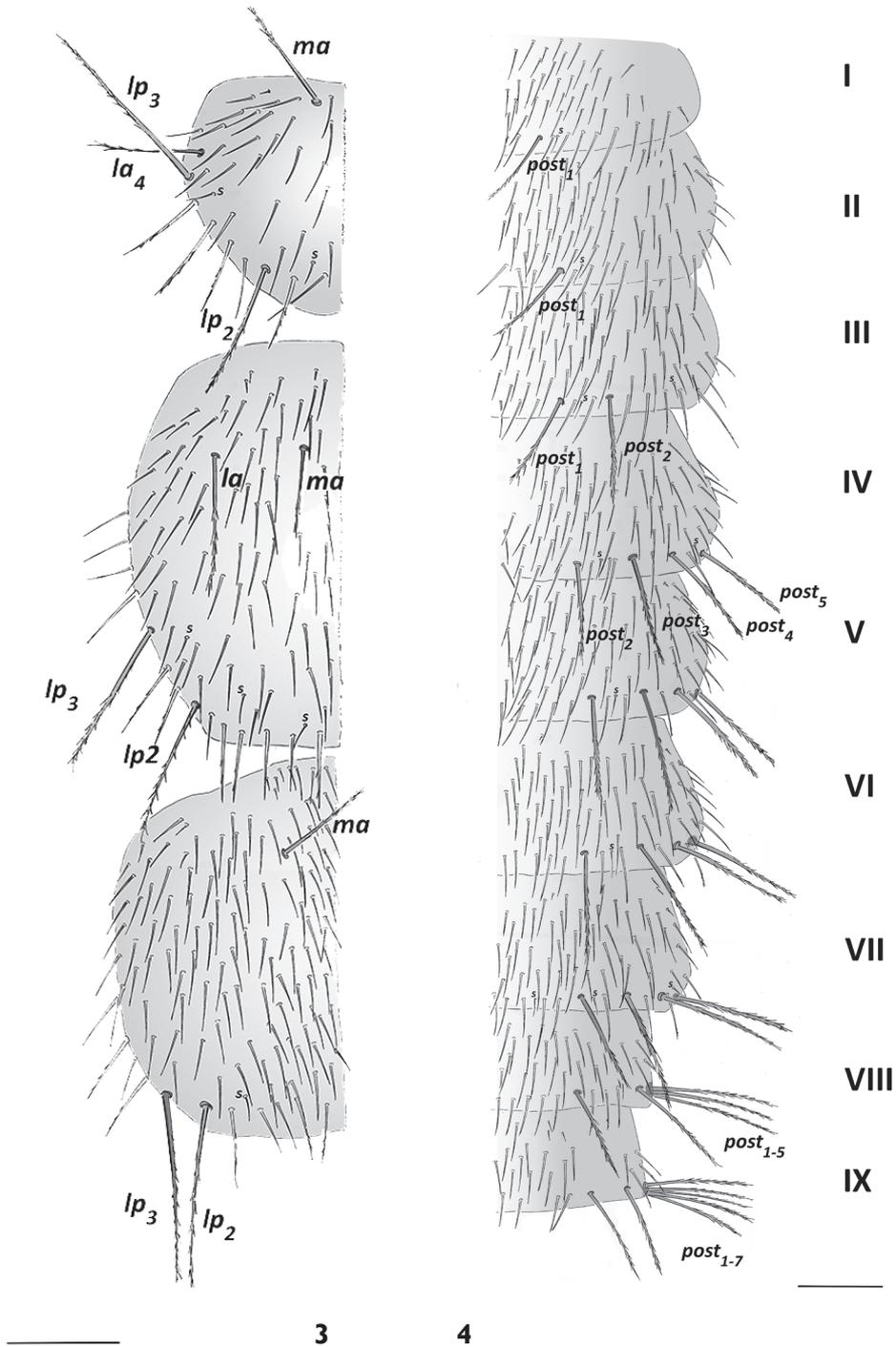
Type species. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n.

Etymology. *Turkmenocampa* is a composite name comprising “Turkmeno”-referring to the type locality and the suffix ‘-campa’ traditionally used in Campodeidae taxonomy. Gender: feminine.

Diagnosis. Head with a frontal process without tuberculate setae (Fig. 1); mentum and submentum short (Fig. 2). Cupuliform organ shallow, having three types, large oval, smaller oval and tree shaped, olfactory chemoreceptors (Figs 8–12). Thorax with 4+4 (*ma*, *la*, *lp*_{2,3}) macrosetae on pronotum and mesonotum, 3+3 (*ma*, *lp*_{2,3}) on metanotum (Fig. 3). Femur having one dorsal macroseta; tibia with one ventral macroseta. Claws simple, with a medial external expansion with laminar lateral processes covered with long barbs on the ventral side (Figs 17–18). Abdomen entirely lacking lateral-anterior macrosetae, with 1+1 to 4+4 *post* macrosetae on I to VII tergites (Fig. 4). Sternal macrosetae: I sternite: 7+7; II-VII sternites: 4+4 (Fig. 7), VIII sternite: 1+1. Sexual secondary characters almost absent; *a*₁ glandular setae present in both sexes in the distal part of subcylindrical appendage (Figs 5–6).



Figures 1–2. *Turmenocampa mirabilis* Sendra & Stoev, sp. n. **1** Dorsal view of the frontal process and right side of the head, holotype **2** Head, ventral view, E23 female paratype. Scale bars: 0.2 mm.



Figures 3–4. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n. **3** Pro-, meso- and metanotum, left side, holotype **4** Urotergites I-IX, right side, holotype. Scale bars: 0.2 mm

A key to the genera of Plusiocampinae Paclt, 1957

- 1(2) Claws with lateral crests 3
- 2(1) Claws without lateral crests 13
- 3(4) Telotarsal processes setiform 5
- 4(3) Telotarsal processes lacking or laminar barbed 9
- 5(6) Telotarsal processes pubescent *Hystrihocampa* Condé, 1948
- 6(5) Telotarsal process smooth 7
- 7(8) 4+4 macrasetae on II-VII urosternites, 1+1 macrosetae on VIII urosternite ..
..... *Condeicampa* Ferguson, 1996 and *Plusiocampa* (*Dydymocampa*)
sinensis Silvestri, 1931
- 8(7) Not less than 5+5 macrosetae on II-VII urosternites and 2+2 macrosetae on
VIII urosternite *Plusiocampa* Silvestri, 1912
- 9(10) Telotarsal processes lacking *Plutocampa* Chevrizov, 1978
- 10(10) Telotarsal processes laminar barbed 11
- 11(12) Telotarsal processes broad
..... *Cestocampa* Condé, 1956; *Vandelicampa* Condé, 1955; *Patrizicam-*
pa Condé, 1956 and *Plusiocampa* (*Didymocampa*) *lipsae* Condé, 1993
- 12(11) Telotarsal processes narrow *Simlacampa* Condé, 1956
- 13(14) Simple claws, without telotarsal processes, medial-intermediate and lateral-in-
termediate meso- and metanotal macrosetae *Silvestricampa* Condé, 1950
- 14(13) Claws with a side-shoot sharp, laminar and telotarsal processes, without me-
dial posterior meso- and metanotal macrosetae *Turkmenocampa* gen. n.

***Turkmenocampa mirabilis* Sendra & Stoev, sp. n.**

<http://zoobank.org/DD725FD0-83CD-45F6-994C-A4C103CB9592>

Material examined. Holotype: female, 5.8 mm, Turkmenistan, Lebap Province, Koytendag District, v. Gurshun Magdanly (=Svintsovyi rudnik), cave Kaptarhana, N37°49' E66°24', alt. 550–600 m asl, numerous gypsum boulders, guano heaps, cave lakes, pitfall traps with a bait, 24–30.V.2015, P. Stoev, B. Sket leg. preserved in slide with Marc André II, deposited in the NMNH labelled E01. **Paratypes:** 16 females and 11 males, same locality, date and collectors, preserved in slide with Marc André II, deposited in the NMNH (labelled E02 to E21) and in A. Sendra personal collection (labelled E22 to E28).

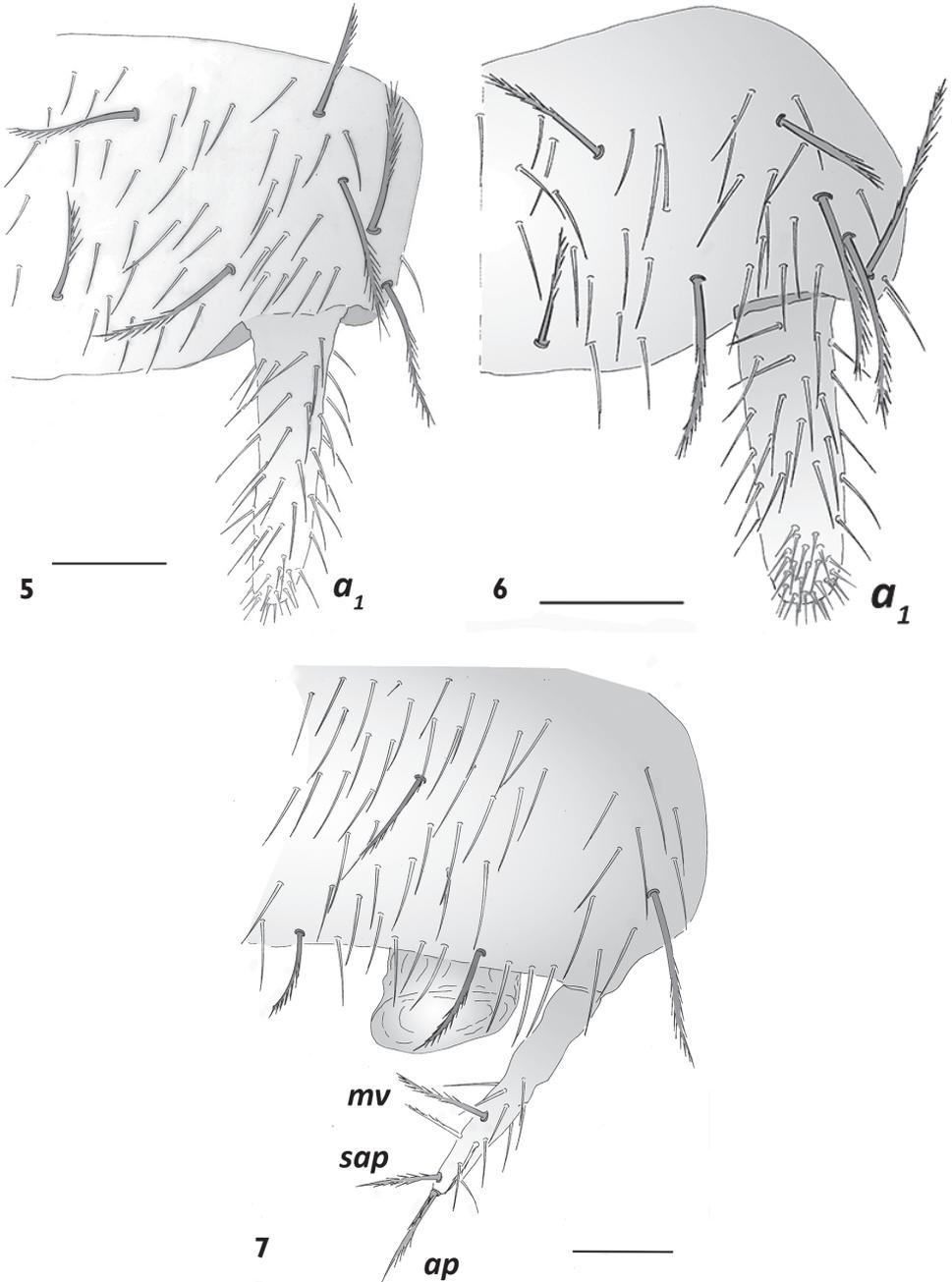
Etymology. ‘*mirabilis*’ is a Latin adjective meaning “unusual, amazing, wonderful, remarkable”. The specific epithet refers to the unique micro-sensilla in the cupuliform organ which resemble sponges and micro-corals.

Description. Body: length of males 3.2–4.9 mm, females 3.5–6.2 mm (Table 1). Epicuticle smooth; body with long, thin and smooth clothing setae (Figs 3–4) which are much shorter and less numerous on the head (Fig. 1); micro-sensilla present on the labial palps and appendages of the first urosternite (Figs 16 and 19).

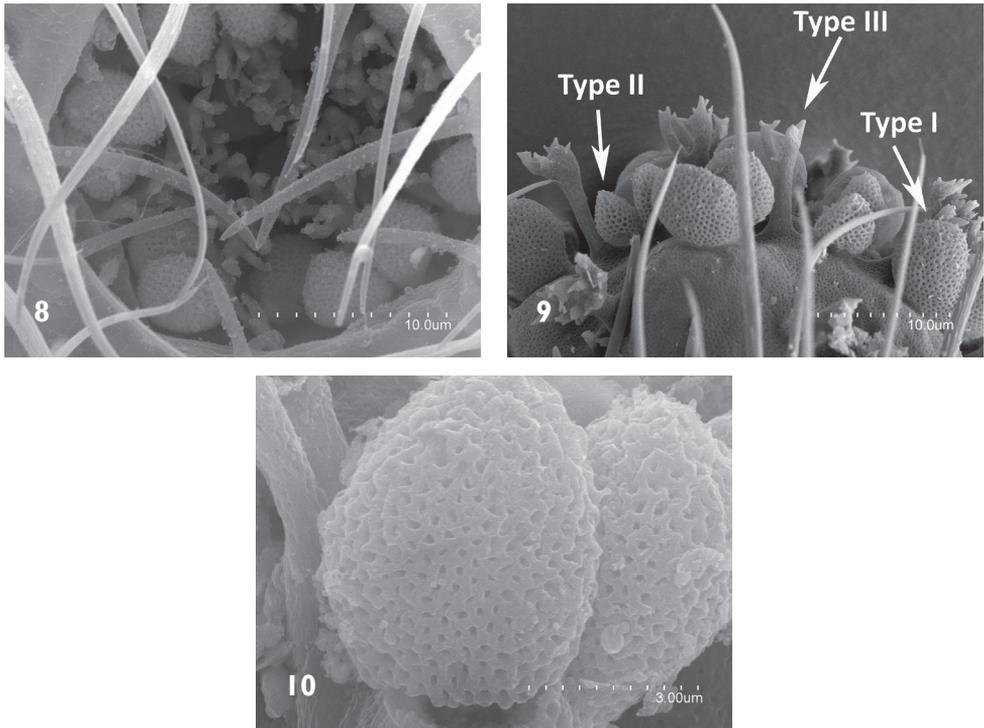
Table 1. Body measurements of *Turkmenocampa mirabilis*. (-) Absent or difficult for observation or measurement trait.

Specimen #	Sex	Length (mm)	Length of antennae (mm)	Number of antennomeres	Leg III length (mm)	Number of <i>aI</i> glandular setae on one appendage
E22, paratype	♂	3.2	1.9	33	1.4	-
E12, paratype	♂	3.3	1.8	33	1.3	8
E28, paratype	♂	3.4	-	-	1.7	-
E17, paratype	♀	3.5	-	-	1.6	9
E24, paratype	♀	3.7	-	-	1.7	-
E08, paratype	♀	3.8	-	-	1.8	12
E27, paratype	♂	4.0	-	-	2.3	23
E11, paratype	♂	4.3	-	-	2.2	-
E14, paratype	♂	4.3	-	-	2.1	26
E07, paratype	♂	4.5	-	-	2.0	22
E18, paratype	♂	4.7	-	-	2.4	29
E20, paratype	♀	4.7	3.1	33	2.3	13
E16, paratype	♂	4.8	3.0	31	2.3	-
E13, paratype	♀	4.9	2.6	32	2.0	15
E03, paratype	♂	4.9	-	-	2.2	25
E19, paratype	♀	4.95	-	-	2.5	-
E15, paratype	♀	5.0	-	-	2.7	20
E06, paratype	♀	5.1	-	-	2.3	20
E04, paratype	♀	5.2	-	-	2.5	15
E21, paratype	♀	5.2	3.6	30	2.3	-
E26, paratype	♀	5.2	-	-	2.4	15
E23, paratype	♀	5.3	-	-	2.3	10
E10, paratype	♀	5.6	3.1	31	2.5	21
E01, holotype	♀	5.8	-	-	2.7	17
E25, paratype	♀	5.8	4.2	32	2.6	19
E09, paratype	♀	5.9	3.9	33	2.6	-
E02, paratype	♀	6.2	4.0	33	2.6	18

Head: Antennae shorter than body; composed of 30–33 antennomeres (Table 1). Sensillum of the third antennomere subcylindrical, slightly swollen, similar in size and shape to the maxilla and labial palps (Fig. 2); sensillum located in ventral position between macrosetae *d* and *e*, middle antennomeres in adults 2–2.5 times longer than wide. Gouge sensilla (Fig. 13) 18–26 μm long, with their outside surface lightly grooved and with a pointed apex. Gouge sensilla distributed in a single distal whorl of 6–10 sensilla on each medial and distal antennomere. Last antennomere is twice the size of the penultimate, with a noticeable shallow cupuliform organ having a wide opening of 25 μm of diameter measuring 1/12th of its length (Fig. 8). Cupuliform organ tightly packed with two types of unknown sensilla and having three different types of olfactory chemoreceptors all covered with pores: about fourteen type I, two oviform structures of 7–8 μm long; about six type II, two oviform structures of 3.5–4 μm long and about



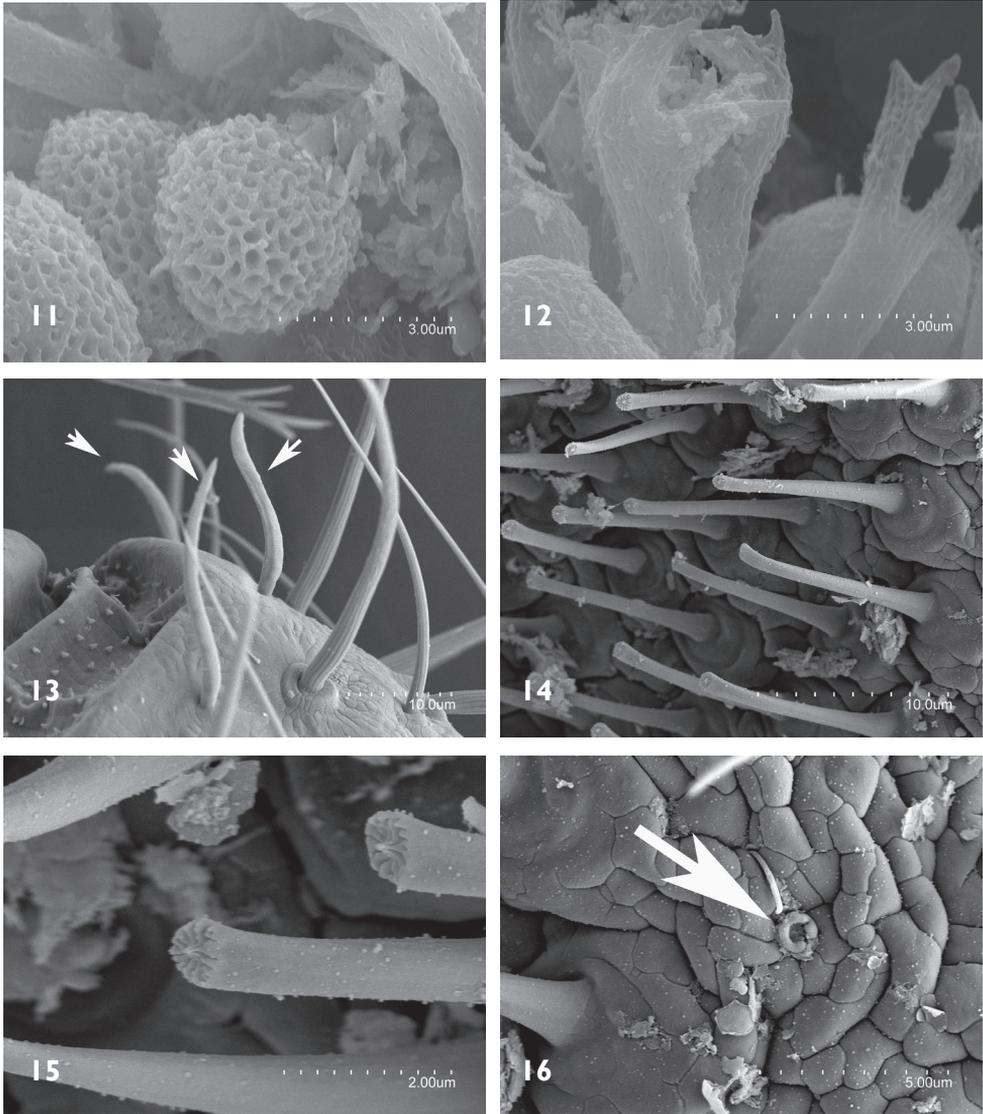
Figures 5–7. *Turkenocampa mirabilis* Sendra & Stoev, sp. n. **5** Urosternite I of male, left side, E03 male paratype **6** Urosternite I of female, left side, E02 female paratype; **7** Urosternite VII, left side, E02 female paratype. Abbreviations: apical (*ap*), subapical (*sap*) and medio-ventral (*mv*) setae, glandular a_1 -setae. Scale bars: 0.1 mm.



Figures 8–10. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n. **8** Cupuliform organ of the latest antennomere in an adult specimen **9** Cupuliform organ of the latest antennomere in an adult specimen with all olfactory chemoreceptors visible after an artificial outpouching of the organ presumably produced by the ethylene glycol in the trap (type I large oval, type II, small oval and type III, tree olfactory chemoreceptors) **10** Type I large oval olfactory chemoreceptor in the cupuliform organ.

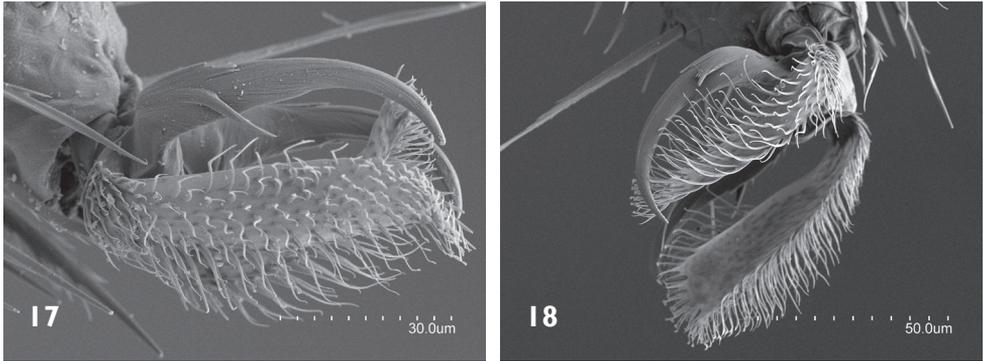
twenty type III, tree-shaped structures with branches that overhang the types I and II sensilla (Figs 8–12). Frontal process slightly developed (Fig. 1), with one long apical and two short posterior setae with 1–2 tiny distal barbs. Three macrosetae along the line of the insertion of antennae and x setae, in female holotype length ratios: *anterior* = 0.7, *posterior* = 0.6, *intermediate* = 1, x = 0.5; all macrosetae with a few thin barbs along the distal one-third. Occiput of the dorsal head with 6+6 macrosetae, including 3+3 *ma*, *la*, *lp* macrosetae (Fig. 1). Labium (Fig. 2) with a short submentum (**sm**) with 2+2 long macrosetae barbed along the distal half and shorter mentum (**m**) with 4+4 short macrosetae with a few distal barbs. Typical labial palps (**lp**) and palpiform processes (**pp**). Labial palps covered by more than one hundred neuroglandular setae ending truncated with radial micro-crests on the top (Figs 14–15); nearby are observed a few micro-sensilla (Fig. 16) adjacent to the row of a few banal setae and the labial sensillum.

Thorax: Slightly elongated thoracic nota. Distribution of macrosetae (Fig. 3): pronotum and mesonotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*_{2,3} and metanotum with 1+1 *ma*, 2+2 *lp*_{2,3}. All macrosetae long, with thin barbs along the distal half to four-fifths; marginal setae longer than clothing setae and with a few distal barbs. Legs slightly



Figures 11–16. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n.: **11** Type II small oval olfactory chemoreceptor in the cupuliform organ **12** Type III tree olfactory chemoreceptor in the cupuliform organ **13** Gouge sensilla on the lateral external side of a medial antennomere in an adult specimen (indicated with arrows) **14** Neuroglandular setae of the labial palp in an adult specimen **15** Tips of some neuroglandular setae on the labial palp in an adult specimen **16** Microsensillum on the labial palp in an adult specimen (indicated with arrows).

elongated, metathoracic legs reaching abdominal segment VIII. Femur II–III with one long dorsal macrosetae barbed along four-fifths. One short ventral macrosetae on tibia I–III well barbed almost from its base. Calcars well barbed from base to tip with long barbs. Tarsus with two ventral rows of setae covered by long thin barbs



Figures 17–18. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n., telotarsal process of the metathoracic leg in an adult specimen: **17** Lateral view **18** Lateroventral view.

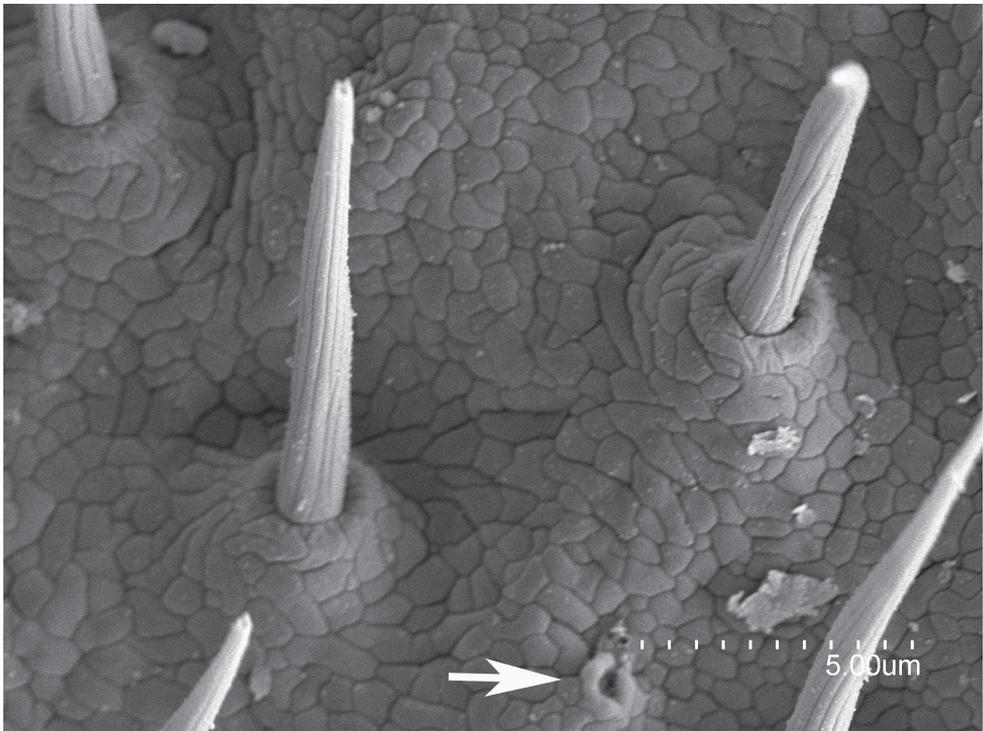


Figure 19. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n.: Apex appendage of the first urosternite in an adult female showing some a_1 glandular setae.

on the medial portion. Distal tarsus with smooth subapical setae or with a few thin distal barbs. Subequal claws curved in the medial distal comprising a thick base and a remarkable sharp-ending external expansion or side-shoot, the whole body of the claws with fine longitudinal and semi-transversal striate laminar telotarsal processes and only ventral face covered with long barbs with tip ending in a hook-shape along

the laminar processes and with a flat expansion-shape at the end of the laminar processes (Figs 17–18).

Abdomen: Abdominal distribution of macrosetae (Fig. 4): 1+1 *post*₁ macrosetae on tergites I–II, 2+2 *post*_{1,2} on III, 4+4 *post*_{2–5} on IV–VII, 5+5 *post* on VIII and 7+7 *post* IX, all long and barbed on the distal two-thirds. Urosternite I with 7+7 (7+8 in three paratypes) well developed macrosetae barbed on the distal two-thirds; II–VII with 4+4; VIII with 1+1 (2+1 in paratype female 5 mm, E05) (Figs 5–7). Styli with a long basal tooth with barbs, apical, subapical and medio-ventral setae well barbed (Fig. 7). One complete cerci isolated: 6.7 mm long, with 9 elongated articles plus base, each article progressively longer and covered with long macrosetae with thin tiny barbs along the distal one-third.

Sexual secondary features: Male urosternite I (Fig. 5) with two subcylindrical appendages, each bearing 8 *a1* glandular setae in paratype E12 (a young male, 3.3 mm long) and up to 29 *a1* in paratype E18 (adult male, 4.7 mm long) (Table 1). Female urosternite I (Fig. 6) with two subcylindrical appendages thinner than in the males, each bearing 9 to 20 *a1* glandular setae (see Table 1 and Fig. 19)

Description of Kaptarhana cave

Turkmenocampa mirabilis is hitherto known only from the cave Kaptarhana situated near the village Gurshun Magdany, Koytendag District, Lebap Province, Turkmenistan (Figs 20, 21). Kaptarhana (also spelt Kaptar-Khana) means ‘house of pigeons’ in Turkmen language as its entrance is used by pigeons for nesting. The cave is located at the foot of Koytendag Mountain (also known as Koytendag, Köýtendag, Kugitang, Koitendag, Kugitangtau, Kugitang-Tay, Kugitangtou) in the northern part of Hojapil Sanctuary, on the left bank of the Koyten river. The cave is approximately 450 m long and is situated in Late Jurassic gypsum (Birstein and Ljovuschkin 1965, Ljovuschkin 1969). There are two main galleries starting from the entrance, one orientated west (160 m long) and the second, approximately 300 m long, in a northeastern direction. Part of the cave is occupied by lakes with saline water. According to Birstein and Ljovuschkin (1965), the salinity is 11.68‰ and the pH is 7.8. The same authors provide a detailed chemical analysis of the water comparing it with the neighbouring river Amu Darya, Aral and Caspian seas and the World Ocean. The ionic composition of the lakes shows a high similarity to that of the ocean water and little resemblance to those of the neighbouring water basins. Additional support to the relict origin of the lakes comes from their rich foraminiferan, harpacticoid, isopod and gastropod fauna comprising a number of endemic species of marine origin.

A list of species known from Kaptarhana

Aquatic: Foraminifera: *Entzia macrescens* (Brady, 1870) =? *Entzia zernovi* (Schmalhausen, 1950), =? *Entzia polystoma* (Bartenstein & Brand, 1938) subsp. *caspicum* Mayer,

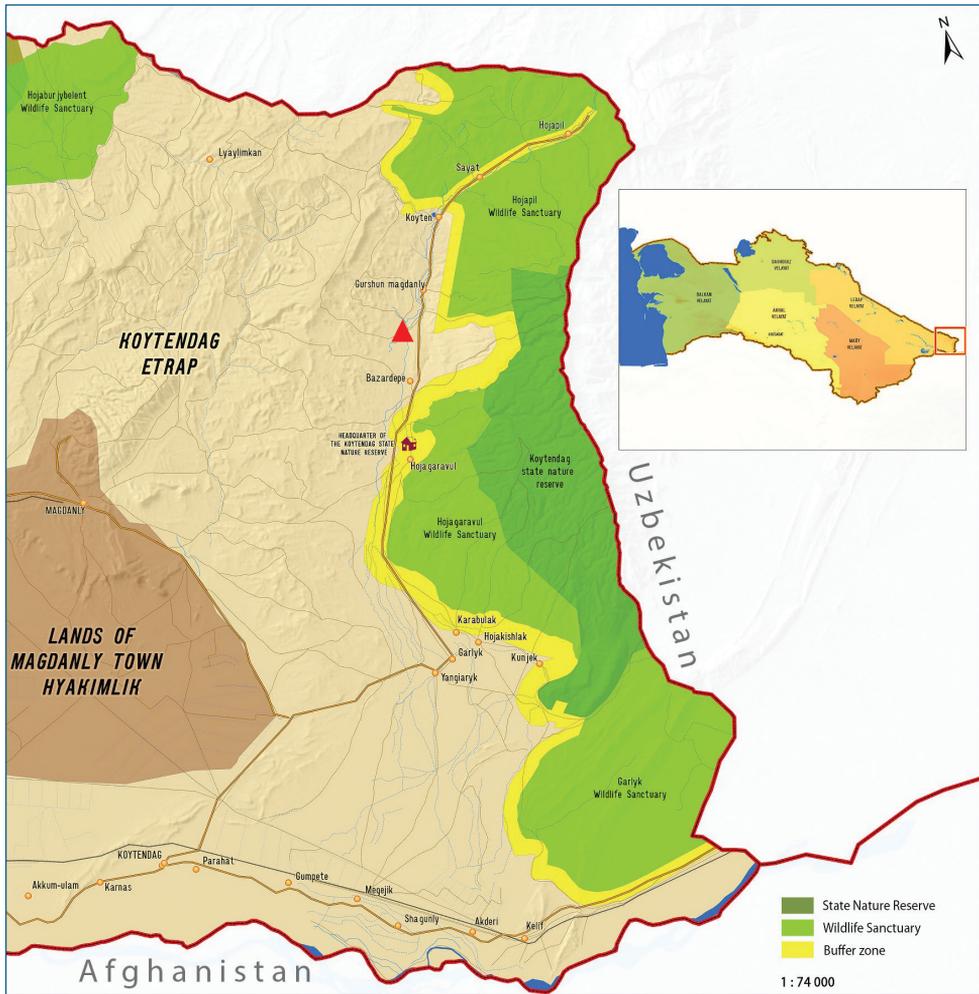


Figure 20. Map of Turkmenistan with location of the cave Kaptarhana (Red triangle). Map credit: Atamyrat Veyisov.

1974 (see Filipescu and Kaminski 2011), *Birsteiniolla macrostoma* Yankovskaya & Mikhalevich, 1972, *Trochamminita* sp., *Miliamina* sp. Nematoda: Oncholaimidae spp.; Gastropoda: Hydrobiidae: *Pseudocaspia ljevuschkini* Y.I. Starobogatov, 1972; Isopoda: *Microcharon halophilus* Birstein & Ljevuschkin, 1965; Maxillopoda: Harpacticoida: *Halectinosoma abrau* (Krichagin, 1877), *Ectinosoma* sp., *Schizopera paradoxa* (Daday, 1904), *Nitocra* sp.

Terrestrial: Isopoda: Oniscoidea gen. sp.; Pseudoscorpiones; Araneae (new record); Collembolla (new record); Diplura: *Turkmenocampa mirabilis*; parasitic Diptera; Coleoptera: Cryptophagidae; Chiroptera: *Rhinolophus bocharicus*.

Habitat

Although *Turkmenocampa mirabilis* has so far been found only in the larger gallery of the cave, some 200–250 m inside the cave, it might well be that it also inhabits the other main passage of the cave. The species is a troglobiont, all records deriving from the aphotic zone of the cave. No specimens were however observed during the exploration of the cave, those that were trapped being found in humid locations, rich in guano.

Discussion

Phyletic affinities

The classifications of Campodeidae (Condé 1956a; Paclt 1957) and Diplura (Pagés 1959) are rather outdated and badly in need of revision. Only some of the higher taxa proposed in Campodeidae seem natural as they appear to receive geographical support. This is particularly so for the diplurans from the Holarctics but, outside this region and towards its edges, most phylogenetic groups appear more or less artificial. The traits currently applied in the taxonomy of the group are of little help in clarifying the natural grouping and for developing a sound phylogenetic hypothesis. The shape and distribution of macrosetae and setae, the shape and complexity of pretarsal structures, as well as the secondary sexual characters, are the major taxonomic traits used for classifying the existing campodeid taxa. Molecular methods have only recently been applied to the group (Sendra et al. 2012) and the data are still insufficient for drawing a more robust phylogenetic analysis. Despite all these taxonomic weaknesses in the current classification, the traits demonstrated by *Turkmenocampa mirabilis* are solid enough to justify the description of a new species and genus within Campodeidae. The new taxon possesses a combination of several features not present in the other genera, one of which – the specific morphology of the olfactory chemoreceptor sensilla of the cupuliform organ – is unique in the whole family.

Plusiocampinae seems to be a paraphyletic taxon with regard to its only diagnostic character – the additional macrosetae on the pronotum – as suggested by Paclt (1957). Nevertheless, many of its genera can be considered monophyletic. This refers to the genera *Cestocampa* Condé, 1956, *Condeicampa* Ferguson, 1996, *Hystrichocampa* Condé, 1948, *Patrizicampa* Condé, 1956, *Plusiocampa* Silvestri, 1912, *Plutocampa* Chevrizov, 1978, *Simlacampa* Condé, 1956 and *Vandelicampa* Condé, 1956, all of which have lateral crests in their telotarsus. The absence of this important taxonomical trait in *Silvestricampa* Condé, 1950 and *Turkmenocampa* clearly distinguish them from the other Plusiocampinae. With regards to the subfamily position of the new genus, the presence of more than 3+3 macrosetae on pronotum (vs. up to 3+3 in Campodeinae Condé, 1956) and the absence of scales covering part of the body (vs. present as in Hemicampinae Condé, 1956 and Lepidocampinae Condé, 1956), places *T. mirabilis* within Plusiocampinae. However, the absence of lateral crests in *T. mirabilis* and all members of genus



Figure 21. Entrance of the cave Kaptarhana. Photo credit: Aleksandr Degtyarev.

Silvestricampa, the latter being solely known from the Afrotropical realm (Silvestri 1913; Condé 1950), raises doubts about their placement in Plusiocampinae.

The high number of macrosetae in *Silvestricampa*, with 7+7 macrosetae on the pronotum and presence of medial and lateral intermediate macrosetae on meso- and metanotum as well as the absence of telotarsal processes, clearly differentiate *Turkmenocampa* from *Silvestricampa*. Close examination of the genera *Plusiocampa* and *Cestocampa*, reveals that several species do not match their original diagnoses. This is the case with subgenus *Dydimocampa* of *Plusiocampa* defined by Paclt (1957) with the presence of two dorsal femoral macrosetae. The subgenus is known with two species from China (Condé 1993; Silvestri 1931): the soil-dwelling *Plusiocampa* (*Dydimocampa*) *sinensis* Silvestri, 1931 and the cave-dwelling *Plusiocampa* (*Dydimocampa*) *lipsae* Condé, 1993. Their chaetotaxy show close similarities with *T. mirabilis* except for the additional macrosetae on II-VII urosternites present in *P. lipsae*. Furthermore, *P. lipsae* has laminar telotarsal processes although with a short sternal pubescence, while they are setiform in *P. sinensis*. *P. sinensis* has clear lateral crests while they are very small in *P. lipsae*.

Another allied species, the soil-dwelling *Plusiocampa kashiensis* from West China (Chou and Chen 1980), was recently transferred from *Cestocampa* (Sendra et al. 2012). Despite its poor original description, *P. kashiensis* shares some similarities with *T. mi-*

rabilis in the distribution of macrosetae on the nota and abdomen and also in having barbed laminar telotarsal processes and claws without crests. However, the species can readily be distinguished from *T. mirabilis* by the short and abundant clothing setae (vs. long and thin in *T. mirabilis*) and the lack of extension of the claws or side-shoot (at least not mentioned in its original description). It might well be that *P. kashiensis* is actually a member of *Turkmenocampa* but, until a new or type material is studied, a formal transfer has not been suggested at this time. This also refers to the genus *Anisuracampa* Xie & Yang, 1990 which was described from subtropical China (Xie and Yang 1991) and shows morphological similarities with *Dydimocampa*.

Finally, worthy of special mention is the presence of the latero-outside side-shoot of the claw in *T. mirabilis*. It can be considered as a convergent character as it is known in *Metriocampa* (*Notocampa*) *afra* Condé, 1950 and is also present basally in *Oreocampa minutella* (Silvestri, 1918), as well as in *Haplocampa* Silvestri, 1912. It has never been found in combination with telotarsal processes (Condé 1956a) until the discovery of *T. mirabilis*.

Derived morphological characters, troglomorphies

It should be emphasised that all Diplura are without external eyes, although George (1963) presumably gave a light-perceptive function to its lateral sense organs, each one being below the integument in the latero-ventral position in the head. Furthermore, Diplura and Campodeidae, in particular show thin integument with no pigment or sclerotized cuticle. These traits are in all soil- and cave-inhabiting species. Nevertheless, the features which clearly define the troglobiotic campodeids are: increased body size, elongation of appendages and body, more numerous antennomeres and cercal articles, as well as specialisation of sensory organs. Considering all these features, *Turkmenocampa mirabilis* is undoubtedly a strict cave-dweller showing slightly elongated body and appendages (including the cercal articles and the antennomeres); and a moderate increase in the number of antennomeres reaching up to 33 and up to 10 elongated gouge sensilla in the medial and distal antennomeres. Furthermore, the species possesses three striking features which could also be related to its subterranean living environment (see also Condé 1956a; Sendra et al. 2017).

Firstly, the olfactory chemoreceptors within the cupuliform organ, which are usually present in troglobiotic campodeids. In *T. mirabilis*, the shape of these olfactory chemoreceptors have no analogue in any other Campodeidae (Figs 8–12). All troglobiotic campodeids show an increase in size and complexity of the olfactory chemoreceptors and their surface. Troglobionts have more and larger pores than soil-dwellers (Juberthie-Jupeau and Bareth 1980). The increase in complexity demonstrates a similar pattern showing a multiplication of tiny folds (or collarets) around a spheroid sensilla (Condé 1956a). In the most complex cases (Bareth and Condé 1984; Condé 1974; Condé and Sendra 1989), these folds have a sheet-like shape, in *Plusiocampa dallai* Bareth & Condé, 1984 and *Plusiocampa alhamae* Condé & Sendra, 1989; or digit-shape, in *Campodea* (*Paurocampa*) *pretneri* Condé, 1974.

Inside the cupuliform organ, *T. mirabilis* has three types of olfactory chemoreceptors, about forty sensilla tightly packed in a shallow cuticular invagination perforated by tiny pores (Figs 8–9). These sensilla are produced by microscopic evagination at the bottom of the cupuliform organ producing three different types of olfactory chemoreceptor sensilla. Type I and II have a wide and very short base, difficult to observe, which increases in size into two oval-shaped structures completely covered by pores. In type I, the oval structures are 7–8 μm long by 5–6 μm wide with pores of 0.1–0.25 μm diameter (Figs 9–10); in type II, the oval structures are 3.5–4 μm by 3–4 μm with pores of 0.25–0.35 μm (Figs 9, 11). Type III are tree-shaped sensilla covered by irregular pores (0.05–0.08 μm diameter) that start from the cupuliform organ base with a trunk-shaped structure 4.5–6 μm high and 1.1–1.4 μm wide, that it is divided into 2, 3 or 4 branches of 1.1–2.6 μm long extending into 1-2-3-4 spines (Figs 9, 12). The type III sensilla slightly overhang the types I and II and are mostly (Fig. 8) in the centre of the cupuliform organ surrounded generally by types I and II.

Thus in *T. mirabilis*, the increase in number, complexity and porous surface in olfactory chemoreceptors sensilla follow another evolutionary path, different from the pattern observed in numerous troglolithic species in *Plusiocampa* and *Cestocampa*, where these sensilla have been examined (eg., Condé 1956a).

The other two remarkable features of *T. mirabilis* refer to the telotarsus and both could be an adaptation for walking on wet and soft surfaces in subterranean environment. The claws are 50–60 μm long and curved only at the distal end where they are also slightly thinner. The whole surface of the claws is marked with fine longitudinal and semi-transversal striate of 0.3 μm thickness. At approximately 15 μm from the base on the lateral external side of the claw, there is a pointed side-shoot process of 12–15 μm length (Figs 17–18). If side-shoots of the claws have a similar function to the function of lateral crests present in several troglolithic species of *Plusiocampa*, *Cestocampa*, *Paratachycampa* and *Juxtacampa*, which are usually regarded as adaptations to subterranean lifestyle (see, for example Conde 1956a; Bareth and Pagés 1994), then they should also be considered derived traits resulting from the long cave evolution. The third interesting feature is the shape of the barbs (about 120 thin barbs 3–18 μm long) on the ventral side of the laminar telotarsal processes, ending mostly in a hook but in a flat extension in the apical barbs (Fig. 17). These two types of laminar barbs have also been observed in other troglolithic campodeids (Sendra et al. 2012, 2016) and were considered as an adaptation to facilitate movement on wet surfaces (Sendra et al. 2017).

Biogeography

The cave fauna of Central Asia is outstanding with its poverty of terrestrial trogloliths (Birstein and Ljovuschkin 1967, Ljovuschkin 1969). Kniss (2001) enumerated from the Central Asian caves altogether 80 species, of which 27 were stygo- and trogloliths. However, out of 27 strict cave-dwellers, only the springtail *Pseudacherontides stachi* (Ljo-

vuschkin, 1972), found from the Amir-Temir Cave on the western spur of Zeravshan Range of Uzbekistan, is considered troglobiont (Turbanov et al. 2016b). All others, including one fish, inhabit underground waters. Likewise, in adjacent Iran, the cave fauna comprise only 89 species, of which 16 are strict cave-dwellers. Of these, only three are terrestrial troglobites – the spider *Trilacuna qarzi* Malek Hosseini & Grismado, 2015, the millipede *Chiraziulus troglopersicus* Reboleira, Malek Hosseini, Sadeghi & Enghoff, 2015 and the isopod *Protracheoniscus gakalicus* Kashani, Malek Hosseini & Sadeghi, 2013 (Malek-Hosseini and Zamani 2017).

Based on climatic, lithological and soil characteristics, Turkmenistan is divided into thirteen ecological regions. Koytendag Mountains form a region of its own and is characterised by desert landscapes on mountainous relief, highly dissected by ravines, foothills with ridges and cuetas and fan plains. Karst processes are well developed in the region. The average annual temperature is about 17°C and annual precipitation is approximately 150 mm (Babaev 1994). The flora contains more than 1,900 species, including 332 endemics (see Rustamov et al. 2009). Lying at the intersection of three biomes – the Eurasian high mountains (Alpine and Tibetan), the Irano-Turanian mountains and the Sino-Himalayan temperate forests – the area supports a high faunal and floral diversity with a number of endemic plant, fish and invertebrate species (UNESCO Nomination dossier 2015).

Due to its remote location, difficult accessibility and restricted border control, as well as the lack of active speleobiologists in Turkmenistan, the biological aspect of the Koytendag caves has only been marginally studied. Despite the great number of caves in the area (some estimates give 300), until now only the invertebrate fauna of the caves Kaptarhana, Gap-Gotan, Hashym Oyuk and Gulshirin, an unnamed cave near v. Svincovyi rudnik, have been explored from the biological viewpoint (Birstein and Ljovuschkin 1965, Ljovuschkin 1969, Starobogatov 1972, Kniss 2001, Turbanov et al. 2016a, b, c). Kniss (2001) reviewed the existing knowledge in his catalogue “Fauna of the caves of Russia and adjacent countries” and Turbanov et al. (2016a, b, c) provided a checklist of all cave species known from Russia and the former Soviet republics. Until the present time, terrestrial troglobionts have not been registered in Koytendag.

The specific composition of the brackish lake in the cave Kaptarhana and its unique stygofauna comprised of species of marine origin suggest a completely different geological history of the cave compared to the rest of the region. It is very likely that the saline waters belong to another hydrographic entity, without connection to the subterranean waters of the neighbouring Koyten and Garlyk areas where the stygofauna is represented by other species such as *Troglocobitis starostini*, *Stenasellus asiaticus*, *Bogidiella ruffoi*, *Gammarus* spp., copepods, etc. (Turbanov et al. 2016 ab, Boris Sket, unpublished).

It is noteworthy that the terrestrial fauna of the cave also shows differences compared to the other caves of Koytendag. The authors’ attempts to find *T. mirabilis* in any of the other caves were unsuccessful despite the fact that the same collecting method (baited pitfall traps) was applied in the cave Gap-Gotan. Furthermore, the ptinid beetle *Niptus hololeucus* (Faldermann, 1835), which is otherwise very abundant in the Gap-Goutan cave (mostly on porcupine scats), is missing in Kaprahana, where the group is repre-

sented by an unidentified species of family Cryptophagidae. The unique character of the fauna of Kaptarhana is supported by the finding of very likely new species of Collembola (L. Deharveng, in progress). It may well be that the existing hydrological barrier between Kaptarhana and the other caves also prevents distribution of terrestrial organisms.

Taking into consideration that the caves of Central Asia are poorly studied, the possibility is not excluded that this taxon or new species of *Turkmenocampa* will be found in future in other caves in Koytendag or in the neighbouring parts of Uzbekistan and Afghanistan.

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The first troglolithic species of the family Pudeoniscidae (Crustacea, Isopoda, Oniscidea), with descriptions of a new genus and two new species

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Abstract

Approximately 170 species of terrestrial isopods are known from Brazil, but only 12 are considered trogloliths. The family Pudeoniscidae comprises four species in two genera, *Brasiloniscus* and *Pudeoniscus*. After the examination of material collected in caves in the state of Bahia, a new genus and two new species have been recognized, *Iansaoniscus iraquara* **gen. et sp. n.** from Buraco do Cão cave, Iraquara, and *Iansaoniscus georginae* **gen. et sp. n.** from Borboletas cave, Paripiranga. The new genus and new species are placed in Pudeoniscidae on the basis of some morphological characteristics, such as antennal flagellum with second and third articles divided by a slender suture, epimera of pereonite 1 with dorsolateral furrow reduced or absent, and shape of uropods. The Brazilian subterranean environments are now under potential threat because of recent legislation for cave exploitation, and the knowledge of the subterranean biodiversity of the country is thus of primary importance for its effective conservation.

Keywords

New species, terrestrial isopods, Pudeoniscidae, Neotropical, Brazilian Atlantic Forest

Introduction

Terrestrial isopods (Oniscidea) constitute one of the most diverse groups within Isopoda, including more than 3,700 described species (Sfenthourakis and Taiti 2015). Among this diversity, more than 300 species of troglobiotic terrestrial isopods are known in the world (Taiti 2004, 2014, 2016; Taiti and Gruber 2008; Taiti and Xue 2012; Tabacaru and Giurginca 2013; Campos-Filho et al. 2014, 2015a, 2016, in press; Souza et al. 2015; Taiti and Wynne 2015a).

Brazil is considered to be one of the most biodiverse countries in the world due to its great diversity of ecosystems (Mittermeier et al. 2005), with high rates of endemism, and most of them are classified as priorities for conservation (Myers et al. 2000). Brazil has more than 15,000 caves in different lithologies, including limestone, sandstone, magmatic and iron ore, representing 7% of the total estimated number of caves in the country (Auler 2002; Williams 2008; Sallun Filho and Karmann 2012; CECAV 2015).

To date, approximately 170 species of terrestrial isopods are known from Brazil, of which 34 are recorded from caves (Souza-Kury 1993; Souza et al. 2006, 2015; Campos-Filho and Araujo 2011; Campos-Filho et al. 2014, 2015b, 2016, 2017, in press; Souza et al. 2015; Cardoso et al. 2016; Bastos-Pereira et al. 2017). Among these cave dwelling species, only 12 are considered to be troglobionts, i.e. *Cylindroniscus flaviae* Campos-Filho, Araujo & Taiti, in press, *Iuiuniscus iuiuensis* Souza, Ferreira & Senna, 2015, *Spelunconiscus castroi* Campos-Filho, Araujo & Taiti, 2014, *Xangoniscus aganju* Campos-Filho, Araujo & Taiti, 2014, *Xangoniscus itacarambiensis* Bastos-Pereira, Souza & Ferreira, 2017 and *Xangoniscus odara* Campos-Filho, Bichuette & Taiti, 2016 (Styloniscidae), *Leonardoscia hassalli* Campos-Filho, Araujo & Taiti, 2014 (Philosciidae), *Amazoniscus eleonora* Souza, Bezerra & Araújo, 2006, *Amazoniscus leistikowi* Campos-Filho, Araujo & Taiti, 2014, *Circoniscus buckupi* Campos-Filho & Araujo, 2011, *Circoniscus carajasensis* Campos-Filho & Araujo, 2011 (Scleropactidae), and *Trichorhina guanophila* Souza-Kury, 1993 (Platyarthridae).

The family Pudeoniscidae Lemos de Castro, 1973 comprises four species in two genera, *Brasiloniscus* Lemos de Castro, 1973, and *Pudeoniscus* Vandel, 1963 (Lemos de Castro 1973). The family has a restricted distribution in the Atlantic Forest of Brazil.

In the present work, a new genus and two new species of Pudeoniscidae from limestone caves in the state of Bahia are described, representing the first troglobiotic taxa within the family. Moreover, additional characters are proposed as diagnostic to the family, in order to accommodate the new taxa described here.

Material and methods

The material was stored in 75% ethanol and identifications were based on morphological characters. The species were illustrated with the aid of a camera lucida mounted on Wild M5 and M20 microscopes. The final illustrations were prepared using the software GIMP with the method proposed by Montesanto (2015, 2016). The material used in this study is deposited in the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP) and Laboratório de Estudos Subterrâneos, Universidade Federal de São Carlos (LES/UFSCar).

Study area

Espinhaço Supergroup, Una Group, Irecê metasedimentary Basin, Salitre Formation: Iraquara, Buraco do Cão cave

Buraco do Cão cave is located in an area geographically known as Chapada Diamantina, in the central portion of the state of Bahia, northeastern Brazil (Fig. 1). The Chapada

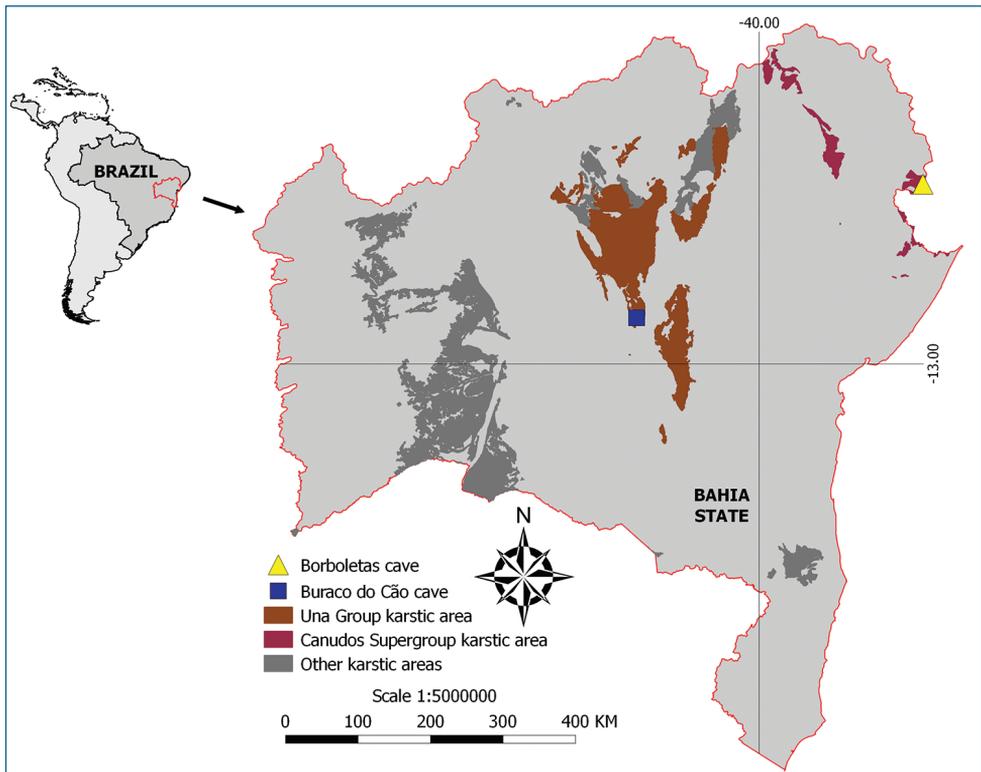


Figure 1. Locality map of Buraco do Cão and Borboletas caves.

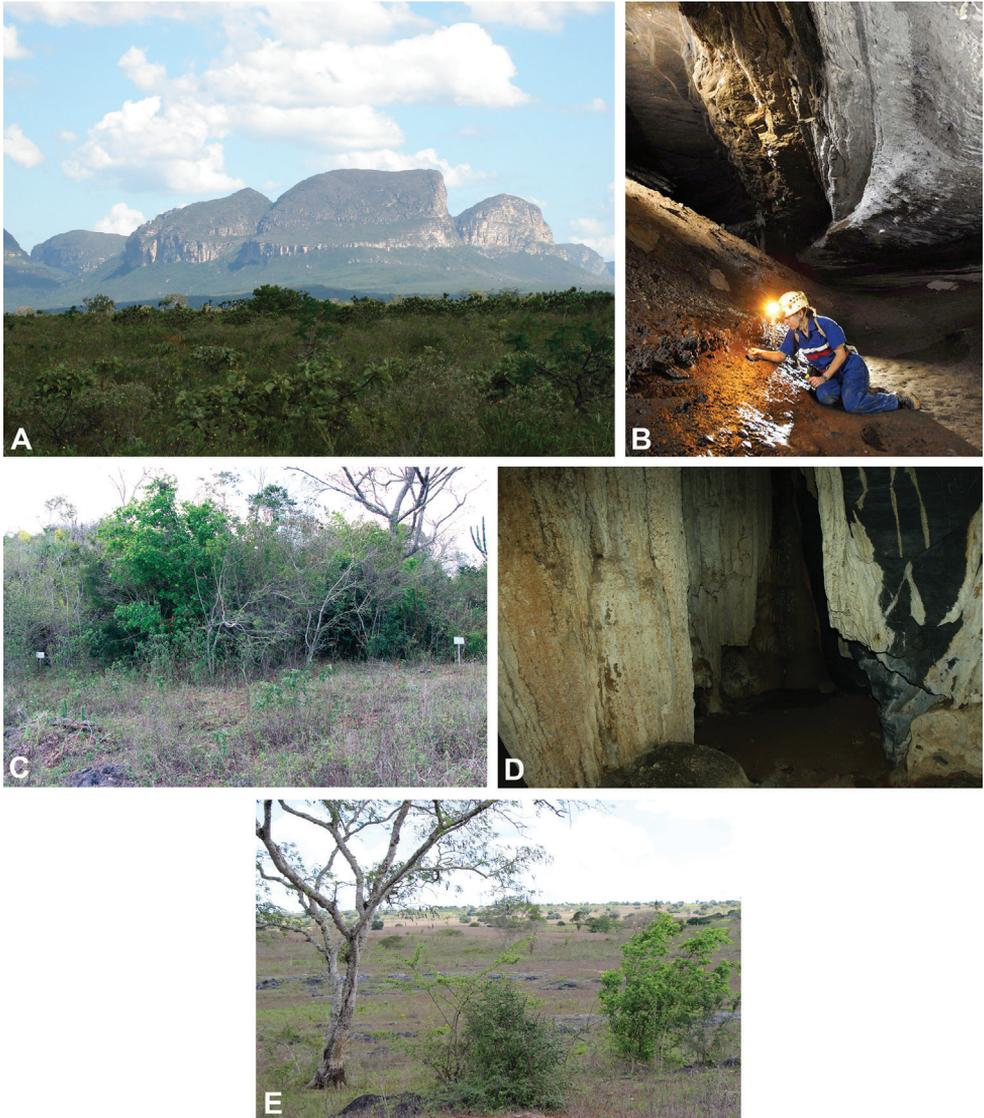


Figure 2. **A** Landscape of Chapada Diamantina, central portion of the state of Bahia, Caatinga vegetation in the foreground **B** Buraco do Cão cave, type locality of *Iansaoniscus iraquara* sp. n., silt and rocky substrates, humid environment **C** Caatinga vegetation close to Borboletas cave, Paripiranga, Bahia **D** Borboletas cave, type locality of *Iansaoniscus georginae* sp. n., silt and rocky substrates, humid environment **E** Deforested landscape from Paripiranga region.

Diamantina landscape is dominated by karst landforms formed by the dissolution of carbonatic and, to a lesser extent, siliciclastic rocks. The carbonatic rocks (limestones) date from Neoproterozoic age (1,000 to 541 million years ago). The climate domain is Aw, Tropical Savanna climate (Köppen and Geiger classification), with average temperature of 22.1 °C and annual rainfall of 761 mm concentrated between November

and April (Kottek et al. 2006). The cave is inserted in the Caatinga domain (Ab'Saber 1977), with typical dry vegetation interspersed by Atlantic Forest remnants (Fig. 2A).

Buraco do Cão is part the Talhão-Buraco do Cão-Gruta da Santa system with ca. 6.5 km of mapped passageways (Grupo Bambuí de Pesquisa Espelológicas, ME Bichuette, pers. comm.), and shows a high diversity of substrates that can be exploited by fauna – silt, guano piles, parietal substrate, etc. (Fig. 2B). To date, at least two exclusively troglobiotic species have been recorded in this cave, a pseudoscorpion (DM von Schimonsky and ME Bichuette, in prep.), and the terrestrial isopod in the family Pudeoniscidae described herein.

Buraco do Cão cave is located outside the Chapada Diamantina National Park (CDNP) and part of the cave galleries are visited by tourists since the '90s. The cave has no management plan and is subject to local environmental impacts related to poorly regulated speleotourism (Trajano et al. 2016). However, the main threats in Iraquara region are the drastic and uncontrolled exploration of the subterranean waters and the pollution of the aquifers by pesticides. The level of subterranean waters is decreasing drastically in the last two years (ME Bichuette, pers. obs.), something that could alter not only the aquatic ecosystem functions but also the habitats related to the system, including terrestrial ones.

Canudos Supergroup, Vaza Barris Group, Olhos D'água Formation: Paripiranga, Borboletas cave

The region of Paripiranga is located in the state of Bahia, northeastern Brazil (Fig. 1). The region consists of carbonated phyllite intensely sheared hills with a maximum elevation of 430 m. In this area one may also find meta-calcareous rocks, which are in tectonic contact with the carbonated phyllite. The limestone dates from the Neoproterozoic (1,000 to 541 million years ago) (Pereira et al. 2017). The climate domain is Aw, Tropical savanna climate (Köppen and Geiger classification), with average temperature of 22.6 °C and annual rainfall of 897 mm concentrated between March and September (Kottek et al. 2006). The cave is inserted in the Caatinga domain (Ab'Saber 1977), with typical dry heterogeneous vegetation in the surroundings, named “Campo Rupestre”, and with Atlantic Rainforest present in the highlands (Fig. 2C). To date, 82 caves are recorded in the region (CECAV 2015), including Borboletas cave with an extension of about 100 m (Fig. 2D). The region has not legal protection, suffers impact by agriculture and pastures (Fig. 2E) and, more recently, by extraction of limestone for cement production.

Results

Pudeoniscidae Lemos de Castro, 1973

***Iansaoniscus* Campos-Filho, Araujo & Taiti, gen. n.**

<http://zoobank.org/59969B35-C6D0-4E10-94AC-C2150E02DDE8>

Type species. *Iansaoniscus iraquara* Campos-Filho, Araujo & Taiti, sp. n. by present designation.

Diagnosis. Body convex. Animals unable to roll up into a ball. Cephalon with well-developed antennary lobes, slightly developed triangular frontal shield, laterally interrupted by antennal grooves, frontal line delimiting frontal shield on upper portion, suprantennal line absent. Pereonite 1 epimeron with dorsolateral furrow reduced or absent. Pleon outline continuous with that of pereon. Telson triangular, surpassing uropod endopods. Antenna with flagellum of three articles, second and third articles divided by thin suture. Mandible with molar penicil dichotomized. Maxillula outer branch with some cleft teeth. Uropod protopod sub-quadrangular. Pleopod exopods with no respiratory structures.

Etymology. The new genus is named after Iansá Orisha, the Afro-Brazilian divinity of the winds and thunderbolts, known as the divinity who commands the storms and the spirit of the dead.

Remarks. *Iansaoniscus* gen. n. is included in the family Pudeoniscidae by having the cephalon with a triangular frontal shield, pereonites 1 and 2 with small ventral lobes, telson with distal portion surpassing the uropod endopods, antennal flagellum with second and third articles divided by a slender suture, and the characteristic Pudeoniscidae-type shape of uropods (see Schmidt 2003).

Iansaoniscus gen. n. differs from the other genera of the family in lacking or having a reduced dorsolateral furrow on the epimeron of the pereonite 1 and in pleopod exopods without respiratory structures.

The dorsolateral furrow on the epimeron of the pereonite 1 and pleopodal exopods with uncovered lungs were considered to be diagnostic characters for the family Pudeoniscidae (Vandel 1963; Lemos de Castro 1973). Thus, regarding these two characters, the diagnosis of the family must be emended as follows: epimera of pereonite 1 with dorsolateral furrows to fit antennae during conglobation, sometimes reduced or absent; pleopodal exopods with respiratory structures, absent in troglotic taxa.

The absence of respiratory structures in the pleopodal exopods of the species of *Iansaoniscus* gen. n. may be due to secondary reduction due to the humid environment in the caves. Other families of Oniscidea are known to have genera with and genera without respiratory structures, e.g. Scyphacidae, Philosciidae, Scleropactidae, and Armadillidae (Ferrara et al. 1994; Taiti et al. 1998; Schmidt 2002, 2007).

***Iansaoniscus iraquara* Campos-Filho, Araujo & Taiti, sp. n.**

<http://zoobank.org/1F152A88-CE7A-4698-9570-47636CD3835A>

Figs 3–5

Type locality. Bahia, Iraquara, Buraco do Cão cave (12°23'37.32"S, 41°36'8.28"W).

Type material. *Holotype* male (MZUSP 27533), Bahia, Iraquara, Buraco do Cão cave, 20 July 2009, leg. ME Bichuette.

Description. Body length: 6.5 mm. Body pigmentless, eyes absent. Body outline in lateral view as in Fig. 3A. Pereonite 1 epimeron without dorsolateral furrow; pere-

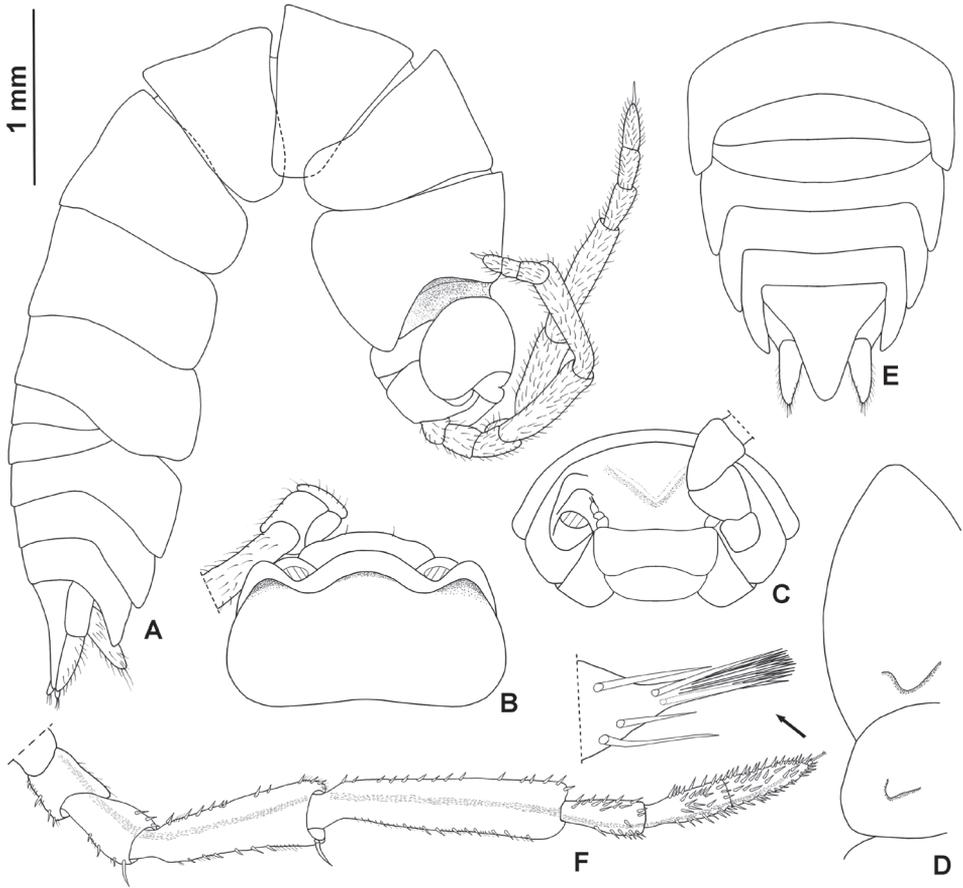


Figure 3. *Iansaoniscus iraquara* sp. n., ♂ holotype, MZUSP 27533. **A** Habitus in lateral view **B** Cephalon, dorsal view **C** Cephalon, frontal view **D** Pereonites 1 and 2, ventral view **E** Pereonite 7, pleon, telson and uropods, dorsal view **F** Antenna.

onite 1 and 2 with ventral triangular lobes (Fig. 3D); pereonite 3–7 with subquadrangular epimera. Cephalon as in Fig. 3B, C. Pleonites 3–5 with epimera subquadrangular and directed backwards (Fig. 3A, E). Telson (Fig. 3E) slightly wider than long with slightly concave sides, narrowly rounded apex. Antennula missing. Antenna (Fig. 3F) with flagellum as long as fifth article of peduncle. Mandibles (Fig. 4A, B) with molar penicil with 5–7 branches, left mandible with 2+1 penicils, right with 1+1 penicils. Maxillula (Fig. 4C) inner endite with distal margin rounded bearing two long penicils; outer endite of 4+5 teeth (two apically cleft). Maxilla (Fig. 4D) outer lobe twice as wide as inner lobe, rounded and covered with thin setae; inner lobe bearing thick setae. Maxilliped (Fig. 4E) basis rectangular; basal article of palp with two setae distinct in length; endite subrectangular, medial seta surpassing distal margin. Uropod (Fig. 5A) protopod with glandular pores on outer groove, exopod as long as endopod. Pereopod 1–7 (Fig. 5B, C) merus and carpus with slightly

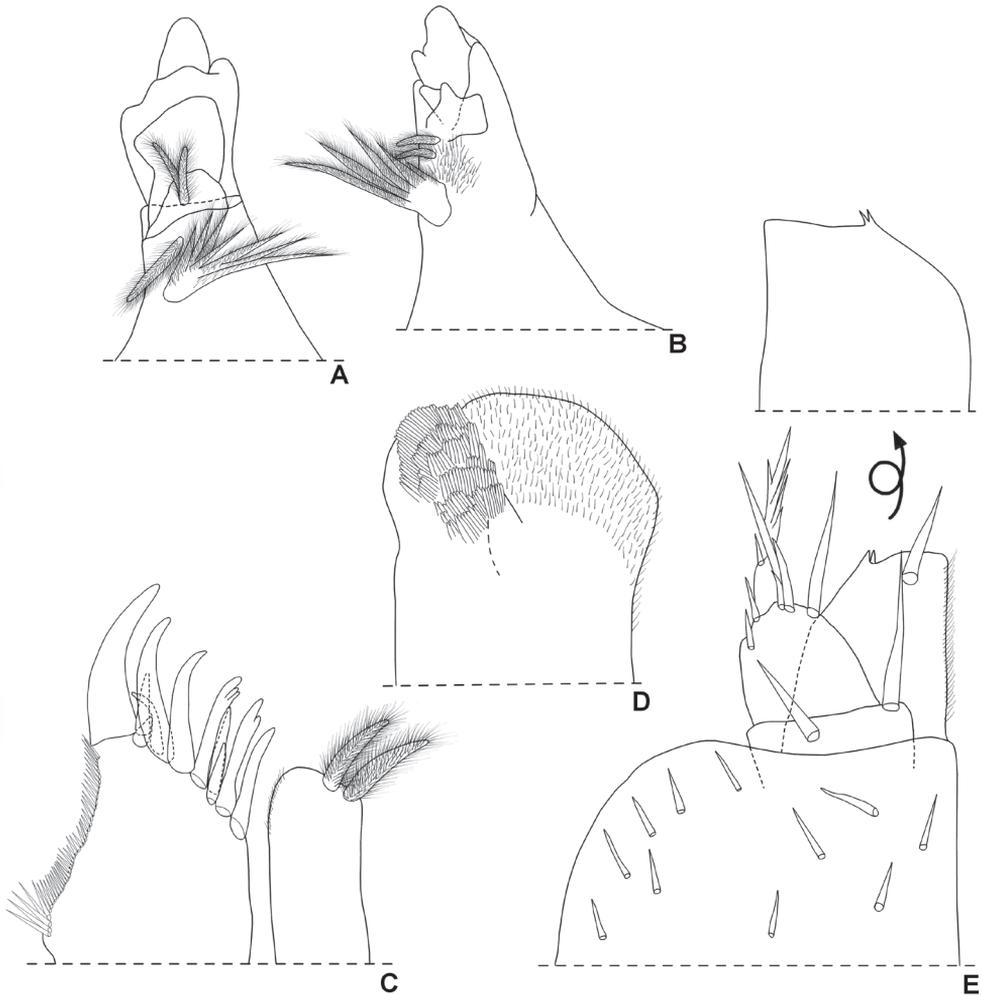


Figure 4. *Iansaoniscus iraquara* sp. n., ♂ holotype, MZUSP 27533. **A** Left mandible **B** Right mandible **C** Maxillula **D** Maxilla **E** Maxilliped.

sparse setae on sternal margin; carpus 1 with antennal grooming brush transverse, distal seta apically with four points; dactylus with dactylar seta and unguar seta simple not surpassing outer claw. Genital papilla missing. Pleopod 1 (Fig. 5D) exopod ovoid, twice as wide as long; endopod almost three times as long as exopod, distal portion slightly bent outwards, inner margin bearing small setae. Pleopod 2 exopod (Fig. 5E) triangular bearing three setae on outer margin. Pleopod 3–5 exopods as in Fig. 5F–H.

Etymology. The new species is named after the Tupi language, spoken by the Brazilian native people, that inhabited the littoral zone. In Tupi, Iraquara means Honey Cave (“*Ira*” = honey + “*quara*” = cave). Actually, the city of Iraquara is also known as the “City of the Caves”.

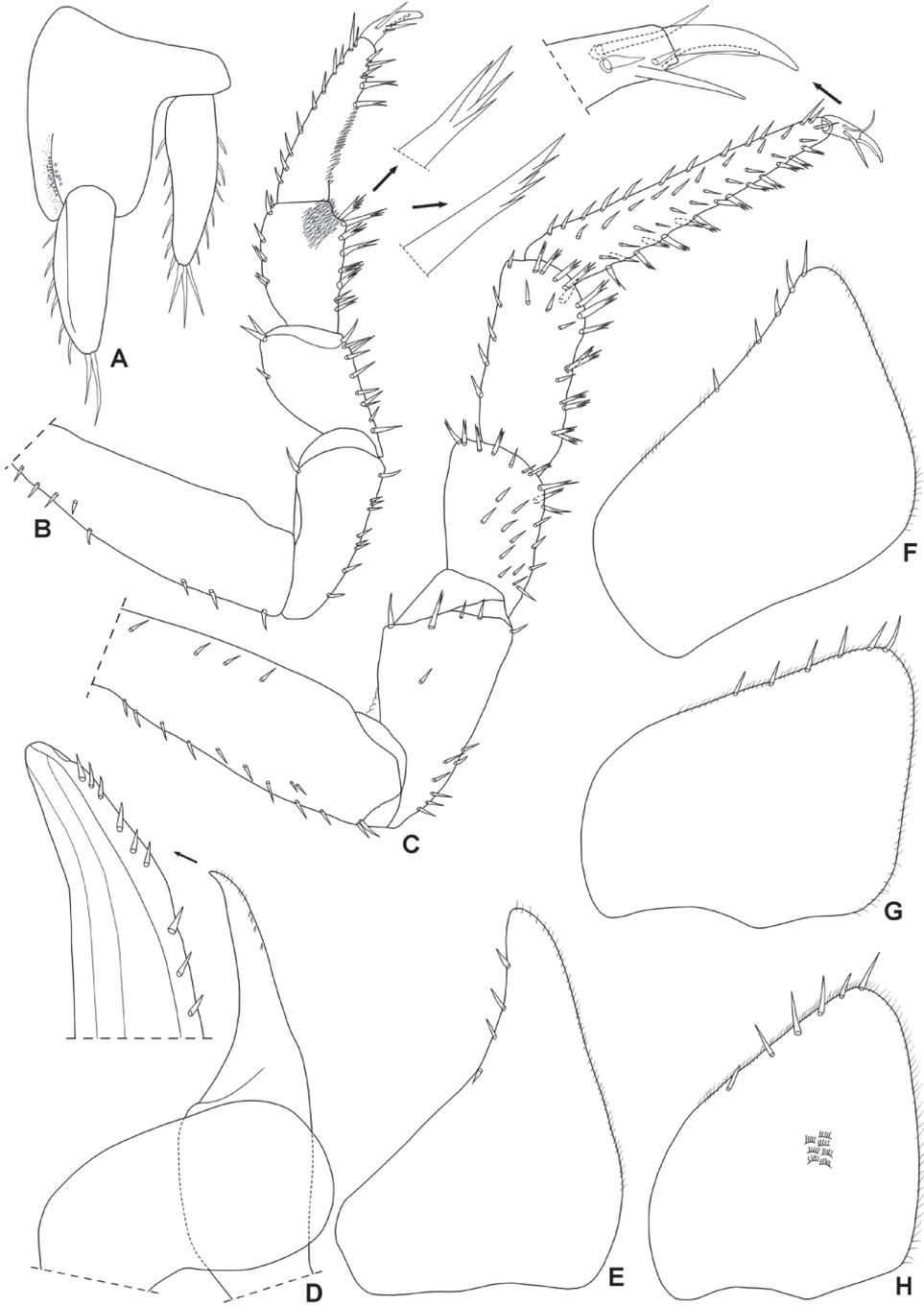


Figure 5. *Iansaoniscus inaquara* sp. n., ♂ holotype, MZUSP 27533. **A** Uropod **B** Pereopod 1 **C** Pereopod 7 **D** Pleopod 1 **E** Pleopod 2 exopod **F** Pleopod 3 exopod **G** Pleopod 4 exopod **H** Pleopod 5 exopod.

***Iansaoniscus georginae* Campos-Filho, Araujo & Taiti, sp. n.**

<http://zoobank.org/85D9F0DD-2B40-45C0-A650-C2F98F809813>

Figs 6–8

Type locality. Bahia, Paripiranga, Caverna das Borboletas cave (10°38'12.75"S, 43°51'43.68"W).

Type material. *Holotype* male (part in micropreparations) (MZUSP 35114), Bahia, Paripiranga, Borboletas cave, leg. JE Gallão, MP Bolfarini, MJ Rosendo, R Moreira.

Description. Body length: 5 mm. Body pigmentless, eyes absent. Body outline in lateral view as in Fig. 6A. Dorsum covered with triangular, elongated scale-setae (Fig. 6B). Pereonite 1 epimeron with dorsolateral furrow weakly developed, anterior and posterior corners triangular; pereonite 1 and 2 ventrally with weakly developed lobes (Fig. 6A, E); pereonite 2–7 with subquadrangular epimera. Cephalon as in Fig. 6C, D. Pleonites 3–5 (Fig. 6A, F) with subrectangular epimera directed backwards. Telson (Fig. 6F) almost as wide as long, not surpassing uropod exopods. Antennula (Fig. 6G) with second article bearing thick lateral setae, distal article with 4 lateral aesthetascs plus apical pair. Antenna missing. Mandibles (Fig. 7A, B) with molar penicil with 6–7 branches, left mandible with 2+1 penicils, right with 1+1 penicils. Maxillula (Fig. 7C) inner endite with two penicils, distal margin rounded; outer endite of 4+6 teeth (two apically cleft). Maxilla (Fig. 7D) outer lobe twice as wide as inner lobe, rounded and covered with thin setae; inner lobe bearing thick setae. Maxilliped (Fig. 7E) with basal article of palp bearing two setae distinct in length; endite subrectangular, medial seta surpassing distal margin. Uropod (Fig. 8A) protopod with glandular pores on outer groove, exopod slightly longer than endopod. Pereopod 1–7 (Fig. 8B, C) merus and carpus with slightly sparse setae on sternal margin; carpus 1 with antennal grooming brush transverse, distal seta apically with five points; dactylus with dactylar seta and unguis simple not surpassing outer claw. Genital papilla (Fig. 8D) with triangular ventral shield and subapical orifices. Pleopod 1 (Fig. 8E) exopod subquadrangular, twice as wide as long; endopod almost three times as long as exopod, inner margin bearing small setae. Pleopod 2 (Fig. 8F) exopod triangular bearing one seta on outer margin; endopod very long, more than three times as long as exopod. Pleopod 3–5 exopods as in Fig. 8G–I.

Etymology. The new species is named after Dr. Georgina Bond-Buckup for all her contributions to the knowledge of crustaceans, including Oniscidea.

Remarks. *Iansaoniscus georginae* sp. n. is readily distinguishable from *I. iraquara* sp. n. in the shape of the cephalon, epimeron of pereonite 1 with reduced dorsolateral furrow, shape of ventral lobes on pereonites 1 and 2, and shape of the male pleopods 1 and 2.

Considerations about conservation

Iraquara and Paripiranga show different historical sampling efforts: Iraquara has been sampled since 1990, and Paripiranga after 2014 (M.E. Bichuette, pers. obs.). The two species are extremely rare and represent the first records of troglobiotic species in the family Pudeoniscidae. These records increase the taxonomic distinctness of these two

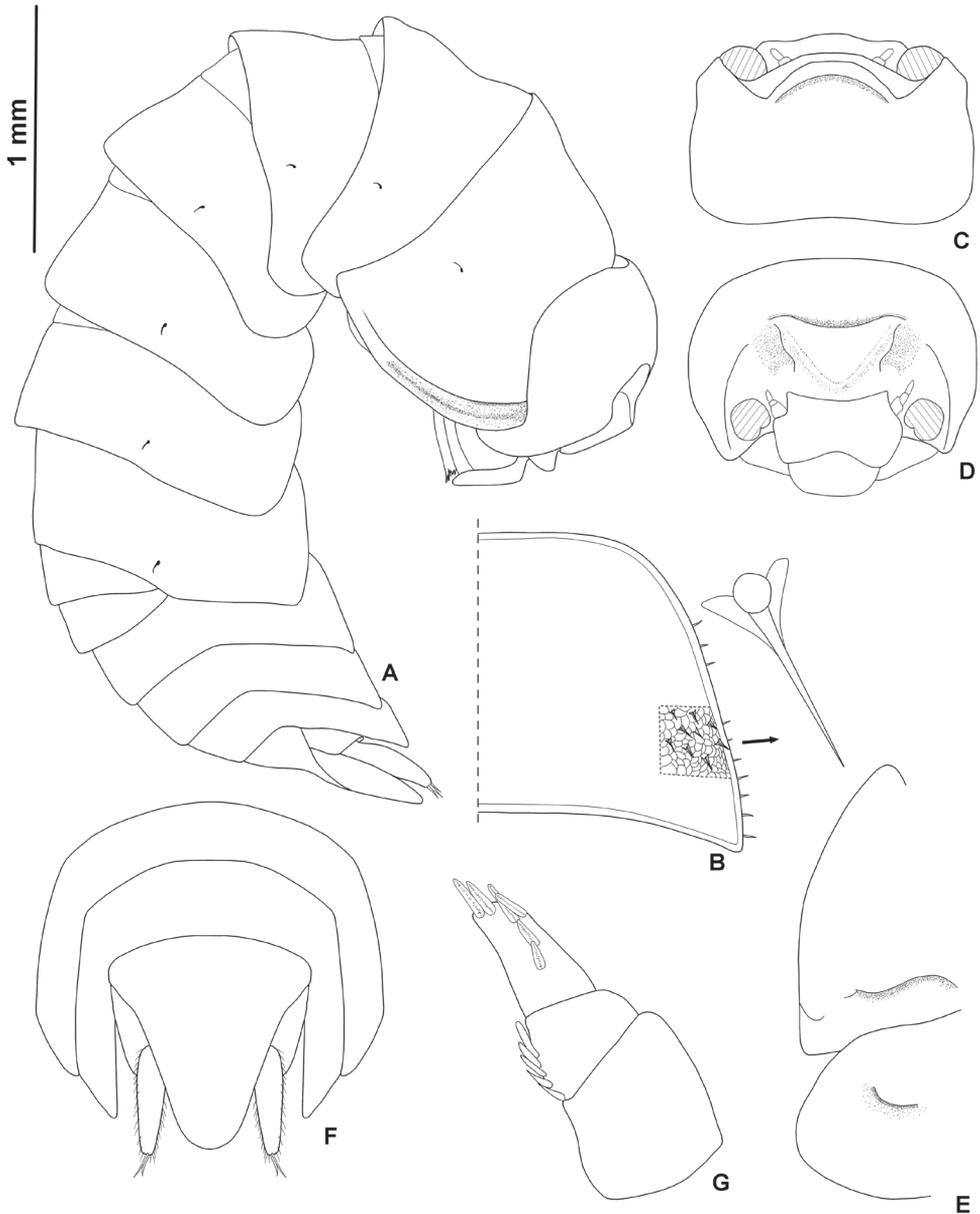


Figure 6. *Iansaoniscus georginae* sp. n., ♂ holotype, MZUSP 35114. **A** Habitus in lateral view **B** Pereonite 1 and scale-seta, dorsal view **C** Cephalon, dorsal view **D** Cephalon, frontal view **E** Pereonite 1 and 2, ventral view **F** Pleonites 4 and 5, telson, and uropods, dorsal view **G** antenna.

regions and, consequently, their importance for conservation (BRASIL 1990, 2008). Both regions have no legal protection acts and have been suffering with serious impacts. The Iraquara region is affected by touristic activities, lowering and pollution of the phreatic water due to agriculture activities. The Paripiranga region suffers deforestation due to agriculture and pastures (Fig. 2E), but the main threat is the use of the limestone

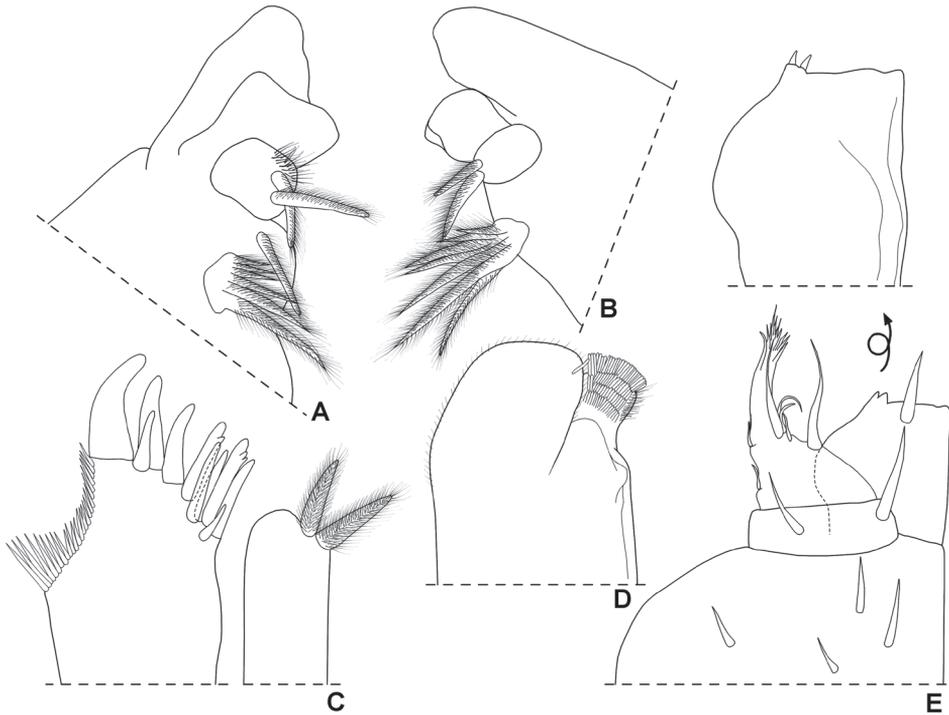


Figure 7. *Iansaoniscus georginae* sp. n., ♂ holotype, MZUSP 35114. **A** Left mandible **B** Right mandible **C** Maxillula **D** Maxilla **E** Maxilliped.

rocks for cement production. In conclusion, considering the rarity and a possibly relictual distribution of both species, *Iansaoniscus iraquara* sp. n. and *I. georginae* sp. n. can be considered as highly threatened and conservations actions studies about their distribution and ecology are urgently needed in order to effectively preserve these fragile species.

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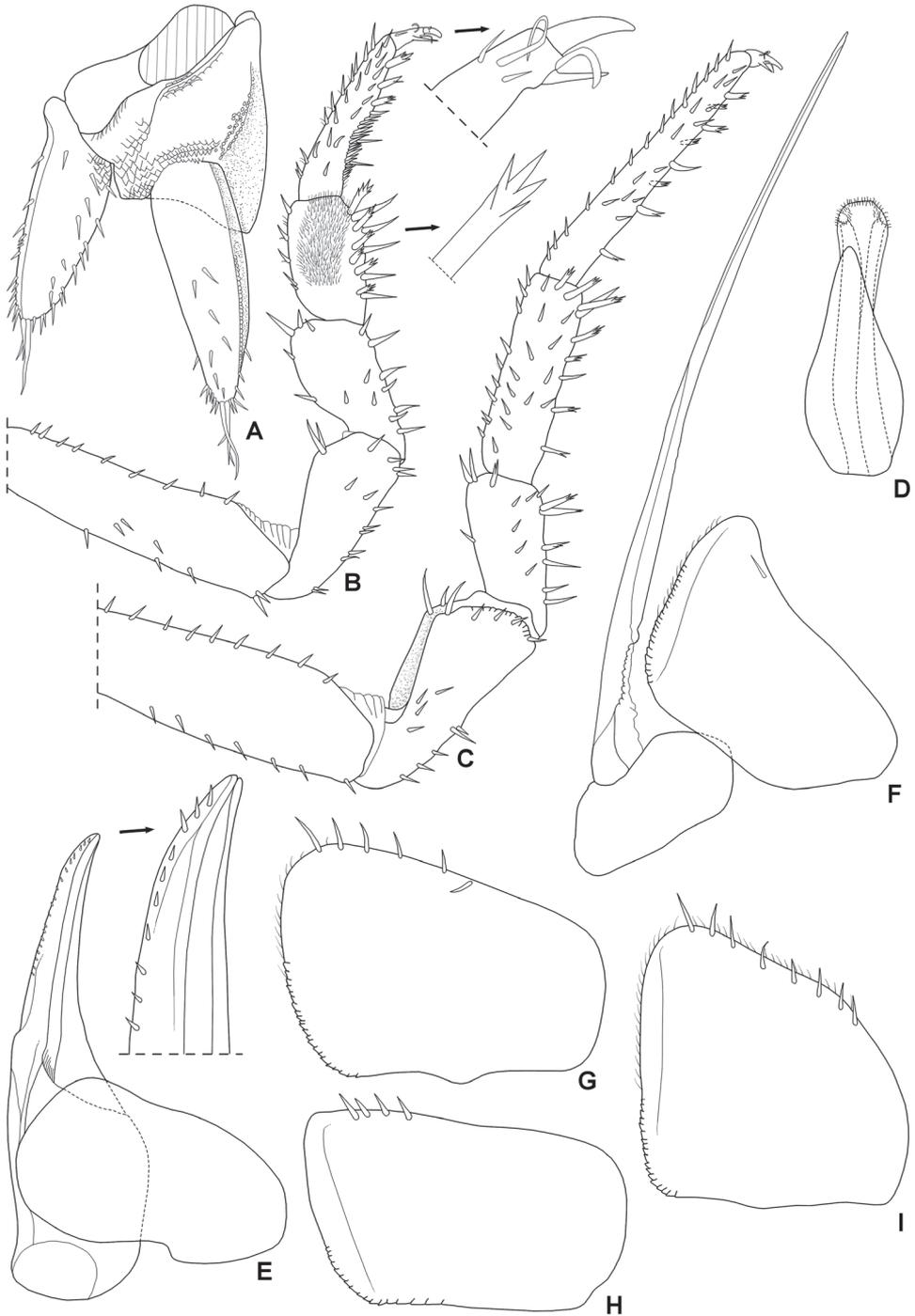


Figure 8. *Iansaoniscus georginae* sp. n., ♂ holotype, MZUSP 35114. **A** Uropod **B** Pereopod 1 **C** Pereopod 7 **D** Genital papilla **E** Pleopod 1 **F** Pleopod 2 **G** Pleopod 3 exopod **H** Pleopod 4 exopod **I** Pleopod 5 exopod.

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Six new subterranean freshwater gastropod species from northern Albania and some new records from Albania and Kosovo (Mollusca, Gastropoda, Moitessieriidae and Hydrobiidae)

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Abstract

During a field trip to the western part of the Balkan Peninsula in 2016, investigations of several caves and karstic springs revealed six new gastropod species living in subterranean waters and resulted in some noteworthy faunistic records. Five of the new species are assigned to the genus *Paladilhiopsis* Pavlović, 1913, namely *P. prekalensis* **sp. n.**, *P. lozeki* **sp. n.**, *P. szekeresi* **sp. n.**, *P. wohlberedti* **sp. n.**, *P. falniowskii* **sp. n.** and one to the genus *Plagigeyeria* Tomlin, 1930, namely *P. steffeki* **sp. n.** New Albania and Kosovo distribution records are given for *Iglica illyrica* Schütt, 1975, *Plagigeyeria zetaprotogona* Schütt, 1960, *Vinodolia matjasici* (Bole, 1961), and the first georeferenced record is given for *Saxurinator schlickumi* Schütt, 1960. The most important environmental factors influencing habitat selection of these subterranean freshwater gastropods are briefly discussed.

Keywords

cave, spring, Kosovo, *Paladilhiopsis*, *Iglica*, *Plagigeyeria*, *Saxurinator*, stygobiont, interstitial water

Introduction

It is known that the Balkan Peninsula is one of the most significant hotspots in terms of subterranean freshwater gastropod diversity (Radoman 1983, Bole and Velkovrh 1986; Kabat and Hershler 1993; Strong et al. 2008). In light of this, the number of the species known from Albania is surprisingly low, which might be due to the fact that the Albanian fauna is still very poorly explored compared to the other parts of Balkan Peninsula. The majority of hitherto known subterranean gastropod records is concentrated to the Lake Skadar area (also known as Lake Scutari or Lake Shkodër) with only a few additional records from the northeastern and southern parts of Albania (Reischütz and Reischütz 2008; Eröss and Fehér 2009; Pešić and Glöer 2013a; Glöer et al. 2015; Reischütz et al. 2013, 2014, 2016). Live collected specimens remain very scarce, therefore, most of the studies are based only on shell morphology. Likewise, all of the descriptions in this study based exclusively on shell characters, and therefore, these genus assignments remain somewhat uncertain and provisional until they are confirmed by anatomical and molecular data. In addition to the new subterranean freshwater gastropod taxa, our investigations of spring and cave localities in Albania and Kosovo also resulted in interesting novel distributional data. Due to the hitherto scarce records of all subterranean species from Albania, they significantly contribute to a better understanding of their zoogeography and distributional pattern.

Material and methods

The studied material was collected during a field trip in June and July of 2016 in northern Albania and Kosovo (Fig. 1). Various cave outflows and karstic springs were studied, where we preferred the following micro-habitats for sampling: (i) sedimentation zones of springs immediately at (or close to) the spring outlet zone, (ii) calm sedimentary spots of cave streams and (iii) from the scarce fine sand and gravel trapped among larger stones in higher water velocity sections of cave streams. In the case of dried-out intermittent springs and cave rivulets the dry sand sediments from the bed had been sampled in the same way. Sampling was carried out by a metal sieve of 3 mm mesh size combined with a polyamide knee-sock or pantyhose of ca 0.2 mm mesh size. Sand and fine gravel were sifted through the sieve. The material retained in the hosiery was further washed *in situ* by fresh water to remove the muddy and the very fine sand fractions of the sediment (Fig. 2H). We have used new hosiery at each sampling site. About 0.05–0.5 kg samples were collected per locality and immediately fixed in ca. 75% ethanol. Samples were sorted under Olympus SZ-11 stereo microscope. In the first round, the samples were sorted wet and if shells containing soft parts were found, they were transferred into fresh 75% ethanol with 20% ambient amount against the estimated specimen volume. After this, the samples were then dried and sorted through again to gain a second crop of dry shells which might have

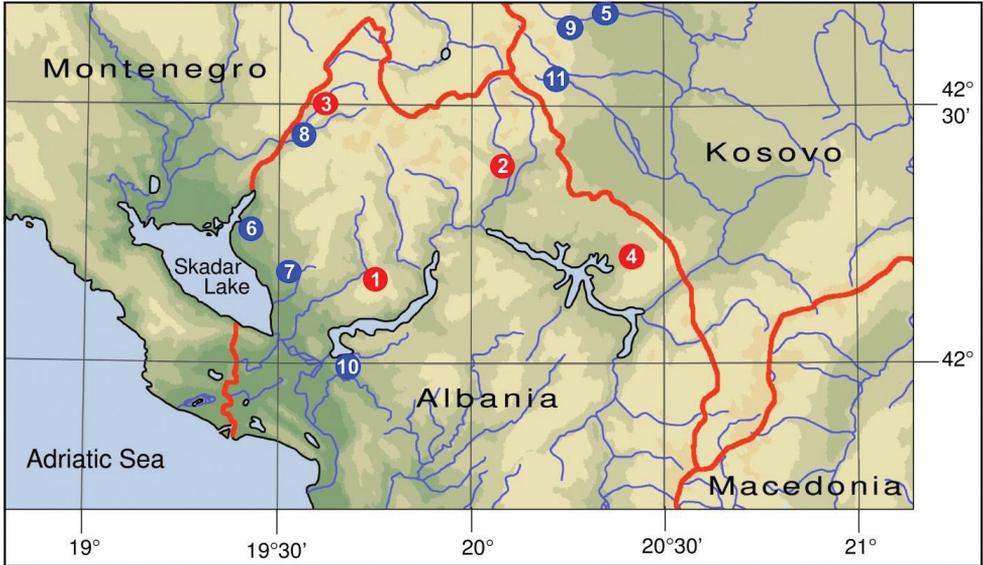


Figure 1. Distribution of the new species and faunal records mentioned in this paper. Red dots indicate type localities of new the species. **1** Prekal, Zhyla Cave (*Paladilhiopsis prekalensis* sp. n.) **2** Shoshan (*Paladilhiopsis lozeki* sp. n.) **3** Tamarë (*Paladilhiopsis szekeresi* sp. n. and *P. wohlberedi* sp. n.) **4** Krumë, Vrela Spring (*Paladilhiopsis falniowskii* sp. n., *Plagigeyeria steffeki* sp. n. and *Paladilhiopsis szarowskæ*) **5** Novosellë, White Drin Spring (type locality of *Plagigeyeria gladilini* and *Iglica illyrica*) **6** Bajzë, Syri i Sheganit Spring (*Plagigeyeria zetaprotogona*) **7** Rrash, Vrak Spring (*Plagigeyeria zetaprotogona*) **8** Tamarë, Dverpte Cave (*Plagigeyeria zetaprotogona*) **9** Kosovo, Pejë, Rugova Gorge, (*Saxurinator schlickumi*) **10** Vau i Dejës (type locality of *Paladilhiopsis gittenbergeri*) **11** Kosovo, Decani Valley (*Iglica illyrica*).

been overlooked during the wet sorting. Frontal, ventral and lateral view images were made by a digital camera system (Leica R8, Leitz Photar 21mm objective with Novoflex bellows and by Olympus DP-10 camera) and ImageJ scientific image analyzing software was used for making the measurements together with direct measurement with eye-piece micrometer.

Abbreviations

HNHM	Hungarian Natural History Museum, Budapest
NHMW	Naturhistorisches Museum, Wien
H	Shell height
W	Shell width
WB	Width of the body whorl
HA	Aperture height
HB	Height of the body whorl



Figure 2. Various habitats where subterranean gastropods were found: **A** Prekal, Zhyla Cave **B** Shoshan Spring **C** Tamarë, spring above the trout farm **D** Krumë, Vrela Spring **E** Novosellë, White Drin Spring **F** Bajzë, Syri i Sheganit Spring **G** Dverpte Cave south of Tamarë **H** sampling from sand and fine gravel by a sieve combined with polyamide pantyhose (photos: Zoltán Fehér, Maroš Grego, Dávid Murányi).

Results

The shells of the genus *Bythiospeum* and *Paladilhiopsis* are very similar and it is not possible to distinguish between these genera by shells only. An ongoing molecular study of the *Moitessieriidae* Bourguignat, 1863 following the earlier studies of Szarowska (2006) could not confirm the presence of genus *Bythiospeum* Bourguignat, 1892 in the Balkans, while the genus *Paladilhiopsis* Pavlović, 1913 was proved to be very diverse over the studied territory (Hofman et al, in MS). Thus, we place all the species described here as new with the shell shape like *Bythiospeum*/*Paladilhiopsis* to the genus *Paladilhiopsis*. For the same reason the *Bythiospeum szarowskiae* Glöer, Grego, Eröss & Fehér, 2015 is treated as *Paladilhiopsis szarowskiae*. In addition, a molecular phylogenetic reconstruction using the nuclear Histone H3 marker revealed that *Bythiospeum blihensis* Glöer & Grego, 2015 as well as *Iglica gittenbergeri* Reischütz and Reischütz, 2008 belong to the genus *Paladilhiopsis* (Andrzej Falniowski, personal communication) as well. The *Plagigeyeria steffeki* sp. n. shell morphology is well aligned with the related species hitherto assigned to that genus.

Superfamily Truncatelloidea J.E.Gray, 1840

Family Moitessieriidae Bourguignat, 1863

Genus *Paladilhiopsis* Pavlović, 1913

Paladilhiopsis prekalensis sp. n.

<http://zoobank.org/59D6C1B8-7543-4ED9-AAB2-CAF2D17A443B>

Figures 3–4

Diagnosis. Can be compared to *Paladilhiopsis szekeresi* sp. n. (Albania, Tamarë), from which it differs by a blunter apex, more convex whorls, more elongated and more declined aperture from the columella and by upper aperture edge more prominent in the shell outline as well as by the narrower umbilicus. It differs from *Paladilhiopsis lozeki* sp. n. (Albania, Shoshan) by its smaller and less elongated shell, blunter apex, more tumid body whorl and by the shape of the aperture. *P. wohlberedti* sp. n. (Albania, Tamarë) and *Montenegrospeum bogici* Pešić & Glöer, 2012 (Montenegro, Podgorica) differ markedly by their larger more conical shells, more prominent body whorls and shape of their apertures. The shell shape of the new species is somewhat similar to that of *Bosnidilhia vreloana* Boeters, Glöer & Pešić, 2013 (Bosnia, Banja Luka) which differs from the new species by its more slender shape, narrower elongated aperture and more flattened whorls.

Type locality. Albania, Shkodër district, Prekal, Shpellë e Zhylyt (Zhyly Cave), 210 m, near junction of Kiri and Prroni i Cise, 205 m, 42.1782°N; 19.7200°E (Fig. 2A).

Type material. Holotype, Type locality: leg. Eröss, Fehér, Grego, Szekeres, 28.06.2016 (HNHM 100167). Paratypes, same data (HNHM 100168/6; NHMW 111656/4; coll. Glöer 1 specimen and coll. Grego 5 specimens).



Figures 3–8. 3–4 *Paladilbiopsis prekalensis* sp. n. (holotype) 5–6 *Paladilbiopsis lozeki* sp. n. (holotype) 7–8 *Paladilbiopsis szekeresi* sp. n. (holotype); (photos: Peter Glöer, Jozef Grego).

Measurements. H 1.7 mm; W 0.8 mm; WB 0.65 mm; HA/H 0.36, HB/H 0.26 (holotype). Paratypes have broken apices, measurements not provided.

Etymology. Derived from the name of Prekal village, where the type locality is situated.

Description. The whitish and silky shell has 5 tumid convex whorls with a deep suture and a blunt apex. The surface is smooth and shiny. The shell is elongated, slightly conical, and almost subcylindrical. Umbilicus is slit-like. In frontal view, the palatal side of the aperture protrudes laterally. Aperture is ovoid, slightly attached to the body whorl and slightly extended left of the columella line, its major diameter deviates by ca. 30 degrees from the plane of the columella. The peristome margin is sharp, slightly reflexed outwards. The evenly thick outer lip is sinuated and the lower part of the aperture protrudes forward in such a way, that in the lateral view the labral margin deviates ca. 13 degrees from the plane of the columellar axis.

Habitat. The Zhyla Cave is a prominent spring cave acting as a temporary water overflow channel during high water outlets in the main spring (Burimi i Zhylës) situated underneath the cave close to bank of Kiri River. The approximately 70 m long cave is formed in a dark grey limestone by a single phreatic tunnel of 10 × 5 meters average diameter and ends in a terminal siphon. The underground water stream is acoustically detectable under the large boulders close to the terminal siphon. The cave is flushed by the frequent water outflows leaving only fine sandy sediment on the bottom. Empty and fragmented shells were found inside the cave; in a large sand sediment deposits close to the terminal siphon at the end of the hitherto known main dry cave passage. Therefore, it is supposed to live deeper in the cave as a typical underground species colonizing also the appropriate water caverns and cave habitats.

Distribution. Only known from the type locality.

Remarks. Most of the collected specimens were empty shells of white color, but it is likely that the shells of living specimens have translucent yellowish color like all other related species known from live-collected material.

***Paladilhiopsis lozeki* sp. n.**

<http://zoobank.org/796A594D-A35A-4655-8B61-FE461F31160D>

Figs 5–6

Diagnosis. Differs from *Paladilhiopsis szekeresi* sp. n. (Albania, Tamarë) and *P. prekalensis* sp. n. (Albania, Prekal) by its larger and more elongated shell, less tumid more flattened whorls, its more acuminate apex, its narrower umbilicus and the shape of the aperture. *P. wohlberedti* sp. n. (Albania, Tamarë) has a significantly more conical shape with fewer whorls and different proportions as well as its larger, differently shaped aperture. *Montenegrospeum bogici* (Montenegro, Podgorica) from family Hydrobiidae has a larger conical shell with more tumid whorls and proportionally larger aperture. *Bosnidilhia vreloana* (Bosnia, Banja Luka) has a similar shell shape with fewer whorls, more tumid apical whorls, blunter apex, and a proportionally smaller, more elongated aperture.

Type locality. Albania, Tropojë district, Shoshan, Burimi i Shoshanit (Shoshan Spring), 270 m, 42.3862°N; 20.0795°E (Fig. 2B).

Type material. Holotype, Type locality, leg. Eröss, Fehér, Grego, Szekeres, 01.07.2016 (HNHM 100169).

Measurements. H 2.00 mm; W 0.85 mm; WB 0.75mm; HA/H 0.30, HB/H 0.26 (Holotype).

Etymology. Named after the well renowned Czech malacologist and an ever-helpful friend, Vojen Ložek (Prague, Czech Republic), who contributed significantly to the knowledge of Recent and Pleistocene mollusc fauna of Europe.

Description. The whitish shell has 5 ½ convex, slightly flattened whorls with a smooth surface, a semi-deep suture and a blunt apex. The shell has slim, elongated, subconical shape with ovoid aperture and closed umbilicus. The left side of the aperture extends very slightly beyond the columellar axis, declining from it by ca. 25 degrees. Aperture is situated under the last whorl and is not prominent on the shell periphery outline. The slightly outward reflexed peristome is equally thick along its outline. The labral lip is sinuous with forward declining lower end by 13 degrees from the columellar axis. The aperture is detached from last whorl by a tiny gap at the suture.

Habitat. Shoshan Spring is situated in a natural limestone amphitheatre close to left bank of the Valbona River, and it forms a prominent spring-fed lake supplied by water from multiple debris outlets at its southern side and from the adjacent waterworks outlet at its eastern side. A small side spring can be found at the northern side of the path to the waterworks building. An old watermill is located at the spring lake outlet to the Valbona River. The new subterranean species likely inhabits the interstitial water of the underground gravel sediment layer. Empty shell of the new species were collected in the sandy sediment of spring water outlet at the left side of the broad spring zone south of the waterworks building.

Distribution. Only known from the type locality, where it was found together with a spring gastropod that most likely belongs to the genus *Graeconatolica*. The latter species could be described once representative material becomes available.

***Paladilhiopsis szekeresi* sp. n.**

<http://zoobank.org/60C0D5CC-3825-4608-942C-B5D5A6B9271D>

Figs 7–8

Diagnosis. Differs from *Paladilhiopsis lozeki* sp. n. (Albania, Shosan) by its smaller and less elongate shell, more tumid whorls, less conspicuous apex, broader umbilicus, and the shape of the aperture. From *Paladilhiopsis prekalensis* sp. n. (Albania, Prekal) it differs by a more prominent apex, less convex whorls, less elongated and less declined aperture from the columella and by the broader umbilicus. The sympatric *Paladilhiopsis wohlberedti* sp. n. has a much more conical shell. *Montenegrospeum bogici* (Montenegro, Podgorica) from family Hydrobiidae has a slightly larger, more conical shell with more tumid whorls and proportionally larger aperture. *Bosnidilbia vreloana* (Bosnia, Banja Luka) has a somewhat similar shell with fewer, more tumid whorls, blunter apex, and a smaller, more elongate, oval aperture.

Type locality. Albania, Malësia district, Tamarë, a spring above the trout farm at the right side of valley, north of the village, 360 m, 42.4745°N; 19.5693°E (Fig. 2C).

Type material. Holotype: Type locality, leg. Eröss, Fehér, Grego, Szekeres, and 27.06.2016 (HNHM 100170), Paratypes: same data (NHMW 111657/1, further 1 specimen in coll. Glöer and 1 specimen in coll. Grego).

Measurements. Holotype H 1.7 mm; W 0.8 mm; WB 0.65 mm; HA/H 0.34; HB/H 0.28; Paratypes H: 1.5–1.8 mm, W: 0.7–0.9 mm. WB: 0.6–0.7 mm. Paratypes have broken apices, measurements not provided.

Etymology. Named after our colleague and friend, a prominent specialist of the family Clausiliidae, Miklós Szekeres (Szeged, Hungary), who accompanied us on the field trip in 2016

Description. The shell is whitish, consisting of 5, slightly convex whorls with a semi deep suture and a blunt rounded apex. The rapidly expanding first apical whorl makes the shell shape oval-elongate. The aperture is ovoid expanded on its right side, and the umbilicus is semi-opened and deep. The left side of the aperture is situated slightly left of the columellar axis. The upper part of the aperture is slightly detached from the body whorl at the suture.

Habitat. Empty shells of the new species were collected at sand among stones and inside a small concrete well-built directly on the spring zone. The only known locality is a permanent spring that arises at the junction of a large debris zone and the limestone massif (concrete well) with a second permanent outflow from a large debris about 30 m upstream the small valley. The lower active spring and well are connected to a pipeline and an aqueduct supplying a trout farm on the right bank of the Cem (Cijevna) River. A large temporary spring outlet is situated under a vertical limestone wall at the end of the deeply cut gorge about 100 m northwest of the two permanent springs, and the large oval boulders indicate a significantly higher temporary water flow during wet seasons and during the snow melting. The morphology of the gorge indicates its genesis by the collapse of a cave portal. The new species likely inhabits the

interstitial water of the debris and the flooded caverns within a cave system present behind the debris.

Distribution. Only known from the type locality, where it was found syntopically with the more abundant *Paladilhiopsis wohlberedi* sp. n.

***Paladilhiopsis wohlberedi* sp. n.**

<http://zoobank.org/8D8EA590-FE46-4BE7-AB2F-7BCAC0B85F3B>

Figs 13–14

Diagnosis. *Paladilhiopsis wohlberedi* sp. n. differs from *P. prekalensis* sp. n. (Albania, Prekal), *P. lozeki* sp. n. (Albania, Shoshan) and *P. szekeresi* sp. n. (sympatric) by its more conical shell and proportionately much larger body whorl. The new species can be compared by shell shape to *Paladilhiopsis grobbeni* Kuščer, 1928 (Slovenia, Sevnica), from which it differs by a more robust shell, more tumid whorls, blunter apex and by its differently positioned and shaped aperture. From *Paladilhiopsis szarowskiae* it differs by its more conical shape, less ($4\frac{1}{2}$) and more tumid whorls, the more prominent body whorl and the larger aperture. *Montenegrospeum bogici* (Montenegro, Podgorica) has a more slender shell with more prominent and proportionally larger aperture situated more to the left of the columellar axis compared to the new species.

Type locality. Albania, Malësia district, Tamarë, a spring above the trout farm at the right side of valley, north of the village, 360 m, 42.4745°N; 19.5693°E (Fig. 1C).

Type material. Holotype: Type locality, leg. Eröss, Fehér, Grego, Szekeres, 27.06.2016 (HNHM 100171), Paratypes: same data (NHMW 111658/5; HNHM 100172/5; further 1 specimen in coll. Glöer and 14 specimens in coll. Grego).

Measurements. H 2.0 mm; W 1.0 mm; WB 0.9 mm; HA/H- 0.39, HB/H 0.33 (holotype).

Etymology. Named after Otto Wohlberedt (Triebes, Thüringen), who within his large work (1909) about Montenegro and northern Albania Mollusca (and Isopoda, Chilopoda, Diplopoda) contributed much to the knowledge of Invertebrate fauna of the Balkan peninsula.

Description. The whitish smooth shell has $4\frac{1}{2}$ slightly tumid whorls with a semi-deep suture and a blunt apex. The shell shape is elongate-conoid with proportionally large body whorl. The oval aperture does not deviate from the conoid shell peripheral outline and is reflected, attached to the body whorl by its upper left side and extends slightly over the columellar axis on its left side. The umbilicus is narrow and deep. On the lateral view, the labral peristome is straight and deviates backward by ca 8 degrees by the plane of columella.

Habitat. See *P. szekeresi* sp. n.

Distribution. Only known from the type locality, where it occurs syntopically with *P. szekeresi* sp. n.



Figures 9–14. 9–10 *Paladilhiopsis falniowskii* sp. n. (holotype) 11 *Paladilhiopsis gittenbergeri* (holotype) 12 *Paladilhiopsis szarowskiae* (holotype) 13–14 *Paladilhiopsis wohlberedti* sp. n. (holotype); (photos: Peter Glöer, Jozef Grego, Zoltán Fehér).

***Paladilhiopsis falniowskii* sp. n.**

<http://zoobank.org/C65B4812-FEBA-4BF0-B70C-882B5E8BC7A0>

Figs 9–10

Diagnosis. Easily distinguished from the sympatric *Paladilhiopsis szarowskiae* (Fig 12) by its larger and more oval shell, the more tumid and proportionally larger body whorl and the aperture shape. Compared to *Paladilhiopsis gittenbergeri*, (Albania, Vau i Dejes) (Fig 11) this species has slightly larger shell with a less prominent apex, less conical shape, and a differently shaped body whorl and aperture. *Paladilhiopsis haduophylax*, Schütt, 1959 (Bileća, Hercegovina) shows some similarity, but its shells size is significantly larger, and the position and shape of the aperture is significantly different. *Paladilhiopsis blihensis* from Donji Kamengrad, Bosnia, has more slender shell with more (5) whorls, more acuminate apex and a different aperture shape. The *Iglica kanalitensis* A. Reischütz, N. Steiner-Reischütz & P.L. Reischütz, 2016, differs from the new species by its much more slender shape, smaller aperture and its aperture axis being less declined from the columella.

Type locality. Albania, Has district, Krumë, Vrela Spring, 450 m, 42.1921°N; 20.4166°E (Fig. 2D)

Type material. Holotype: Type locality, leg. Eröss, Fehér, Grego, Szekeres, 30.06.2016 (HNHM 100173), Paratypes: same data (NHMW 111662/1, one specimen in coll. Grego, two alcohol preserved specimens were destroyed during ongoing molecular studies at Jagellonian University).

Measurements. Holotype, H 2.4 mm; W 1.0 mm; WB 1.0 mm; HA/H 0.37; HB/H 0.35. Paratypes H: 2.3–2.4 mm, W: 0.9–1.0 mm, WB: 1.0–1.1 mm

Etymology. Named after the honored malacologist and friend, Andrzej Falniowski (Jagellonian University, Kraków), who has greatly contributed to the knowledge of the Balkan Hydrobiidae and Moitesseriidae.

Description. The white translucent smooth shell has 4 convex whorls with a semi-deep suture. The shell is elongate-ovoid, and the tumid whorls are regularly tapering towards the blunt apex. The aperture is ovate with very slightly reflexed margins, its palatal side does not exceed the shell periphery, and its columellar side extends beyond the columellar axis. The peristome is detached from the body whorl by, the umbilicus is a tiny furrow. The labrum is straight-not sinuated laterally

Habitat. The type locality is a karstic spring at the foot of a scree slope. It has a permanent outflow from within the right side of a shallow pond and an intermittent upper spring outflow, situated at about 5 m higher level, 50 m from active spring. The new species had been collected in the sandy sediment of the spring water outlet at bottom of the broad and shallow spring zone. There is a large communal waste deposit site near the spring zone, which poses a direct threat to the spring habitat and the fauna of the outflowing rivulet.

Distribution. Only known from the type locality. Within the type locality the new species co-occur with the subterranean *Plagigeyeria steffeki* sp. n., *Paladilhiopsis szarowskiae* and several spring surface dwelling species: *Radomaniola curta* (Küster, 1852), *Ancylus fluviatilis* O.F. Müller, 1774, *Pseudamnicola krumensis* Glöer, Grego, Eröss and Fehér, 2015.

Genus *Iglica* A. J. Wagner, 1910

Iglica illyrica Schütt, 1975

Iglica (Rhaphica) illyrica Schütt, 1975: 8, figs 26–27.

Iglica illyrica – Glöer et al. 2015: 71, fig. 3.

Material. Kosovo, Gjakova (Đakovica) district, Deçan (Dečani), Deçani luginë valley (dolina Dečani) 2 km NW behind the Visoki Dečani Monastery, along the left bank of Lumbardh i Deçanit (Deçanska Bistrica), W of the trout farm. 710 m, 42.5533°N; 20.2492°E; leg. Angyal, Eröss, Fehér, Grego, 25.6.2014

Remarks. This species is known only from the three locations, namely the spring of the White Drin River in Kosovo (Burimi i Drinit të Bardhë or Beli Drin Izvor, Fig. 2E), which is the type locality, from Kosovska Mitrovica in Kosovo and from Soljani near Rožaj in Montenegro (Schütt 1975). This new record extends its distribution range southwards along the foothills of Prokletije Mountains. We have to note, that during our visit in 2016, we observed significant disturbance of the spring habitat compared to 2014, when we first found this species. The extraordinary floods of near rivulet Lumbardh i Deçanit removed a large part of the left bank stone debris under the spring resulting in leaking the spring waters directly to the rivulet sediment and almost drying out the spring. As a result, no specimen of the species was found in the locality during our 2016 visit. We believe that the species is still present inside the underground waters and in the nearby waterworks installation.

Family Hydrobiidae Stimpson, 1865**Genus *Plagigeyeria* Tomlin, 1930*****Plagigeyeria steffeki* sp. n.**

<http://zoobank.org/98763707-6C77-4400-B1FD-CE58FA321BA0>

Figs 15–17

Plagigeyeria gladilini – Glöer et al. 2015: 80, figs 32–35.

Diagnosis. Compared to the most closely related *Plagigeyeria gladilini* Kuščer, 1937 (Kosovo, Novosellë) (Figs 18–20), the new species differs by its more slender shape, blunter apex, less prominent protoconch and narrower umbilicus as well as by the broader and more reflexed peristome with a wing-like columellar expansion. The lateral shape of the outer lip has a different situation in the two species. From *Plagigeyeria procerula* Angelov, 1965 (Bulgaria, Opizvet), it differs by its much larger shell and blunter apex as well as by the much wider and differently shaped reflexed peristome.

Type locality. Albania, Has district, Krumë, Vrela Spring, 450 m, 42.1921°N; 20.4166°E (Fig. 2D)

Type material. Holotype: Type locality: leg. Eröss, Fehér, Grego, Szekeres, 20.06.2016 (HNHM 100174), Paratypes: same data (NHMW 111659/40, HNHM 100175/62. Also 1 specimens in coll. Glöer and 69 specimens in coll. Grego).

Other material. Same locality, leg. Eröss, Fehér, Grego, 02.07.2015 (coll. Grego and coll. Eross).

Measurements. Holotype H 2.8 mm; W 1.7mm; WB 1.1 mm; HA/H 0.47, HB/H 0.28. Paratypes H: 2.2–3.1 mm, W: 1.5–1.9 mm., WB: 1.0–1.2 mm.

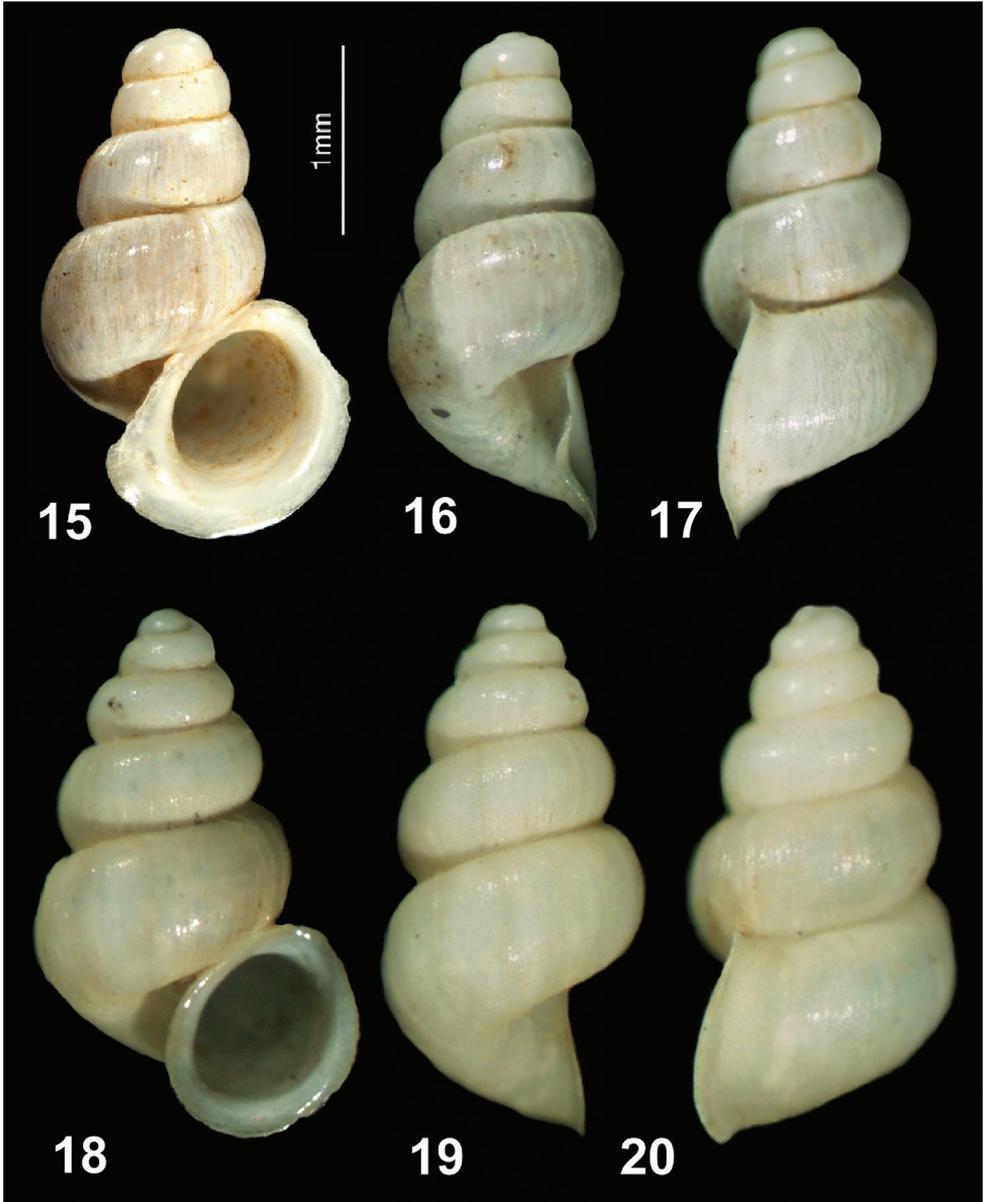
Etymology. Named after our untimely deceased excellent friend Jozef Šteffek (Banská Štiavnica, Slovakia) whose multidisciplinary activities dominated in the fields of malacozoology, ecosozology and zoogeography of the Slovakian mollusc fauna.

Description. The milky whitish, translucent shell has 4 convex whorls with a deep suture. The surface is smooth with fine axial growth lines. The shell is narrow-conical. The aperture is oval; the peristome expands widely outwards forming a wing-like structure at the columellar peristome. The lateral edge of the labrum is sinuated, and a characteristic situation is present on the wing shaped lower half of its columellar margin. The umbilicus is tiny, hidden behind the aperture and its reflected margins.

Habitat. See *P. falniowskii* sp. n.

Distribution. Only known from the type locality. Within the type locality the new species was found together with the subterranean *Paladilhiopsis falniowskii* sp. n. and *Paladilhiopsis szarowskiae*.

Remarks. The first specimens of the new species were collected in 2015 and were erroneously reported as *P. gladilini* (Glöer et al. 2015). Since then, we collected further individuals from the Krumë population and obtained topotypical *P. gladilini* material at the White Drin Spring (Burimi i Drinit të Bardhë or Beli Drin Izvor, Fig 2E). Having these samples in hand made us conclude that *P. steffeki* is a distinct species, quite separable from *P. gladilini*.



Figures 15–20. 15–17 *Plagigeyeria steffeki* sp. n. (holotype) 18–20 *Plagigeyeria gladilini* (topotype from the White Drin Spring near Novosellë).

Plagigeyeria steffeki sp. n. together with *P. gladilini* from Kosovo (Kuščer 1937) and *P. procerula* from Bulgaria (Angelov 1965), belong to a morphologically distinct group within the genus *Plagigeyeria* which is also geographically isolated from the other species of the genus. It would not be surprising if further molecular studies confirmed their separation at the genus level.

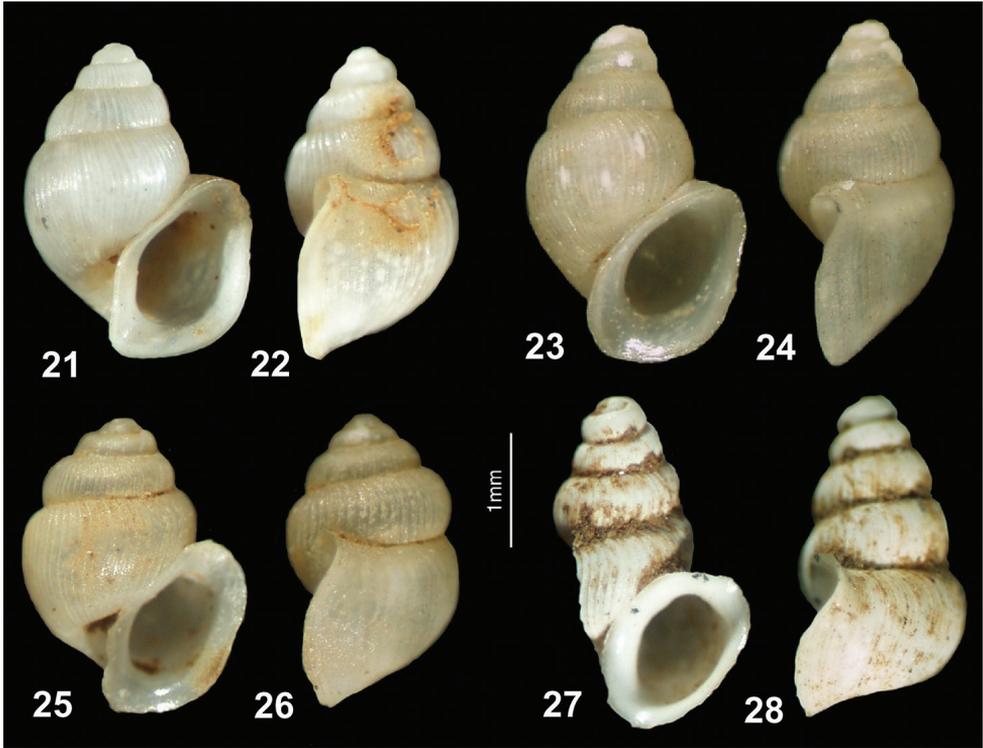
***Plagigeyeria zetaprotogona* Schütt, 1960**

Figs 21–28

Plagigeyeria zetaprotogona Schütt, 1960: 148–149, fig. 3 (Zetaquelle bei Tunjevo)*Plagigeyeria zetadidyma* Schütt, 1960: 149–150, fig. 4 (Zetaquelle bei Tunjevo).*Plagigeyeria zetatrityma* Schütt, 1960: 150, fig. 5 (Zetaquelle bei Tunjevo)*Plagigeyeria montenigrina* Bole, 1961b: 207, fig. 3 (Obodska pećina bei Rijeka Crnojevića)? *Plagigeyeria pageti* Schütt, 1961: 134–136, fig. 3 (Velika Spilja bei Risan)? *Plagigeyeria pageti minor* Schütt, 1961: 136, fig. 3 (Velika Spilja bei Risan)*Plagigeyeria zetaprotogona vitoja* Reischütz & Reischütz, 2008: 143, fig. 1 (Östliche Quelle in Vitoja am Ufer des Skadarsko Jezero):*Plagigeyeria zetaprotogona zetaprotogona* – Schütt 1972: 115, fig. 11.*Plagigeyeria zetaprotogona zetadidyma* – Schütt 1972: 115, figs 12–13.*Plagigeyeria zetaprotogona zetatrityma* – Schütt 1972: 116, figs 14–16.? *Plagigeyeria zetaprotogona pageti* – Schütt 1972: 116, figs 17–20.*Plagigeyeria zetaprotogona montenigrina* – Schütt 1972: 116, fig. 10.*Plagigeyeria montenegrina (sic!)* – Radoman 1983: 107–108, figs 122–124.*Plagigeyeria montenigrina* – Bank 2013*Plagigeyeria zetaprotogona* – Bank 2013? *Plagigeyeria zetaprotogona pageti* – Bank 2013*Plagigeyeria zetaprotogona vitoja* – Bank 2013*Plagigeyeria zetaprotogona zetadidyma* – Bank 2013*Plagigeyeria zetaprotogona zetatrityma* – Bank 2013*Plagigeyeria zetaprotogona* – Glöer et al. 2015: 74, figs 7–8.

Material. Albania, Malësia district, Bajzë, Syri i Sheganit Spring by the Shkodër Lake, 10 m, 42.2722°N; 19.3963°E (Fig. 2F); leg. Eröss, Fehér, Grego, Szekeres, 27.06.2016 (coll. Grego, HNHM 100385, NHMW 111661) – Shkodër district, Rrash, Burimi te Vrakut (Kroi i Vrakes, Vrak Spring), 60 m, 42.1457°N; 19.5452°E; leg. Eröss, Fehér, Grego, Szekeres, 28.06.2016 (coll. Grego) – Malësia district, Shpellë e Dverptes (Dverpte Cave), 4.5 km S of Tamarë, 200 m, 42.4262°N; 19.5272°E; Eröss, Fehér, Grego, Szekeres, 27.06.2016 (coll. Grego) (Fig. 2G).

Remarks. The taxonomic identity of this species is not clear. Schütt (1972) associated five subspecies with it, while Radoman (1983) didn't even mention this name in his monograph. In Schütt's (1972) opinion the typical *montenigrina* can be considered the morph from which the others are derived. Bank (2013) mostly follows Schütt's (1972) view, except that treating *montenigrina* a distinct species. The source of uncertainty is that, unlike in other subterranean (and epigeal) truncatelloid snails, striking morphological differences could be observed within the same museum lots (found at the same localities), e.g. three different morphs were described from the Zeta Spring in Tunjevo. Schütt (1972) found that two or three morphotypes can often be detected



Figures 21–28. 21–26 *Plagigeyeria zetaprotogona*: 21–22 Montenegro, Vitoja Spring 23–24 Albania, Bajzë, Syri i Sheganit Spring 25–26 Albania, Rraps, Vrak Spring; *Plagigeyeria* cf. *zetaprotogona*: 27–28 Albania, Dverphte Cave. (photos: Peter Glöer, Jozef Grego).

in the same location. Based on the biological species concept, one could argue that co-existence of these morphs is a strong argument against their distinction at the subspecies level. However, it is also conceivable that the museum lots studied by Schütt (1972) represent thanatocoenoses only, i.e. they were washed together from various, geographically isolated subpopulations, and therefore the co-existence of the various morphs is just artifactual. This makes it questionable how many species and subspecies actually exist, and, if there is more than one species, how large is the geographic range of *Plagigeyeria zetaprotogona* s. str.

We have found three populations that seem to belong to this taxon (or taxon group), which are the first records thereof from Albania. The Syri i Sheganit population is conchologically very similar to that of the Vitoja Spring (Podgorica, Montenegro, type locality of *P. z. vitoja*), and the other two populations further expand the known range of morphological heterogeneity. The specimens from Vrak spring have a more robust shape and could represent a new subspecies, while the single broken shell and few fragments from Shpelle Dverptes are more elongate. Until more material become available we will treat it as *Plagigeyeria* cf. *zetaprotogona*.

Genus *Vinodolia* Radoman, 1973

Figs 29–32

Vinodolia matjasici* (Bole, 1961)Iglica matjašiči* Bole, 1961a: 59–60, fig. 1 (a small spring near Rijeka Crnojevića)*Anagasta matjašiči* – Radoman 1973: 423, fig. 2C.*Iglica (Iglica) matjasici* – Schütt 1975: 7, figs 21–22.*Anagastina matjasici* – Radoman 1983: 54–55, fig. 45.*Vinodolia (Anagastina) matjasici* – Bank 2013*Vinodolia matjasici* – Pešić and Glöer 2013a: 79.*Vinodolia matjasici* – Glöer et al. 2015: 74, fig. 9

Material. Albania, Malësia district, Bajzë, Syri i Sheganit Spring by the Shkodër Lake, 10 m, 42.2722°N; 19.3963°E (Fig.1F), leg. Eröss, Fehér, Grego & Szekeres, 27.06.2016 (coll. Grego).

Remarks. Hitherto only three locations of this species were known, all in Montenegro: the type locality near Rijeka Crnojevića (Bole 1961a), more precisely Lipovik Spring near Rijeka Crnojevića (according to Radoman 1973, 1983); Vilina Cave near Virpazar (Schütt 1975) and Vitoja Spring (Glöer et al. 2015). This new record confirms the presence of this species in Albania and extends its known distribution within the Skadar Lake drainage. All known populations show some difference in the shell size and morphology, but the scarce material does not allow us to understand their significance, and thus, for the time being, we consider the above mentioned populations conspecific.

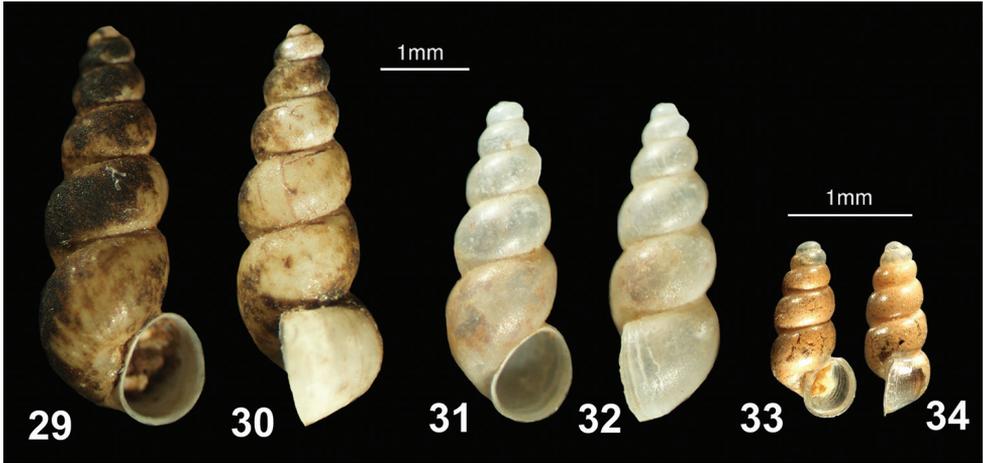
Genus *Saxurinator* Schütt, 1960***Saxurinator schlickumi* Schütt, 1960**

Figs 27–28

Saxurinator schlickumi Schütt, 1960: 148, fig. 2 (Rugovska klisura bei Peć).*Saxurinator schlickumi* – Bank 2013

Material. Kosovo, Pejë (Peć) district, Rugova Gorge, 3.5 km W of the Patriarchate Monastery, spring with travertine waterfalls at the left side of gorge near a resting station, 650 m, 42.6654°N; 20.2307°E; leg. Eröss, Fehér, Grego, Szekeres, 03.07.2016 (NHMW 111660, HNHM 100384)

Remarks. This species was known only from the type locality, which was defined quite inaccurately as "Rugovska klisura bei Peć" (=Rugova Gorge or Gryka e Rugovës, near Pejë) by Schütt (1960). It has not been found since, and, as the Rugova Gorge



Figures 29–34. 29–32 *Vinodolia matjasici*: 29–30 Albania, Bajzë, Syri i Sheganit 31–32 Montenegro, spring Vitoja 33–34 *Saxurinator schlickumi*: Kosovo: Peja, Rugova Gorge; (photos: Peter Glöer, Jozef Grego).

is 25 kilometers long and there are numerous springs along both sides, it remained uncertain where the type material originated and where exactly does the species live. Due to the lack of any recent data to validate the species' distribution, Seddon (2011) assessed it as Data Deficient (DD). The Rugova Gorge is a protected site now, and there is no reason to suppose that there is any threat to its subterranean habitats. This record confirmed the presence of this species and makes us suppose that it might be found also in other springs within the gorge.

Discussion

As before, little is known about how environmental factors influencing the living conditions of subterranean truncatelloid gastropods. Most of our knowledge is based on field observations and partly on intuition of the specific groundwater habitat characterization. We assume that the most important factors determining the appropriate habitat of the subterranean freshwater species include: 1.- *the absence of daylight*; 2.- *the availability of food*; 3.- *oxygen and carbon dioxide concentrations of the water*; 4.- *water chemistry*; and 5.- *water flow velocity*. Combinations of these factors within their optimal range for the snail species determine their living conditions directly and indirectly by influencing the composition of the biotic community (influence on the growth of food species, on predator species, and on the competitors, parasites, etc.) as well.

1. Absence of daylight: By the absence of light, photosynthesizing Cyanobacteria, algae and auxotrophic Labyrinthulomycetes are also absent in the subterranean habitats, while their strong presence on the surface spring zone has allowed the evolution of a wide range of daylight dependent food competitors, predators and parasites. We

assume that the lower number of predators, parasites and competitors for food, together with the more steady environment was the main driving factor for gastropods inhabiting and adapting to underground habitats.

2. Availability of food: Subterranean truncatelloids are presumably feeding on the chemolithotrophic prokaryotes gaining the energy for their biochemical processes (structural proteins, lipids and sugar synthesis) under the absence of light from the oxidation of inorganic cations, in most cases Fe^{2+} or Mn^{2+} . In similar some thermal and mineral waters (and deep sea vents) could host ecosystems based on biological oxidation of sulphurous compounds and H_2S by chemoautotrophic microorganisms (Falniowski et al. 2008). The organic material accumulated by the chemolithotroph/chemoautotroph assemblages is thus a fundament for specific underground ecosystems. The precipitated inorganic residua of chemolithotrophic process (hydroxides/oxides of Fe^{3+} or Mn^{4+} can be frequently found accumulated on the outer shell surface of underground gastropod species as a brown or black overlay indicating the likelihood of our assumption. We have also an indication that some underground valvatiform species (Carpathian populations of *Hauffenia*) can feed on the dense net of soft tiny tree roots penetrating the interstitial water among debris within the spring zone. Likely the flat valvatiform shell shape could better trap those species in the net of roots. Future genetic investigations of gastropod intestine content could most likely prove the above theories.

3. Oxygen and CO_2 saturation: Dissolved oxygen is necessary for gastropod breathing and also to oxidative reactions important for the chemolithotrophic processes within its feed chain, while the dissolved CO_2 is essential as the main carbon source for the feed bacteria. Both saturations are strongly dependent on temperature (saturation increasing by lower temperature) and thus the environment temperature has a secondary effect on optimal saturation range for the gastropod as well as food microorganisms. Furthermore, the CO_2 saturation coupled with dissolved hydrocarbonate equilibrium are the key factors driving the corrosive/accumulation character of the karstic water. Some underground gastropod species are also adapted to thermal extremes and waters with high CO_2 , H_2S content, and low oxygen saturation (Falniowski et al. 2008).

4. Water chemistry: The dissolved ions are important for reactions driving the biomass growth (Fe^{2+} , Mn^{2+}) of the food species. The calcium content is important to the secretion of the gastropod shell and other water-soluble growth factors are essential for the gastropod as well for the food substrate, in addition it stabilizes the pH value (hydrocarbonate equilibrium). As all the underground species are narrowly specialized to their steady chemical habitat, even slight anthropogenic pollution or other environment alternation could have a severe impact on water chemistry and could cause irreversible damages on the whole underground ecosystem.

5. Water flow velocity: The water flow velocity influences the oxygen and CO_2 saturation and distribution. We assume it is also important for the species motility within the

habitat. Stagnant water has lower oxygen saturation and higher CO₂ content coming from decaying organic material. Low flow allows better animal motility towards food and to sexual partners and the opposite for high. High flow also challenges the adhesive strength of gastropod musculature and slime important for attachment of the animal to the substrate. The seasonal very high water flow likely detaches live animals from the substrate and washes them out where they accumulate in the sedimentation zones. The underground species must have adapted to withstand the flowing water within their habitat. We are convinced that the average water flow velocity could also determine the shape of the shell: more slender shells can stand higher velocities of water due to lower hydrodynamic resistance and the more robust forms evolved in habitats with slower or steady water velocity.

Although they are often referred to as cave-dwellers, the subterranean truncatelloids (those discussed in this paper and *Bythiospeum*, *Paladilbia*, *Hauffenia*, *Islamia*, *Lanzaia* etc.) are not restricted only to the caves and cave waters. Based on our two decades of field experience from the Carpathian mountains, the Carpathian basin, Dinarid Alps and southeastern Asia (Šteffek and Grego 2002, 2005; Šteffek et al. 2011; Glöer and Grego 2015; Glöer et al. 2015; Eröss and Petró 2008; Pešić and Glöer 2012, 2013a, 2013b; Glöer and Pešić 2014a, 2014b), we can conclude that their habitat is the groundwater saturated zone, including interstitial spaces within the coarser sand and gravel deposits, among debris as well as inside the crevices and caverns of the bedrock. On limestone substrate they might also occur in larger cavities and caves as well, and these, together with spring outlets and wells, are the usual places where they can be sampled relatively easily.

Some facultative cave-dwelling species (Šteffek and Grego 2005) can mainly be found in the spring zone and spring debris, while their occurrence inside the cave waters is restricted to the passages close to the spring zone and they their occurrence is not extended into the deeper parts of the cave systems. Several taxa/local populations, occurring in non-limestone habitats with optimal water chemistry (e.g. *Hauffenia kissdalmae* Eröss & Petró, 2008 in the volcanic Börzsöny Mts., Hungary; *Bythiospeum oshanovae* (Pintér, 1968) in the gravel of the Danube, Hungary; *Hauffenia* sp. in sandstones of the Rimavská Basin, Slovakia; *Alzoniella slovenica* (Ložek & Brtek, 1964) in the outer Carpathian flysh, Slovakia and Czech Republic, *Bythiospeum carpathicum* (Soós, 1940) on the flysh of Mt. Hoverla, Ukraine) indicate that subterranean truncatelloids are not bound exclusively to karstic systems.

Considering the above discussed very specific range of habitats the discussed gastropod species cannot be called as “troglobiont” species, as this term is preferably used for mostly air breathing species inhabiting the cave areas above the water level. The term “freshwater troglobiont” suggested by Sket (2008) also does not fit to the above described habitat range, as the species are not limited to cave waters. The term “stygo-biont” is also not well defined and very differently interpreted, most frequently used to describe the relevant habitat (Bole and Velkovich 1986). With this respect we would prefer the interim term “subterranean freshwater habitat” which better covers the broad habitat ranges and makes the understanding of the subject clearer, until some other generally accepted and more appropriate term is adopted.

Conclusions

While the neighboring former Yugoslavian territories have been recognized for their large subterranean freshwater gastropod species diversity for a long time, no data had been reported from Albania before the end of the millennium (Radoman 1983, 1985; Bole and Velkovrh 1986; Kabat and Herhsler 1993). As several other molluscan groups, terrestrial gastropods among others, showed a similar pattern in the Balkans, the question arose as to whether Albania is actually a gap in continuation of the Balkan diversity or just *terra incognita* (Sattmann and Reischütz 1994). The malaco-faunistic exploration in Albania gathered momentum only after the political transition of the country in 1990 (Welter-Schultes 1996, Fehér et al. 2004), and this resulted in the discovery of the first subterranean freshwater gastropod population only in 2006. This was first reported as *Paladilhiopsis* cf. *serbica* (Pavlović, 1913) by Fehér and Eröss (2009), but considered later as a presumably distinct species (Reischütz et al. 2013). Since then, including the six new species reported within this article, the number of subterranean freshwater species described from Albania has increased to 11 (Reischütz and Reischütz 2008; Reischütz et al. 2014, 2016, Glöer et al. 2015), and the total known Albanian fauna is now comprised of 16 species including the two new records herein and the 3 known undescribed species. During our field trip in 2016 we sampled 16 springs and cave outflows altogether, and, in fact, we discovered new species in ca. a quarter of them while underground species were detected in almost half of the investigated localities. This suggests that these known species represent just a small fraction of the actual species richness, and most of the Albanian subterranean gastropod diversity is still waiting to be discovered. We hope that this study will stimulate future research toward a better understanding of these cryptic ecosystems in Albania.

Acknowledgements

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