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Simplogonopus rubellus (Attems, 1902) gen. n., comb. n. (Diplopoda: Polydesmida: Trichopolydesmidae): Revealing the Identity of an Enigmatic Eastern-Mediterranean Millipede

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Abstract: The true identity of the millipede *Polydesmus rubellus* Attems, 1902 is revealed more than a century following its original description. Its type material is examined for the first time after 117 years of shelf-life. A lectotype is designated and documented. *Sphaeroparia simplex* Golovatch, 2013 is shown to be a junior subjective synonym of *P. rubellus* **syn. n.** According to the latest concepts in the systematics of the family Trichopolydesmidae, the species does not fit in any of the known genera and should be assigned to a new, monotypic genus, *Simplogonopus* gen. n., described here. The clear Afrotropical affinities of the new genus and the possible explanations for its distribution, currently known to include Crete, the Aegean islands of Kythnos and Chios, and northeastern Bulgaria, are discussed.

Key words: new genus, new synonymy, Afrotropical, introduction, relict, distribution

Introduction

Numerous, often overlooked synonymies at the species level present a common challenge for diplopod taxonomists worldwide. Even the best known European fauna still contains such taxa. Their unresolved status usually results from poor original descriptions, often either accompanied by no illustrations or based solely on females or juveniles, or both, despite the paramount importance of the male copulatory organs long recognised in the taxonomy of most millipede groups (e.g. Minelli 2015). In this work, we attempt to solve one similar issue, clarifying the identity of a remarkable polydesmidan millipede.

The order Polydesmida is by far the most diverse and widely distributed group in the entire class Diplopoda (Hoffman 1980, Brewer et al. 2012, Enghoff et al. 2015). In Europe, the order comprises seven families, 45 genera and over 260 species (excluding unquestioned introductions) (Kime & Enghoff 2011, Golovatch 2013, Antić et al. 2014, Golovatch & VandenSpiegel 2015). Many of these species are small, typically under 1.5 cm in length, and mostly confined to the Mediterranean realm, largely representing narrow endemic, often troglobitic or troglophilic forms. This holds especially true for the family Trichopolydesmidae Verhoeff, of which 31 species and 18 genera are presently encountered in Europe together with the adjacent parts of North Africa (Kime & Enghoff 2011, Golovatch 2013, Antić et al. 2014, Golovatch & VandenSpiegel 2015, Akkari & Mauriès 2018). These species are almost exclusively characterised by strongly developed gonopodal telopodites with transversely oriented bases, considerably protruding from a moderate to small gonocoel (Golovatch 2013).

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Among the European Trichopolydesmidae, one species was referred to an Afrotropical genus: *Sphaeroparia* Attems, 1909, described from two Greek islands (Golovatch 2013). The taxonomic history of this species provides the main objective of the present contribution, as it appears to be quite complex, even though the name of that trichopolydesmid was *Sphaeroparia simplex* Golovatch, 2013. The story actually started when Attems (1902) described *Polydesmus rubellus* Attems, 1902 based on 23 females and 7 juveniles collected from Nerokouros, south of Chania, Crete, Greece. Despite the absence of males, the author considered the small size (5–5.5 mm in length) and the conspicuous reddish colouration of the species to be distinctive enough to recognise it among other local polydesmidans. However, the reason why he assigned this species to *Polydesmus* Latreille, 1802 remains unknown, since neither its minute size nor its bacilliform tergal setae are characteristic of the genus. Lang (1964) put 3 females of *P. rubellus* on record, again from the western part of Crete. Strasser (1970) added two more records of the species from the island, this time from the vicinities of Rethymno (Vrises) and the ruins of Knossos near Heraklion (see also Felesaki et al. 2010). Strasser (1970) also provided descriptive notes, reasonably assuming that this conspicuous polydesmidan belonged to an unknown genus. Hence, the quotation marks he used for the name *Polydesmus*. Three years later, in his third review of the Bulgarian diplopods, Strasser (1973) provided a surprising discovery of "*Polydesmus*" *rubellus* from Kavarna, on the northern Black Sea coast of Bulgaria. Despite the absence of males from the sample, Strasser was confident that the material was conspecific with the Cretan "*Polydesmus*" because it fully matched Attems' (1902) original description.

Four decades later, Golovatch (2013) described *Sphaeroparia simplex* from the caves Katafyki (Katafygi) and Hagiogalousiana (Agiou Galaktos) from the Aegean islands of Kythnos and Chios, respectively, in the context of a reclassification of the superfamily Trichopolydesmoidea. The species was described as uniformly cream to yellowish, thus not at all reminiscent of the reddish "*P.*" *rubellus*. The choice of an African genus to accommodate *simplex* was based on the classification of the Afrotropical Trichopolydesmidae by Mauriès & Heymer (1996). The last piece of the puzzle was found in the form of eight tiny pinkish-orange polydesmidans collected in 2017 from the park of the Euxinograd [Evksinograd] Palace, on the Black Sea coast, near the city of Varna, Bulgaria, this time including three adult males. Their gonopods appear to be identical to those of *Sphaeroparia simplex*. Two years later, another seven specimens, completely matching the external appearance of those from Euxinograd, were found at the beach of Plaka Village, east of Mount Olympus in Greece; this time, however, including females only.

Putting all facts together, it seems most likely that the samples from Crete, Kythnos, Chios, Plaka, Kavarna and Euxinograd belong to the same trichopolydesmid species described and originally assigned by Attems (1902) to *Polydesmus*, with a slight doubt remaining about the species identity of the Cretan samples and the specimens from Plaka which consist of females only.

The latest reclassification of the family Trichopolydemidae in the scope of the Afrotropical fauna (Golovatch et al. 2018) redefines the genus *Sphaeroparia* and characterises it by the presence of small gonopodal coxae with a shallow gonocoel leaving the telopodites considerably exposed, the latter with branched acropodites. Thus, *S. simplex* is clearly not congeneric with *S. minuta* Attems, 1909, the type species of the genus. Considering the clear-cut affinities of *simplex* to the Afrotropical fauna, we propose a new genus to accommodate *simplex* alone.

Materials and Methods

The examined specimens are preserved in 70% ethanol and deposited in the collections of the Naturhistorisches Museum Wien, Austria (NHMW), Institute of Biodiversity and Ecosystem Research, Sofia, Bulgaria (IBER), the National Museum of Natural History, Sofia, Bulgaria (NMNHS) and the Zoological Museum of Moscow University, Russia (ZMMU). The examination and documentation of the type specimens of *Polydesmus rubellus* were performed with a Nikon DS-F2.5 camera mounted on a Nikon SMZ25 stereomicroscope, using NIS-Elements Microscope Imaging Software with an Extended Depth of Focus (EDF) patch. Whole-body pictures of non-type specimens were taken with a Nikon D5500 and a Canon EOS 5D digital camera and stacked using Zerene Stacker software.

Line drawings of the gonopods were made with a Leica stereomicroscope with a built-in camera lucida. Scanning electron micrographs were taken with a JEOL JSM-5510 microscope.

Results

Family Trichopolydesmidae

Genus *Simplogonopus* gen. n.

Type-species: *Polydesmus rubellus* Attems, 1902.

Etymology. To emphasise the conspicu-

osly simple gonopod conformation in this genus. Masculine.

Diagnosis. Both sexes with 20 segments. Gonopodal coxite (***c***) very large, with a broad and deep gonocoel, almost fully concealing the telopodite. Telopodite remarkably simple, consisting of a more or less semi-globose prefemoral part ending in a short solenomere (***s***) devoid of a pulvillus; and a rather short uniramous acropodite (***a***) apically drawn into a very small process barely visible beyond coxite. Both ventral side of segment 2 and coxae 2 in males without modifications. Metatergal setae bacilliform.

Remarks. The shape of the gonopodal telopodite, in particular the apically directed seminal groove and the short retrorse solenomere, are so characteristic of nearly all Afrotropical Trichopolydesmidae, as reviewed recently by Golovatch et al. (2018), that there is no doubt that *Simplogonopus* gen. n. is rooted in the same lineage within the family. The large coxite and gonocoel in the new genus represent the supposed advanced state of trichopolydesmid gonopods, which is also observed in Afrotropical genera like *Eburodesmus* Schubart, 1955 and *Hemisphaeroparia* Schubart, 1955. However, the latter two taxa are characterized by a more or less complex gonopodal telopodite, unlike its very simple condition in *Simplogonopus* (Golovatch et al. 2018). In addition, at least *Hemisphaeroparia* is characterized by a strongly enlarged, finger-shape spiracle placed ventrally on segment 2 in males, while in *Simplogonopus* gen. n. this character is still plesiomorphic, the spiracle remaining unmodified.

***Simplogonopus rubellus* (Attems, 1902) comb. n.**

Figs 2–18

Polydesmus rubellus Attems, 1902: 584–585, no figures.

Polydesmus rubellus: Lang (1965): 239; Felesaki et al. (2010): 364.

"*Polydesmus*" *rubellus*: Strasser (1970): 244–245, fig. 13; Strasser (1973): 414–415, figs 1–3.

Sphaeroparia simplex Golovatch, 2013: 68–74, figs 7–17, **new synonymy.**

Material examined. Type material of *Polydesmus rubellus* Attems, 1902: ♀ lectotype, Inv. No. NHMW9451, designated herewith, 19 ♀♀, 9 fragments, 6 juv. paralectotypes Inv. No. NHMW9445, "Kreta, Nerokuri, zwischen abgefallenen Platanenblättern am Bachrand, leg. Attems C. Mai 1900" [Crete, Nerokouros, in *Platanus* leaf litter, at the edge of a rivulet, V.1900], det. & don. Attems C. **Other material**: 1 ♂, 5 ♀♀ (IBER), 1 ♂ (NMNHS), 1 ♂ (ZMUM), Bulgaria, Black Sea coast, park of Euxinograd [Evksinograd] Palace, under large calcareous stones by a small artificial pond surrounded by various broadleaved trees and shrubs (Fig. 1), hand collecting, 15.V.2017, P. Mitov & B. Vagalinski leg.; 7 ♀♀ (IBER), Greece, Central Macedonia, Pieria regional unit, Plaka Village, near Olympos Beach Camping, small pile of leaf litter mixed with some human-made waste, under a piece of plywood and in a decaying slipper, 23.IV.2019, B. Vagalinski & P. Mitov leg.

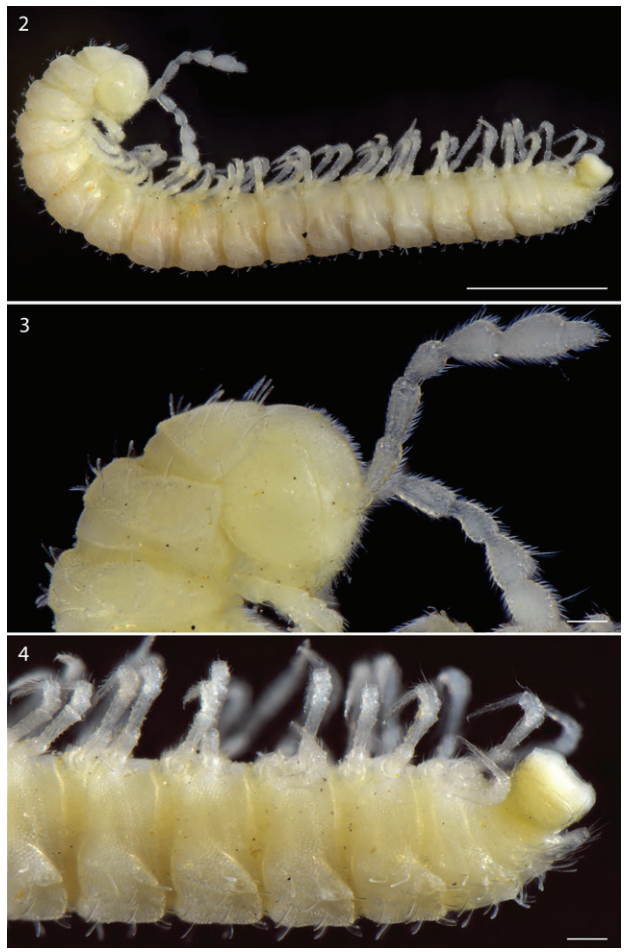
Comment. Since type material has never been revised, lectotype designation is warranted to stabi-

Fig. 1. Habitat of *Simplogonopus rubellus* in the park of Euxinograd Palace.

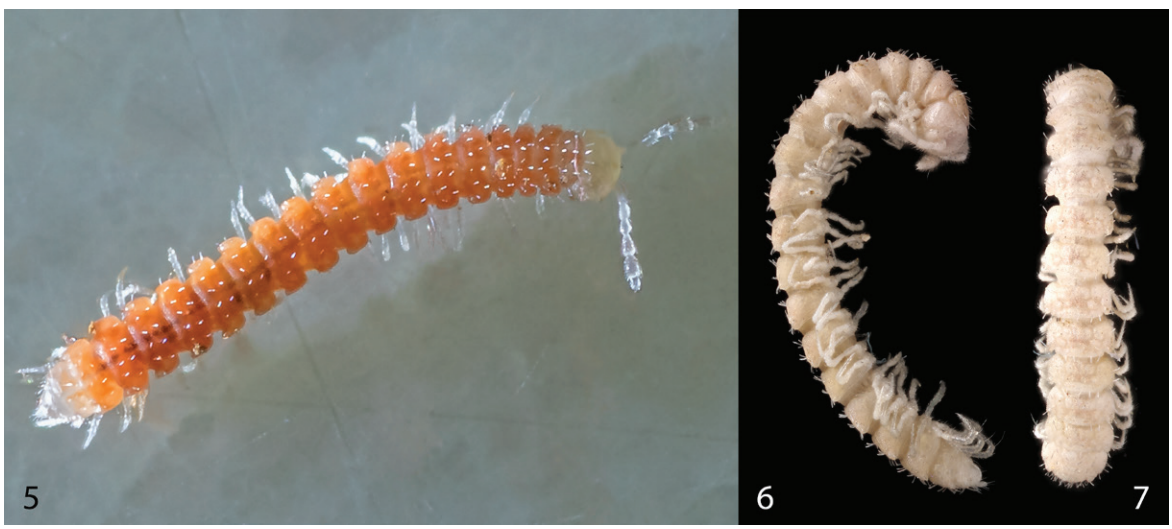
lise the nomenclature of the species. The most intact, well-preserved, adult specimen, albeit a female one, is herewith designated as lectotype, while all other specimens from the type series become paralectotypes.

Descriptive notes. Live colouration pink to light orange (Fig. 5), preserved material faded to yellowish or pallid (Figs 2–4, 6, 7). Tegument (Figs 10–13) densely micro-alveolate. Antennae (Figs 8 & 9): antennomeres 4–7, each with one to several macrosetae distally; 5th and 6th with a distinct crescent-shaped field of bacilliform sensilla dorsally near distal edges; 7th with a distodorsal tuft of very short and erect setae (arrow in Fig. 9). Collum with 3 transverse rows of 3+3, 3+3 and 4+4 setae, from oral to caudal; metatergal rows: 3+3, 4+4 and 4+4 setae, from oral to caudal, ozopore-bearing segments with an additional seta on each side between rows 2 and 3 at paratergal edge. Limbus (Fig. 12) microcrenulate, with alternating stouter and finer denticles. Gonopods (Figs 14–18): coxite (***c***) bearing 2 setae near ventral edge; solenomere (***s***) vestigial – very short and straight, directed caudad; acropodite (***a***) short and stout, drawn into a fine, small, apical process bent dorsad; seminal groove (***g***) running mesally over prefemoral part (***p***), ending ventrally on solenomere.

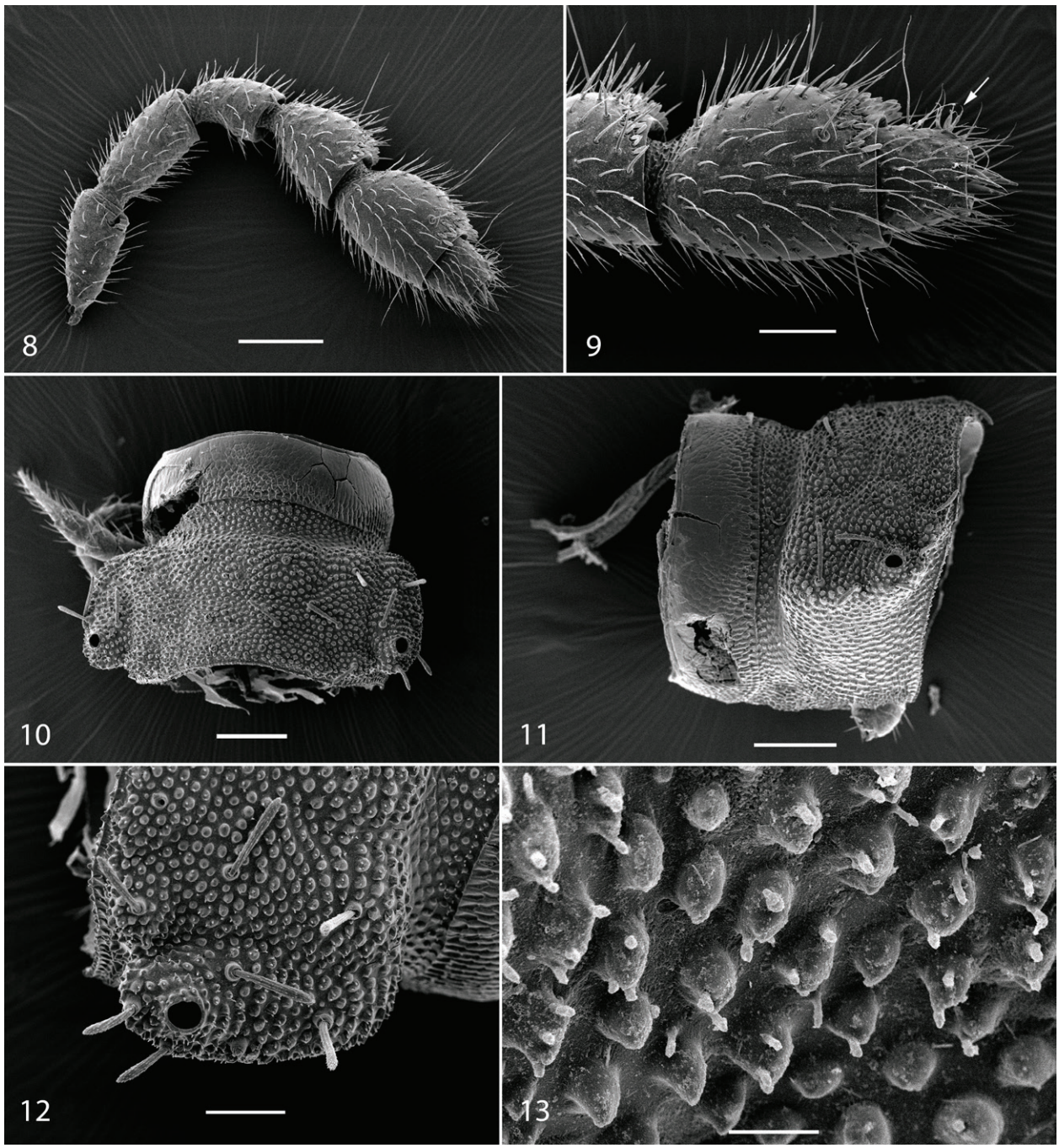
Remarks. The conspicuous pinkish-orange colouration of *S. rubellus* is still another piece of evidence of the Afrotropical roots of this trichopolydesmid, as many taxa from Cameroon also show different tinges of red (Golovatch et al. 2018), while all European trichopolydesmids are uniformly pallid. However, the remarkable pigmentation of *S. ru-*



Figs 2–4. *Polydesmus rubellus* Attems, 1902, lectotype female, inv. no. NHMW9451; (2) habitus, lateral view; (3) close-up of the head and anterior body rings; (4) close-up of body rings 14–19 and the telson. Scale bars: figure 2: 1 mm, 3 & 4: 0.1 mm.



Figs 5–7. Habitus of *Simplogonopus rubellus*: (5) a living female from Euxinograd, dorsal view, picture by V. Zarev, taken not to scale; (6) a male from Euxinograd after alcohol conservation, lateral view; (7) same specimen, dorsal view, pictures by K. V. Makarov, taken not to scale.



Figs 8–13. External morphology of *Simplogonopus rubellus*, male from Euxinograd: (8) antenna; (9) distal part of the same; (10) body ring 9, dorsal view; (11) body ring 7, lateral view; (12) right edge of metatergum 9, dorsal view; (13) tegument under large magnification. Scale bars: figures 8, 10 & 11: 0.1 mm, 9 & 12: 0.05 mm, 13: 0.01 mm.

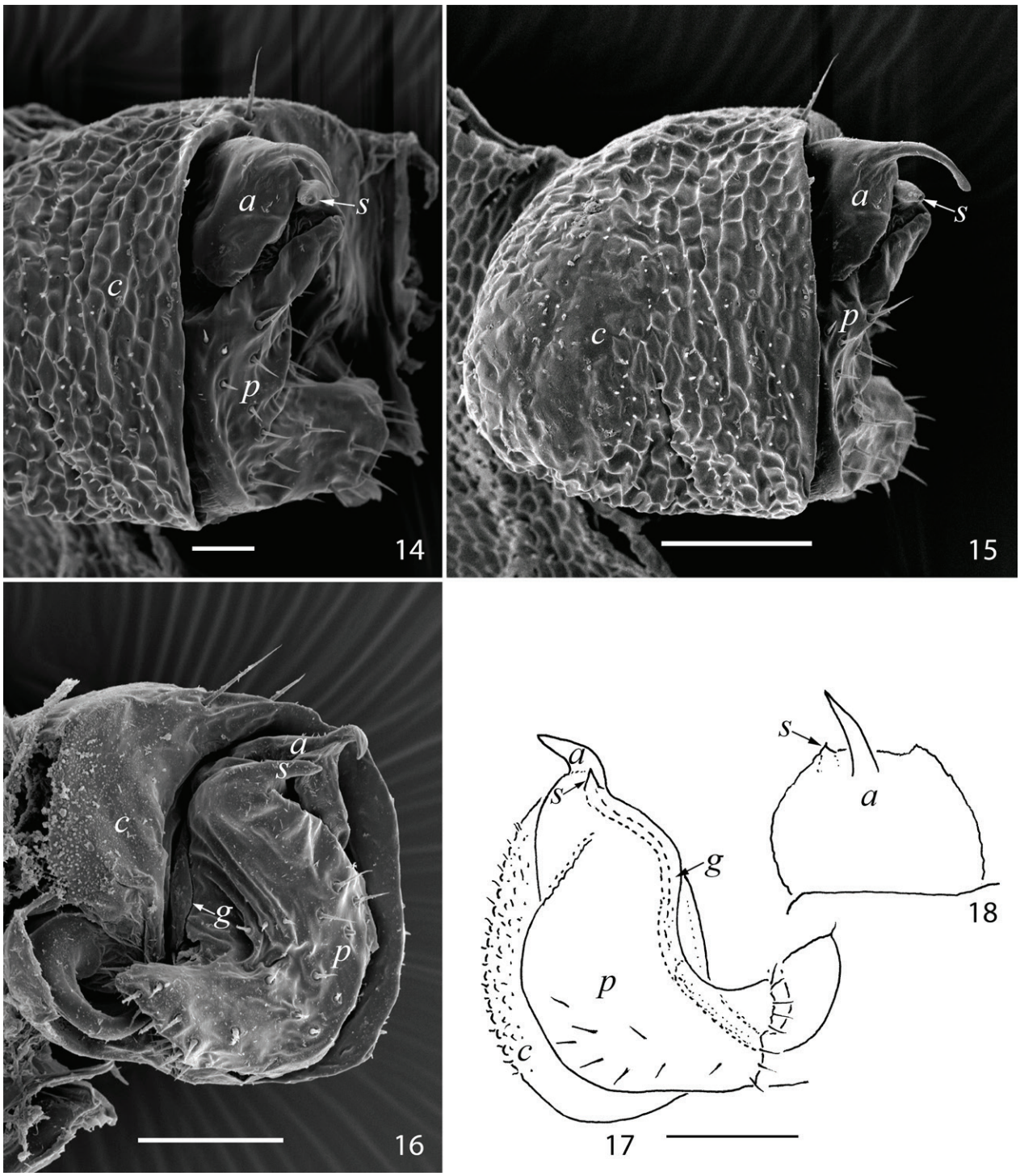
bellus is very easy to fade in ethanol, as the newly collected specimens became uniformly pallid only several days after conservation.

Discussion

There are at least three possible scenarios to explain the known distribution of the species (Fig. 19), as discussed below.

1) Palaeorelict survivor

Millipedes are well-known for their poor dispersal abilities in combination with a generally weak ecological specialisation. These two features make them very suitable for biogeographic studies, as their distributions mostly reflect tectonic events rather than environmental changes (e.g. Enghoff 1993, Golovatch 2009, Golovatch & Kime 2009, Shelley & Golovatch 2011).



Figs 14–18. Gonopods of *Simplogonopus rubellus*, male from Euxinograd: (14) right gonopod, latero-caudal view; (15) right gonopod, lateral view; (16) left gonopod, caudo-mesal view; (17) right gonopod, mesal view; (18) distal part of left gonopod, lateral view. Scale bars: figure 14: 0.02 mm, 15–18: 0.05 mm. Abbreviations: *a*: acropodite, *c*: coxite, *g*: seminal groove, *p*: prefemoral part, *s*: solenomere.

Thus, it seems tempting to believe that *Simplogonopus rubellus* is an indigenous palaeorelict element in the eastern Mediterranean fauna. If we accept this hypothesis, then we may assume that the exclusively Afrotropical trichopolydesmid group the new genus belongs to must have already been diverged by the Late Triassic, before the division between Gondwana and Laurasia was completed. Furthermore, by that time its distribution must have encompassed much of present-day Africa and the southern parts of Laurasia, including the future Mediterranean.

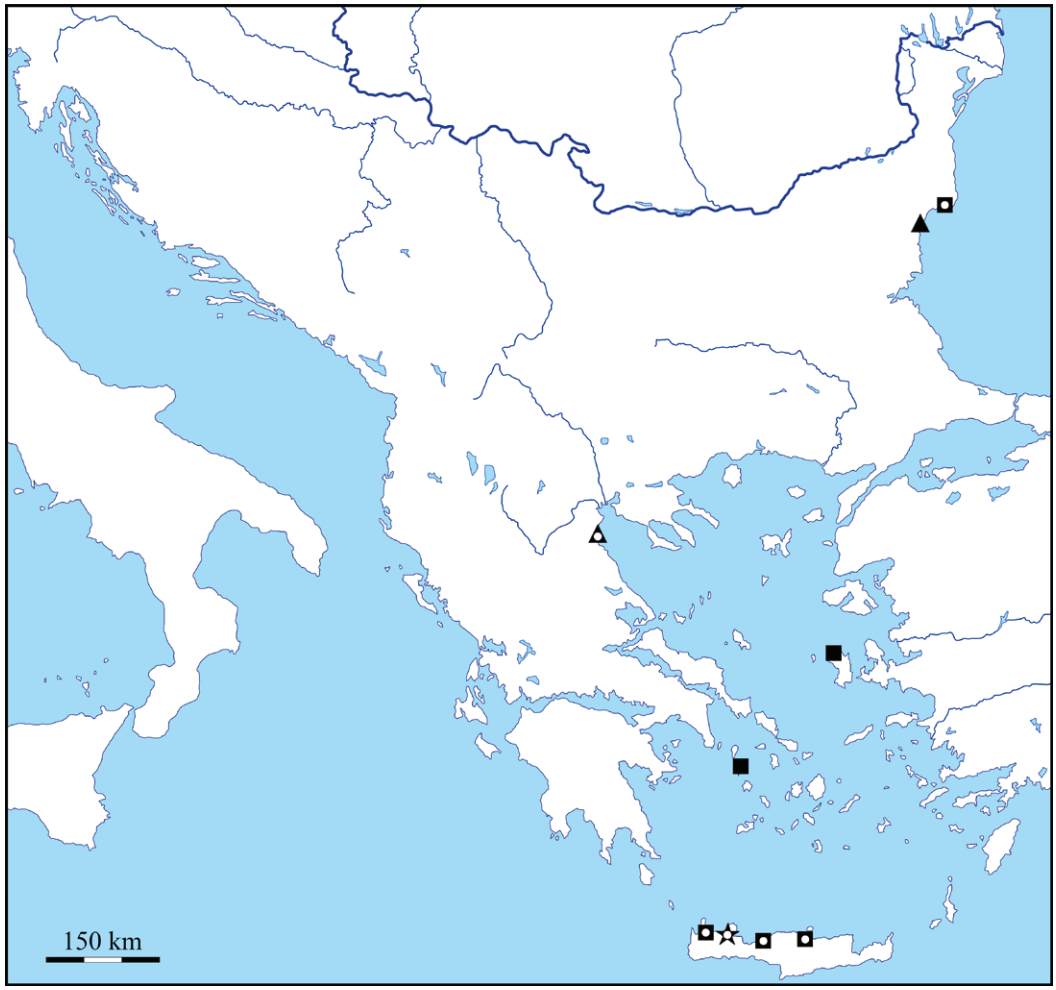


Fig. 19. Distribution of *Simplogonopus rubellus*. Star: type locality of *Polydesmus rubellus* Attems, 1902; squares: other records from literature; triangles: new records; symbols with white dots: records based only on females.

Some relict polydesmidans belonging to taxa showing Gondwanan distribution patterns are known from the western Mediterranean realm. The genus *Tonodesmus* Silvestri, 1925 with its two species from Málaga Province, Spain, the genus *Rharodesmus* Schubart, 1960 known from Morocco and Tunisia with one species each, and the mostly Carribean genus *Cynodesmus* Cook, 1895 with a single species occurring in the Canary Islands, are the only Palaearctic representatives of the otherwise pantropical family Pyrgodesmidae (Akkari & Enghoff 2011, Kime & Enghoff 2011). In addition the paradoxosomatid genera *Boreviulisoma* Brölemann, 1928 and *Jeekelosoma* Mauriès, 1985 from the southern Iberian Peninsula and Morocco, respectively, appear to be northern outposts of the chiefly Afrotropical-Neotropical tribe Eviulisomatini (Reboleira & Enghoff 2013, Enghoff & Reboleira 2019). Another example may be *Cantabrodesmus lorioli* Mauriès, 1971, the sole species of the genus *Cantabrodesmus* Mauriès, 1971, which is a troglobitic endemic from the Santander Province of Spain (Kime & Enghoff 2011, Luque & Labrada 2017). If its placement in the Afrotropical subfamily Prepodesminae of family Chelodesmidae (which is questionable, H. Enghoff, pers. comm.) is to be confirmed, then *C. lorioli* would be the only indigenous Palaearctic member of the family.

Currently no palaeoendemics related to either the Afro- or the Neotropics are known among the Diplopoda from the Aegean region. However, the distribution shown by a particular family of Isopoda, another poorly vagile arthropod group, seems to present such evidence. The Styloniscidae is a predominantly Gondwanan family, except for the genus *Cordioniscus* Graeve, 1914, which is chiefly Euro-Mediterranean, with most of its species occurring on Greek islands, while a single species, *Cordioniscus africanus* Vandel, 1955, is known from Algeria, and another one—*Cordioniscus leleupi* Vandel, 1968—from Ecuador (Schmalfuss & Erhard 1998). Even more interestingly, *Cordioniscus kithnosi* Andreev,

1986 inhabits one of the locations from which *S. rubellus* was recorded, Katafygi Cave, Kythnos. The cave also harbours other troglobiont endemic arthropods, while same holds true for Agiou Galaktos cave on Chios (Paragamian 2018a & b).

However, considering its epigean occurrences in various habitats (including anthropogenic ones) in combination with its vivid colouration, *S. rubellus* is obviously no true troglobiont. Moreover, the significant climatic differences between the Aegean region and the northern Black Sea coast of Bulgaria—especially as regards the mild and humid Mediterranean winter compared to the serious colds (below -10°C) which are rather usual in northeastern Bulgaria during this time of the year—also suggest that the species is not a stenoecious relict, but a more ecologically plastic taxon. Therefore, it is likely that the distribution of *S. rubellus* is either a result of natural dispersal in the more recent geological past or is due to anthropochory.

2) A human-caused introduction could have easily occurred considering that the eastern Mediterranean has been a trade crossroad in the Old World since ancient times. The ancient and medieval history of Crete was particularly turbulent, the island having been ruled successively by the Roman and Byzantine empires, the Arabs and the Venetians, all of which are well known for their long-distance military and trade expansions. As the Romans in particular and, later, the Arabs, established trans-Saharan trade routes (Fenn et al. 2009, Ross 2011), *S. rubellus* may have been brought from tropical Africa to the Aegean region with soil or plant material. This option seems indeed very plausible at least as regards the record from the park of Euxinograd whose vegetation includes many foreign species planted in the late 19th to early 20th century.

3) Recent migration

Another possible scenario is that certain Afrotropical trichopolydesmids, including the presently studied species and/or its direct ancestor, may have inhabited parts of the Sahara Desert during its "green period" either in the Miocene and/or in the Pliocene, when xerophytic shrublands, grasslands or sclerophyll woodlands covered most of the region (Salzmann et al. 2011, Pound et al. 2012). Then, with the desertification of Sahara in the late Pliocene and Pleistocene these trichopolydesmid populations could have become extinct. However, *S. rubellus* may have survived in the eastern Mediterranean after a gradual migration northwards at some point in the past. This could have taken place through the Isthmus of Suez and along the Near East and the Mediterranean coast of Anatolia. In such case, the present distribution of the species could be expected to include also parts of Anatolia, and at least its occurrence on Chios may have resulted from natural dispersal, bearing in mind that the island had been connected to the Anatolian mainland until only ca. 12 thousand years ago (Perissoratis & Conispoliatis 2003).

Alternatively, certain parts of the Mediterranean Basin could have served as transport corridors between North Africa and Aegean Islands during the Messinian salinity crisis (ca. 5.96 Mya), when the marine gateways between the Atlantic Ocean and the Mediterranean Sea closed due to an uplift along the African and Iberian continental margins resulting in (partial) desiccation of the sea basin (Krijgsman 2002, Duggen et al. 2003). The following Zanclean flood (ca. 5.33 Mya), when the Mediterranean Basin was refilled, has already been used for explaining the vicariance events between terrestrial organisms in North Africa and Southern Europe, including invertebrates (e.g. Sanmartín 2003, Graham et al. 2012).

There are some examples of trans-Saharan distributions of millipedes. Most species of the genus *Odontostreptus* Attems, 1914 (Spirostreptida: Spirostreptidae) are found in western tropical Africa, except *O. lepineyi* (Verhoeff, 1938) and *O. maroccanus* (Attems, 1914), both of which are known from Morocco. Likewise, *Archispirostreptus syriacus* (DeSaussure, 1859) of the same family is endemic to Palestine, being the only non-African member of this chiefly tropical eastern African genus (Sierwald 2016).

A mixture of the above presented scenarios should also be considered, that is *S. rubellus* being native (either palaeo- or neoendemic) to Aegean islands, having reached the Balkan mainland with human transport. That the species occurs in natural habitats on Crete, Kythnos and Chios and in anthropogenic ones at Plaka and Euxinograd is in support of such a hypothesis. The distribution of the nearctodesmid *Macrosternodesmus palicola* Brölemann, 1908 presents a similar example. The natural habitat of this species is believed to be ancient deciduous woodland in the European Atlantic zone, while its occurrences east and north of this region are in synanthropic sites (Kime & Enghoff 2011).

In any case, the origin of *S. rubellus* remains doubtful until further material is collected and molecular analysis carried out.

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