



Research article

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A new species of *Speonemadus* from Portugal, with the revision of the *escalerai*-group (Coleoptera, Leiodidae)

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Abstract. Over recent years, intense field work in caves of Portugal has provided new data on the distribution of subterranean Iberian leiodid beetles. *Speonemadus algarvensis* sp. nov. is described from caves of southern Portugal. The new species is included in the *Speonemadus* Jeannel, 1922 *escalerai*-group (Cholevinae; Anemadini). All species of the *S. escalerai*-group are revised and *S. breuili* (Jeannel, 1922) is resurrected as a valid species. A key to identify the species of the *S. escalerai*-group is provided and the distinctive characters are illustrated. The distribution of all species of the group is mapped with new data together with biogeographic considerations.

Key words. Beetles, subterranean, troglobiont, karst, caves, *Speonemadus*.

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Introduction

The genus *Speonemadus* Jeannel, 1922 has been the subject of a comprehensive review by Giachino & Vailati (1993), who established *Hormosacus* Jeannel, 1936 as a synonym of *Speonemadus*, due to close structural homology between morphological characters of the aedeagus.

Speonemadus comprises 10 taxa divided into four species groups, seven of which are distributed in the Iberian Peninsula (Giachino & Vailati 1993; Perreau 2000; Salgado *et al.* 2008).

Recent intense fieldwork in Portuguese caves has provided abundant material of troglobiont beetles (Reboleira 2007; Reboleira *et al.* 2009, 2010a, 2011b; Reboleira & Ortuño 2011). Among this material, a new species of *Speonemadus* belonging to the *escalerai*-group was found. Currently, this species group comprises three Iberian species: *Speonemadus angusticollis* (Kraatz, 1870), *S. bolivari* (Jeannel, 1922) and *S. escalerai* (Uhagón, 1898).

We describe a new southwestern Iberian species of *Speonemadus*, that colonizes caves of southern Portugal, and revise all species of the *escalerai*-group. We also resurrect *Speonemadus breuili* (Jeannel, 1922) as a valid species.

Material and methods

Specimens were collected with baited pit fall traps and by active searching in several caves of the Iberian Peninsula (Reboleira 2012).

Male genitalia were extracted and immersed in a 10% KOH solution for six hours and then dehydrated with a series of ethanol transfers (60% to 96%), followed by a xylene immersion for 12 hours and final mounting in Canada balsam.

The general external morphology of the specimens was photographed with a stereo microscope Olympus SZX16, the aedeagus with an Olympus CH; both using an Olympus C5060WZ camera; photos were combined using CombineZP. For scanning electron microscopy, specimens were critical point dried in a Tousimis Autosamdri 815, series A, and mounted on aluminium stubs, coated with platinum/palladium and studied in a JEOL JSM-6335F scanning electron microscope. Images were processed with Adobe Photoshop CS6.

Habitus length was measured from the apex of the labrum to the tip of the elytra. Mean measurements in Table 1 correspond to six specimens of each sex.

Institutional abbreviations

The material is deposited in the following collections:

- SR = Sofia Reboleira (Portugal)
- ZMUC = Zoological Museum, Natural History Museum of Denmark (University of Copenhagen, Denmark)
- CJMS = J.M. Salgado (Vigo, Spain)
- CFL = Fresneda-Lagar (Llesp, Spain)
- CPB = Pablo Barranco (Universidad of Almería, Spain)
- CZULE = León University Zoological (León, Spain)
- CMCN = Museo de Ciencias Naturales (Barcelona, Spain)
- MNHN = Natural History Museum (Paris, France)

Results

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Family Leiodidae Fleming, 1821
Subfamily Cholevinae Kirby, 1837
Tribe Anemadini Hatch, 1928

Genus *Speonemadus* Jeannel, 1922

Speonemadus escalerae-group; “Gruppo *escalerae*” *sensu* Giachino & Vailati 1993: 205.

Representatives of this group are characterized by a body length between 3.9 to 5.0 mm and have a slightly transverse pronotum (Figs 6–15); the anterior tibia of the males is compressed towards the apical half and has a keel with different shapes on the dorsal edge (Figs 16–20); elytra have a rounded apex in males and a notched one in females. The median lobe of the aedeagus is elongated and bottle-shaped in dorsal view (Figs 21–25) and the inner sac lacks a ventral tooth in the apical region of the middle lobe and has two long parallel rows of fine spines and teeth (Figs 23–24).

All species of the group have similar color patterns, the same antennal shape and development of the membranous wings in both sexes, as well as similar genital segments and aedeagi in males, and similar 7th and 8th urosternites and spermatheca of females.

The life-style of this group is mostly subterranean, they are frequently found under stones or in leaf litter in forests and in caves, walking in bat guano or in the subterranean substrate.

Key to the species of the *Speonemadus escalerae*-group

Note to the key: diversification of the species of the *escalerae*-group is likely to be recent (see below “Speciation and biogeography”). Therefore, morphological differences are not particularly visible and a combination of characters should be used for species recognition. All species and both sexes of the “*escalerae*” group show a similar coloration, shape of the antenna, development of membranous wings, genital segment in the male aedeagus and 7th and 8th uroventrites, as well as spermatheca of the females. Females have no characters to distinguish between species, which also occurs in other genera of the Leiodidae, e.g., *Colon* Herbst, 1797. Only females of *S. angusticollis* can be separated from other species by the shape of the pronotum, being the only one with a bell-shape, as in males. Therefore, in this species group only males provide distinctive characters useful for identification. These characters are identified in all key items and constitute the basis of specific differentiation.

1. Male with a high protibial keel, with the highest point around middle of the tibia (Figs 16, 18, 20) ...2
 - Male with a lower protibial keel, with the highest point at the basal third of the tibia (Figs 17, 19) ...4
2. Protibial keel with sharp vertex and slightly lobed from the margin to the base (Fig. 20); elytra sculpture and pronotum granularity poorly marked; pronotum sexually dimorphic (Figs 14–15)
 -*S. escalerae* (Uhagón, 1898)
 - Protibial keel with a slightly sharp vertex and linear margin to the base (Figs 16, 18); elytra sculpture and pronotum with well marked granularity; pronotum not sexually dimorphic (Figs 6–7, 10–11) ...3
3. Body size generally small (male length around 4.2 mm); protibial keel with sharp apex and basal part of the protibia with a wide keel (Fig. 18); 8th antennomere around 1.5 × longer than wide and 4th one length different from 5th and 7th antennomeres in both sexes ...*S. bolivari* (Jeannel, 1922)
 - Body size generally larger (mean male length around 4.8 mm); protibial keel with rounded apex and the basal area of the protibia with a wider keel (Fig. 16); 8th antennomere more than 1.4 × longer than wide and 4th antennomere equal or almost equal in length to 5th and 7th antennomeres in both sexes*S. algarvensis* sp. nov.
4. Upper margin of protibial keel long, linear medially (Fig. 17); 8th antennomere slightly less than 1.5 × longer than wide, and 4th, 5th and 7th antennomeres of unequal length in both sexes
 -*S. angusticollis* (Kraatz, 1870)
 - Upper margin of protibial keel short, curved medially (Fig. 19); 8th antennomere more than 1.5 × longer than wide and 4th, 5th and 7th antennomeres of almost equal length in both sexes
 -*S. breuili* (Jeannel, 1922)

Speonemadus algarvensis sp. nov.

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Figs 1, 6–7, 16, 21, 26–31

Diagnosis

A species of *Speonemadus* with a total length of 4.0–4.9 mm, belonging to the *escalerai*-group, and with typical features of the group; characterised by having the 2nd, 4th, 5th and 7th antennomeres equal or subequal in length; a slightly transverse and hexagonal pronotum; and a long, raised and elevated protibial keel in males, with the apex moderately sharp.

Etymology

The species epithet is derived from the type locality, the southernmost province of Portugal, the Algarve.

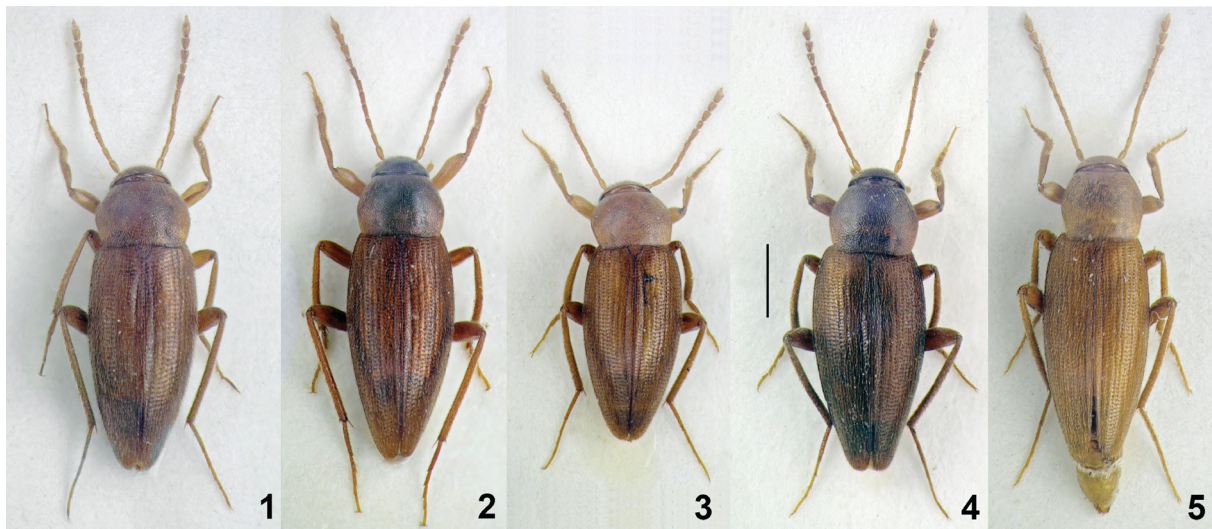
Material examined

Holotype

PORTUGAL: ♂, Algarve, Loulé, Gruta do Vale Telheiro, coordinates: WGS 84: 37°10'14" N, 008°02'06" W, 29 Dec. 2009, S. Reboleira leg. (ZMUC number 00036257).

Paratypes

PORTUGAL: 38 ♂♂ and 30 ♀♀, same data as holotype; 11 ♂♂, 18 ♀♀, same locality as holotype, 13 Mar. 2009, S. Reboleira leg.; 53 ♂♂, 63 ♀♀, 24 May 2009, S. Reboleira leg.; 9 ♂♂, 9 ♀♀, Algarve, São Brás de Alportel, Algarão do Remexido, 15 Mar. 2009, S. Reboleira leg.; 1 ♀, same locality, 23 May 2009, S. Reboleira leg.; 31 ♂♂, 27 ♀♀, same locality, 25 May 2009, S. Reboleira leg.; 1 pupa, 1 ♀, same locality, 5 Sept. 2009, S. Reboleira leg.; 3 ♂♂, 3 ♀♀, same locality, 29 Dec. 2009, S. Reboleira leg.; 4 ♀♀, Algarve, Moncarapacho, Gruta da Senhora, 29 Dec. 2009, S. Reboleira leg.; 1 ♂, same locality, 24 May 2009, S. Reboleira leg. (SR, CASR, CJMS, CZULE, CFL, CPB, ZMUC).



Figs 1–5. *Speonemadus* of the *escalerai*-group habitus. 1. *S. algarvensis* sp. nov. (Gruta do Vale Telheiro, Portugal). 2. *S. angusticollis* (Kraatz, 1870) (Rute, Spain). 3. *S. bolivari* (Jeannel, 1922) (Ardales, Spain). 4. *S. breuili* (Jeannel, 1922) (Motillas, Spain). 5. *S. escalerai* (Uhagón, 1898) (Jumilla, Spain). Scale bar = 1 mm.

Table 1. Mean measurements (in millimeters) of the antennomers of *Speonemadus* of the *escalerai*-group (L) length; (W) width.

		1 st	2 nd	3 rd	4 th	5 th	6 th	7 th	8 th	9 th	10 th	11 th
<i>Speonemadus algarvensis</i> sp. nov.												
holotype ♂	L	0.189	0.195	0.212	0.196	0.194	0.176	0.196	0.117	0.166	0.137	0.221
	W	0.065	0.056	0.056	0.056	0.056	0.056	0.075	0.061	0.088	0.088	0.090
paratypes ♂	L	0.191	0.195	0.208	0.194	0.192	0.170	0.194	0.116	0.163	0.138	0.220
	W	0.065	0.056	0.055	0.055	0.055	0.055	0.074	0.060	0.082	0.082	0.082
paratypes ♀	L	0.185	0.195	0.202	0.181	0.179	0.161	0.179	0.105	0.140	0.122	0.225
	W	0.066	0.057	0.055	0.053	0.053	0.059	0.069	0.064	0.088	0.088	0.092
<i>Speonemadus angusticollis</i> (Kraatz, 1870)												
♂	L	0.182	0.208	0.226	0.195	0.200	0.153	0.192	0.114	0.161	0.143	0.231
	W	0.078	0.066	0.069	0.065	0.068	0.068	0.087	0.078	0.104	0.104	0.107
♀	L	0.177	0.195	0.205	0.191	0.195	0.150	0.190	0.107	0.159	0.143	0.231
	W	0.078	0.068	0.065	0.065	0.068	0.065	0.085	0.073	0.091	0.091	0.094
<i>Speonemadus breuili</i> (Jeannel, 1922)												
♂	L	0.174	0.177	0.217	0.186	0.186	0.170	0.186	0.117	0.163	0.140	0.222
	W	0.078	0.059	0.059	0.056	0.056	0.060	0.072	0.061	0.085	0.088	0.088
♀	L	0.194	0.199	0.228	0.196	0.198	0.179	0.198	0.120	0.155	0.135	0.237
	W	0.074	0.060	0.059	0.057	0.057	0.057	0.072	0.065	0.096	0.100	0.100
<i>Speonemadus bolivari</i> (Jeannel, 1922)												
♂	L	0.182	0.192	0.228	0.192	0.203	0.189	0.205	0.117	0.156	0.135	0.231
	W	0.066	0.059	0.055	0.055	0.060	0.062	0.073	0.064	0.088	0.088	0.094
♀	L	0.177	0.182	0.198	0.169	0.190	0.160	0.191	0.107	0.153	0.134	0.228
	W	0.068	0.061	0.056	0.056	0.059	0.061	0.072	0.061	0.083	0.083	0.086
<i>Speonemadus escalerai</i> (Uhagón, 1898)												
♂	L	0.190	0.194	0.217	0.196	0.195	0.160	0.195	0.114	0.176	0.157	0.246
	W	0.075	0.060	0.062	0.062	0.062	0.065	0.078	0.074	0.101	0.104	0.104
♀	L	0.200	0.207	0.230	0.208	0.208	0.169	0.207	0.120	0.172	0.156	0.248
	W	0.078	0.072	0.073	0.074	0.074	0.077	0.099	0.082	0.109	0.111	0.111

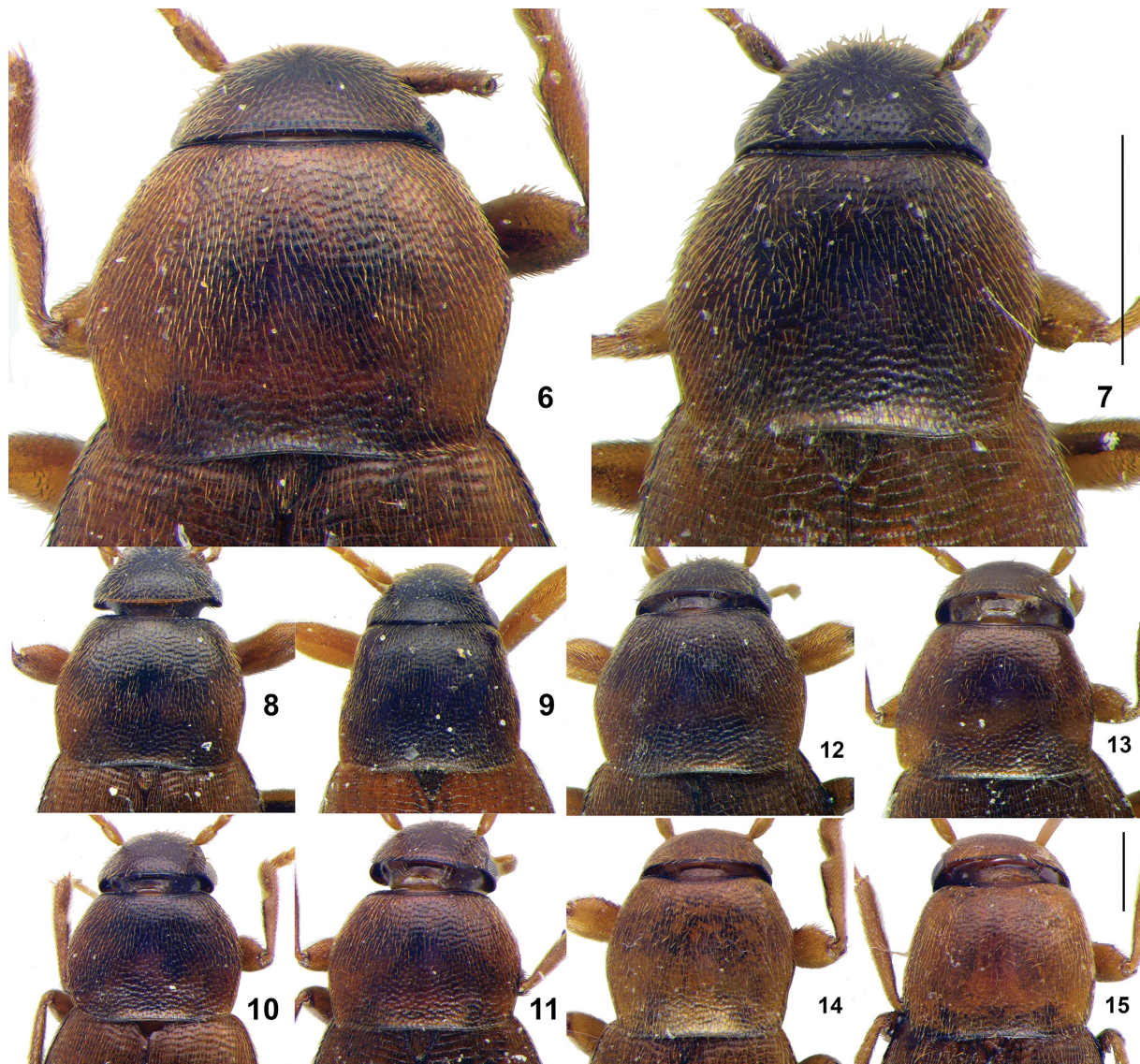
Description

BODY. Length 4.03–4.90 mm (males) and 4.00–4.89 mm (females) width 1.46–1.58 mm (males) and 1.44–1.60 mm (females) (Figs 1, 26–27). Color reddish brown, darker in central area of head and lighter on antennae and legs. Integument evenly covered with a yellowish pubescence, thin, short and flattened, slightly raised in forehead area and clypeus. Head retractable; head sculpture composed of a tight mesh of small dots. Eyes developed with pigmented ommatidia (Fig. 27); antennae long (1.9 mm) and reaching almost one third of basal area of elytra; antennomeres (Figs 26–27, 29) slender, all clearly longer than wide; 2th, 4th, 5th and 7th antennomeres equal, 3rd slightly longer, 6th shorter and 8th almost twice as long as wide (Table 1); tip of antenna with sensorial organ (Fig. 29).

PRONOTUM (Figs 6–7). Slightly transverse, maximum width/length ratio = 1.29–1.43 (males) and 1.28–1.38 (females), with maximum width at middle; almost flattened; basal impressions not observed; lateral and basal margins weakly beaded; pronotal sides regularly curved anteriorly, posteriorly almost straight and converging posteriorly; basal angles obtuse with apex almost rounded. Pronotal base narrower than base of elytra; middle area gently arched, lateral areas almost straight. Pronotum surface uniformly granulate, well defined laterally and more indistinct in disk area.

ELYTRA. Elliptical, very elongate and convex, except along suture where they are flattened in the central area; maximum length/width ratio = 1.85–1.98 in males and 1.95–2.02 in females; elytron apex rounded; transverse striations visible, clearly separated, shallow and perpendicular to elytral suture (Fig. 28); sutural groove present and well marked along entire elytron, sub-parallel to suture and clearly convergent. Metathoracic wings fully developed.

LEGS. Relatively long and thin; protibial keel (Fig. 16), which is high and long, elevated distally, with a well marked vertex, sharp at apex; first three protarsomeres dilated (Fig. 30) in males, first slightly narrower than apical area of protibia (tarsus/tibia ratio = 0.86); mesotibia curved, metatibia straight.



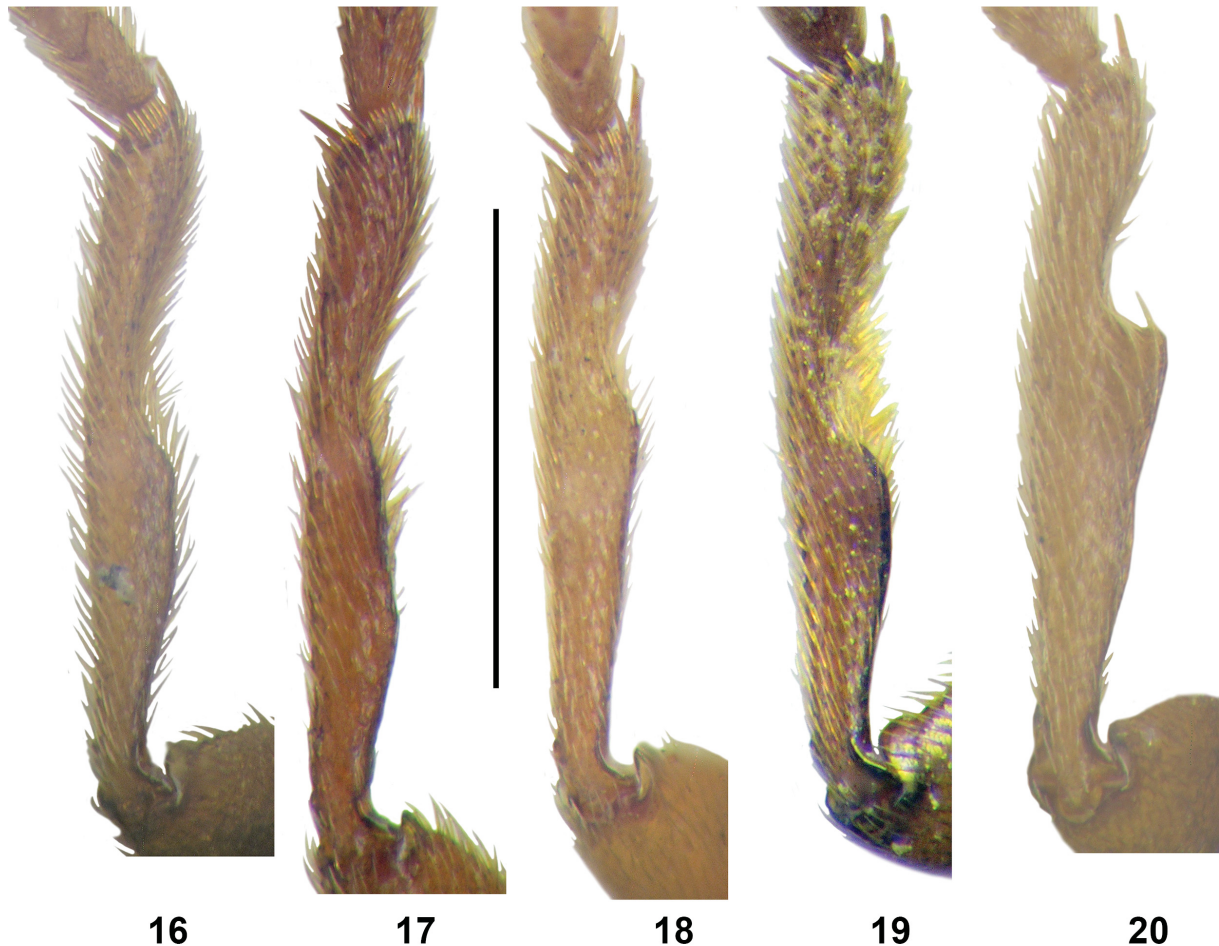
Figs 6–15. *Speonemadus* of the *escalerae*-group pronotum. **6–7.** *S. algarvensis* sp. nov. (Gruta do Vale Telheiro, Portugal), respectively ♂ and ♀. **8–9.** *S. angusticollis* (Kraatz, 1870) (Rute, Spain) respectively ♂ and ♀. **10–11.** *S. bolivari* (Jeannel, 1922) (Ardales, Spain) respectively ♂ and ♀. **12–13.** *S. breuili* (Jeannel, 1922) (Motillas, Spain) respectively ♂ and ♀. **14–15.** *S. escalerae* (Uhagón, 1898) (Jumilla, Spain) respectively ♂ and ♀. Scale bars = 1 mm.

Male

Some variability is observed in male paratypes (Table 1). Genital segment elongate, $1.5 \times$ longer than wide; composed of a tergum and two pleurites, all with small setae in apical area; sternum reduced to a long, narrow longitudinal piece, sharp apically. Aedeagus length = 1.2 mm (1.3 if parameres are included) (Fig. 21). Median lobe, lanceolate in dorsal view, with elongate and curved apex close to dorsal face; sharp apex with marked shoulders at margins; basal lamina developed, almost two times shorter than middle lobe; ventral blade of tegmen short and poorly defined. Parameres, in dorsal view, sub rectilinear, slightly curved medially on inner side, with apical areas rounded and slightly truncated on inner side; four thin setae at apex, three subequal upper setae and a larger one, close to largest setae, another seta, shorter, more robust, tooth-like and highly sclerotized. Inner sac with two long rows of spinules surrounding two long parallel rows of sclerotized teeth arranged in a zipper-shape (Figs 21, 31).

Female

Generally smaller, with a less transverse pronotum (Fig. 7) and longer elytra, but same body width. No sexual dimorphism observed in colour, pubescence, sculpture, granularity, striation, mesotibia or metatibia. Females have a slender protarsus; antennomeres proportionally thicker and elytral apex



Figs 16–20. *Speonemadus* of the *escalerai*-group male protibia. **16.** *Speonemadus algarvensis* sp. nov. (Gruta do Vale Telheiro, Portugal). **17.** *S. angusticollis* (Kraatz, 1870) (Rute, Spain). **18.** *S. bolivari* (Jeannel, 1922) (Ardales, Spain). **19.** *S. breuili* (Jeannel, 1922) (Motillas, Spain). **20.** *S. escalerai* (Uhagón, 1898) (Jumilla, Spain). Scale bar = 0.5 mm.

notched and serrate. Seventh uroventrite with a narrow slit in middle of posterior margin and 8th uroventrite with posterior margin as a soft membranous arc, its ventral spine is short, wide and slightly sharp at apex. Ratio of first tarsus to apical part of tibia: 0.84–0.89. Female genitalia typical of genus as described by Giachino & Vailati (1993) and Salgado *et al.* (2008).

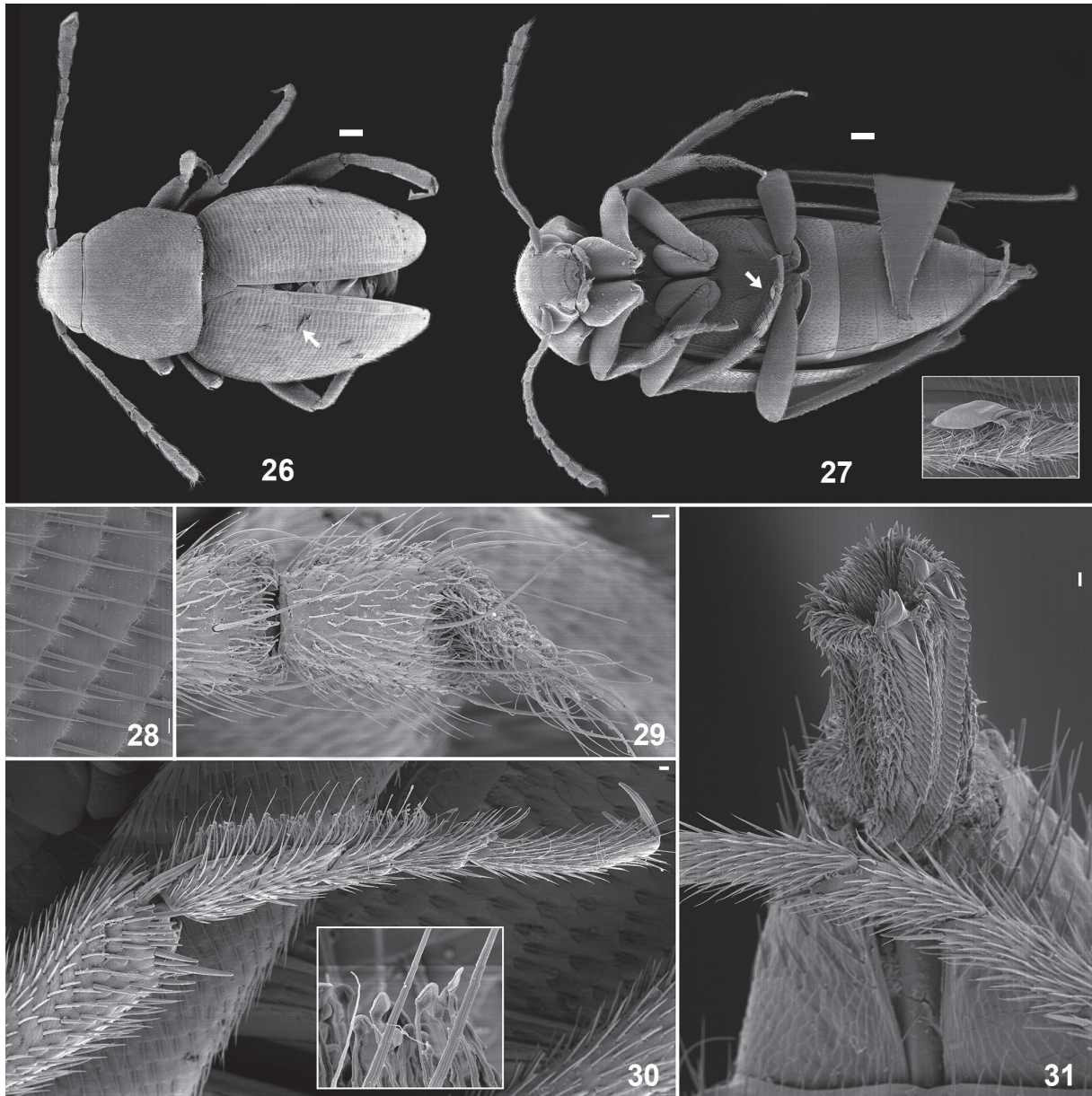


Figs 21–25. *Speonemadus* of the *escalerai*-group, aedeagus. **21.** Paratype of *S. algarvensis* sp. nov. (Gruta do Vale Telheiro). **22.** *S. angusticollis* (Kraatz, 1870) (Rute). **23.** *S. bolivari* (Jeannel, 1922) (Ardales). **24.** *S. breuili* (Jeannel, 1922) (Motillas). **25.** *S. escalerai* (Uhagón, 1898) (Jumilla). Scale bar = 0.5 mm.

Affinities

The morphological differences that separate *Speonemadus algarvensis* sp. nov. from all other species of the *S. escaleraei*-group are pointed out in the key for the group.

Morphologically, the most closely related species are *Speonemadus bolivari* and *S. breuili*, which are also the closest geographically (Fig. 32). However, *S. algarvensis* sp. nov. can easily be distinguished from *S. bolivari* by the different shape of the male protibial keel, by the antennomeres ratio and the shape of the aedeagus, with the median lobe apically more narrow and elongate. Differences can also



Figs 26-31. *Speonemadus algarvensis* sp. nov. scanning electron micrograph. **26.** Dorsal view with Laboulbeniales *Stichomyces conosomatis* pointed out. **27.** Ventral view, with detail of phoretic acari. **28.** Details of elytra stria and setation. **29.** Tip of the antenna. **30.** Male protarsus with detail of the ventral pads of the first tarsomere. **31.** Posterior dorsal view of the evaginated aedeagus. Scale bars 26-27 = 100 μ m, 28-31 = 10 μ m.

be observed in the females of *S. algarvensis* sp. nov., with the median posterior slit of the 7th uroventrite slightly narrower and the apex of the ventral spine of the 8th uroventrite less sharpened. The differences regarding *S. breuili* are much more clear in the shape of the protibial keel.

There is a strong geographic isolation between karst areas colonized by the previous three species, which have the most southern distribution of the group (Fig. 32).

The male specimen collected on 4 Jan. 1940, in the cave Igrejinha da Soidos, located in Alte, municipality of Loulé (Jeannel 1941), deposited in the Natural History Museum of Paris (MNHN), has been examined and belongs to the new species *S. algarvensis* sp. nov., it had previously been identified as *S. angusticollis*. The remnants of another specimen collected in the cave “Berrocal do Esguincho”, also in the Loulé municipality, on 6 Dec. 1983 and cited by Blas (1985, 1989), are also included in this new species. Both aforementioned caves are included in the same karst area as the type localities of *S. algarvensis* sp. nov., where only this species of *Speonemadus* has consistently been collected. The specimens reported from the Algarve massif as *Speonemadus angusticollis* by Jeannel (1941), Blas (1985, 1989), Reboleira *et al.* (2010a, 2010b, 2011b, 2012a) and Reboleira (2012) should now be included in *S. algarvensis* sp. nov.

Biology and ecology

Despite lacking some of the typical traits of cave-adapted species, i.e., eyes, severe depigmentation and extreme body and appendages elongation, *Speonemadus algarvensis* sp. nov. was never found at the surface, leading us to classify it as a subterranean species. It has been sampled all year round and it has never been collected at the surface in the areas surrounding the sampled caves. The largest population was found in Vale Telheiro Cave, which matches with the general high biodiversity pattern for other groups of troglobionts in Portugal (Reboleira 2012; Reboleira *et al.* 2015).

Some specimens of *S. algarvensis* sp. nov. have the ectoparasitic fungus *Stichomyces conosomatis* Thaxt., 1901 (of the order Laboulbeniales) attached to the cuticle (Santamaria pers. com.) (Fig. 26); this represents the first record of the fungal species for the Portuguese territory. This fungus species has only been previously found in Staphylinidae beetles of the genus *Sepedophilus* Gistel, 1856 (Haelewaters *et al.* 2015), that was also found in these caves (Reboleira unpublished). The remarkable discovery of this Laboulbeniales species on a new host of the family Leiodidae is the first case of host shifting following an ecological opportunity (*sensu* De Kesel & Haelewaters 2014), in the subterranean environment. Also phoretic undetermined mites were observed on some specimens (Fig. 27).

Speonemadus algarvensis sp. nov. shares its habitat with highly subterranean-adapted species such as the detritivorous woodlice *Cordioniscus lusitanicus* Reboleira & Taiti, 2015 and *Troglehuma machadoi* (Vandel, 1946); the millipedes *Acipes machadoi* Enghoff & Reboleira, 2013, *A. bifilum* Enghoff & Reboleira, 2013, *Boreviulisoma barrocalense* Reboleira & Enghoff, 2013 and a new species of *Archipolydemus* Attems, 1898; the campodeid *Litocampa mendesi* Sendra & Reboleira, 2010; the nicoletiid *Squamatinia algharbica* Mendes & Reboleira, 2012; and some predators: the pseudoscorpions *Chthonius minutus* Vachon, 1940; *Titanobochica magna* Zaragoza & Reboleira, 2010 and *Lusoblothrus aenigmaticus* Zaragoza & Reboleira, 2012; the spiders *Harpactea stalitoides* Ribera, 1993, *Teloleptoneta synthetica* (Machado, 1951) and *Anapistula ataecina* Cardoso & Scharff, 2009, as well as a species of centipede, *Lithobius* Leach, 1814 (Enghoff & Reboleira 2013; Reboleira *et al.* 2010a, 2010b, 2010c, 2011a, 2012a, 2012b, 2013, 2015; Reboleira & Enghoff 2013, 2014).

Distribution

Speonemadus algarvensis sp. nov. was collected in three caves of the southernmost province of Portugal, the Algarve (Fig. 32), where it seems to be endemic to the central and eastern part of the Algarve karst massif. The species was not found in the most western part of the Algarve massif, where fieldwork

was also conducted. The karst included in this region is also known as “Barrocal” and is the richest area for subterranean-adapted fauna of the country (Reboleira 2012; Reboleira *et al.* 2011a, 2013, 2015; Reboleira & Enghoff 2013, 2014).

Speonemadus angusticollis (Kraatz, 1870)

Choleva angusticollis Kraatz, 1870: 98.

Catops angusticollis – Marseul 1884: 69.

Anemadus angusticollis – Reitter 1885: 60.

Speonemadus angusticollis – Jeannel 1936: 220.

Type locality

“Cordova” (Kraatz 1870).

Material examined

SPAIN: Córdoba: many ♂♂ and ♀♀, Luque, Sima de Fuente del Espino I, 22 Nov. 2009 and 1 Aug. 2010, GES-Priego leg. (CFL, CPB, CJMS, CZULE); 1 ♂, 2 ♀♀, Sima Fuente de Alhama, 3 Apr. 2010, GES-Priego leg. (CFL); many ♂♂ and ♀♀, Priego de Córdoba, Cueva de la Solana, 6 Dec. 2009 and 7 Feb. 2010, GES-Priego leg. (CFL, CPB, CJMS). — Guadalajara: 1 ♂, 1 ♀, Tamajón, Cueva de Remigín, 10 Apr. 1994, Carabajal leg. (CZULE). — Huelva: 6 ♀♀, Fuenteheridos, Cueva del Guerrero, 23 Mar. 2013 CDP leg. (CPB, CJMS); 3 ♂♂, 4 ♀♀, same locality, 5 Jun. 2013, CDP leg. (CPB, CJMS). — Jaén: 11 ♂♂, 28 ♀♀, Hornos, Cueva de la Murcielaguina, 15 Nov. 2009, GEV leg. (CFL, CJMS); 5 ♂♂, 4 ♀♀, La Iruela, Sierra de Cazorla, Cueva Secreta del Sagreo, 30 May 1953, Mateu & Cobos leg. (CMCN); 4 ♂♂, 2 ♀♀, Sierra de Cazorla, Cueva del Nacimiento de Guadalquivir, 8 Aug. 1964, Castells leg. (CMCN); many ♂♂ and ♀♀, Siles, Cerro de Bucentaina, Sima de los 30 años, 8 Sep. 2008 and 16 Jan. 2010, GEV leg. (CFL, CPB, CJMS). — Sevilla: many ♂♂ and ♀♀, Alanís, Sima del Paro, 23 Jan. 2013, CDP leg. (CFL, CPB, CJMS).

PORTUGAL: 1 ♂, Alandroal, Estremoz-Cano massif, Algar de Santo António, 30 Mar. 2009, A.S. Reboleira leg. (SR).

Previous records

SPAIN: Albacete: Riópar, Cueva del Farallón (Blas 1989; Giachino & Vailati 1993; Fresneda *et al.* 2007); Riópar, Sierra de Segura, Cueva de la Umbria de Santiago (Blas 1989; Pérez 2014). — Ávila: Villarejo del Valle (Uhagón 1890, 1898; Jeannel 1922; Blas 1977, 1979, 1989; Giachino & Vailati 1993). — Badajoz (Uhagón 1890, 1898; Jeannel 1922, 1936; Fuente, 1925; Blas 1979): Cabeza la Vaca, Los Cortinales (Sáez & Blanco 2010); Calera de León, Monasterio de Tentudía (Sáez & Blanco 2010). — Cáceres (Fuente 1925): Navalmoral de la Mata (Uhagón 1898; Blas 1977, 1979). — Ciudad Real: Horcajo de los Montes, P.N. de Cabañeros, Pinar de las Llanas (Fresneda *et al.* 2007); Pozuelo de Calatrava (Uhagón 1898; Blas 1989; Giachino & Vailati 1993); Retuerta del Bullaque, P.N. de Cabañeros, Los Palillos (Fresneda *et al.* 2007). — Córdoba: Cabra, Cueva-Mina de Jarcas (Fresneda *et al.* 2007; Pérez 2015); Cabra, La Nava (Fresneda *et al.* 2007); Cabra, Cueva Ca-2 (Blas 1989; Tinaut 1998); Córdoba (Kraatz 1870; Uhagón 1890; Jeannel 1922, 1936; Blas 1979; Giachino & Vailati 1993); Luque, Abuchite, L-14 (Fresneda *et al.* 2007, 2011); Priego de Córdoba, Cueva de los Mármoles (Fresneda *et al.* 2007, 2011; Pérez 2015); Priego de Córdoba, Castillo, in archaeological excavations under the castle (Fresneda *et al.* 2007); Rute, Cueva la Negra (Fresneda *et al.* 2007); Zagrilla, Manantial (Fresneda *et al.* 2007); Zuheros, Cueva de los Murciélagos (Fresneda *et al.* 2007; Pérez 2015). — Huelva: Aracena, Gruta de las Maravillas (Blas 1979, 1989). — Jaén: Hornos, Cueva de la Murcielaguina (Fresneda *et al.* 2007); La Iruela, Sierra de Cazorla, Cueva Secreta del Sagreo (Mateu 1953; Ribera 1970; Blas, 1976,

1977, 1979, 1989; Giachino & Vailati 1993; Tinaut 1998, Pérez & Tinaut 2005; Pérez & Pérez 2006; Pérez *et al.* 2013); Peal de Becerro, Cueva del Arroyo de la Rambla, PB-4, (Tinaut 1998; Fresneda *et al.* 2007); Santa Elena (Blas 1977, 1979, 1989); Sierra de Cazorla, Cueva del Nacimiento de Guadalquivir (Ribera 1970; Blas 1976, 1977, 1989; Tinaut 1998; Pérez & Tinaut 2005; Pérez 2015); Siles, Cerro de Bucentaina, Sima de los 30 años (Fresneda *et al.* 2007; Ribera *et al.* 2010). — Madrid: Escorial (Uhagón 1890, 1898; Jeannel 1922, 1936; Blas 1977, 1979, 1989); Sierra de Guadarrama, Navacerrada (Uhagón 1890, 1898; Jeannel 1922, 1936; Fuente 1925); Robledo de Chavela (Blas 1989). — Sevilla: Alanís, Sima los Coscojales (CFL) (Fresneda *et al.* 2007); Almadén de la Plata, Cueva de los Covachos (Pérez 2015).

Redescription

BODY. Length 4.0–4.6 mm (males) and 4.1–4.6 mm (females), body width 1.3–1.4 mm (males) and 1.4–1.6 mm (females). Body shape elongate and very slim (Fig. 2). Integument color light brown to darker brown, the legs, antennae and palpi of similar color; pubescence arranged uniformly, golden, moderately long and adpressed, only erected on the clypeus. Head retractable, with well-developed eyes. Antennae quite long, greyish in color, reaching the basal $\frac{1}{5}$ part of the body; all antennomeres longer than wide, 3rd antennomere longer than 2nd antennomere, 4th and 6th antennomeres shorter than 5th one, and 8th almost $1.5 \times$ longer than wide (Table 1).

PRONOTUM. Slightly transverse with surface slightly punctured (Figs 8–9), maximum width/length ratio = 1.20–1.32 (males) and 1.18–1.25 (females), with maximum width in the middle third and the lateral edges regularly arcuate, converging towards the base; posterior angles obtuse and slightly rounded at apex. Pronotal base sinuate and narrower than elytral base.

ELYTRA. Elliptical and very elongated, maximum length/width ratio = 2.04–2.19 (males) and 1.97–2.11 mm (females); apex of each elytron rounded; elytral disk slightly convex and flattened in the middle. Elytral sculpture formed by very strong sutural striae and transverse striae with regular arrangement, sunken, well marked and perpendicular to the suture.

Male

The structure of genital segment corresponds to the typical pattern of the genus, formed by an urotergite with the apex in sharp bow, two uropleurites with apically narrow, sharp, slightly outwardly and short shaped handle ventrite. Aedeagus robust and long, between 1.2 and 1.3 mm (Fig. 22); basal lamina almost $2 \times$ shorter than middle lobe; ventral blade of tegmen short and poorly defined. Median lobe in dorsal view, similar to other species of the group, although it has the triangular apex with less protruding edge and narrower at its distal third part. Parameres robust and wide with a marked hump on the outside of distal and the apical area is beveled with a blunt tip, in this area four setae are inserted, of which three are short and thin, and the fourth is longer with a small tooth, coarse and finely sclerotized. Inner sac showing two longitudinal chains of small sclerotized pieces, surrounded by a longer structure formed by numerous fine spines that are joined at the apex, but not tooth-shaped. Legs long with a peculiar structure of the keel protibial (Fig. 17) which is long, slightly elevated, with a straight area, and fuzzy projections; in addition, the first three protarsomeres are dilated, although first protarsomere is narrower than anterior area of protibia; mesotibia arched and metatibia straight.

Female

The most significant external differences are observed on the antennae, pronotum, elytra, protibia and protarsomeres. Antennae very similar to those observed in males (Table 1); the 2nd antennomere equal to the 5th one, and the 8th almost $1.5 \times$ longer than wide. Pronotum slightly transverse and clearly narrower than in males (Fig. 9), its sides almost straight and divergent on the posterior part; the maximum width is near the base and bell-like in form; posterior angles are almost straight with rounded angles; pronotal

base is almost as wide as base of elytra. Elytra are elliptical and elongated and proportionally slightly shorter than in males. Apex of elytra is notched and toothed. Protibiae lacking keel and protarsi slender. 7th and 8th uroventrites and genital segment typical of the genus (see Giachino & Vailati 1993).

Variability

The most significant variation was observed in the samples from the two caves of Huelva (Gruta de la Maravillas and Cueva del Guerrero), specimens from both caves show intermediate characteristics between *S. angusticollis* and *S. breuili*, with the protibial keel more close to the first one and female pronotum most similar to the second species. Systematic position of the specimens collected from these two caves will be solved only by further study of specimens from caves near the Sierra de Aracena.

Biology and ecology

This species is found in a forest environment, in leaf litter or under stones. In arid climates it tends to colonize the subterranean ecosystem, being frequently found in caves, as in Spanish Andalusia and now also in the Portuguese region of Alentejo. In less dry regions it is found to be more associated with the soil ecosystem (Blas 1977). It has been also been reported (Giachino & Vailati 1993) from the Superficial Subterranean Habitat (*sensu* Giachino & Vailati 2010).

Distribution

Described from Spanish Córdoba (Kraatz 1870), this is an Iberian endemic with a scattered distribution in the central area of the peninsula, being more common in its southern and western parts. It is known from the Spanish provinces of Albacete, Ávila, Badajoz, Cáceres, Ciudad Real, Córdoba, Huelva, Jaén, Madrid and Sevilla and now also from southeastern Portugal (Fig. 32). The present finding in a cave of Alandroal, in the Alentejo province, is the first confirmed record of this species for the Portuguese territory as previous records for Portugal (Jeannel 1941, Blas 1985, 1989, Reboleira 2012, Reboleira *et al.* 2010a, 2010b, 2011a, 2012a) refer to *S. algarvensis* sp. nov.

Speonemadus breuili (Jeannel, 1922)

Anemadus (*Speonemadus*) *breuili* Jeannel, 1922: 60.

Anemadus (*Speonemadus*) *verneri* – Jeannel 1922: 61.

Anemadus (*Speonemadus*) *angusticollis breuili* – Jeannel 1936: 221.

Anemadus (*Speonemadus*) *angusticollis vernerii* – Jeannel 1936: 221.

Type locality

“Cueva de las Motillas, Jerez de la Frontera, provincia de Cádiz” (Jeannel 1922).

Material examined

SPAIN: Cádiz: 3 ♂♂, 2 ♀♀, Villaluenga del Rosario, Cueva Aljibe (= Cueva del Aljibe, Jul. 1970, Ribera & Viñas leg. (CMCN). — Málaga: many ♂♂ and ♀♀, Cortés de la Frontera, Cueva del Berrueco, 12 Sep. 2009 and 6 Jun. 2010, GIEX leg. (CFL, CPB, CJMS, CZULE); 15 ♂♂, 9 ♀♀ Cortés de la Frontera, Peñón del Berrueco, Cueva del Humo, 22 Dec. 2012, GIEX leg. (CFL, CJMS); many ♂♂ and ♀♀, Cortés de la Frontera, Complejo Motillas, Cueva Motilla fósil, 13 Sep. 2009 and 8 Nov. 2009, GIEX leg. (CFL; CPB; CJMS); many ♂♂ and ♀♀, Cortés de la Frontera, Complejo Motillas, Cueva Motilla Parralejo, 13 Sep. 2009, 8 Nov. 2009 and 5 Jun. 2010, GIEX leg. (CFL, CPB, CJMS, CZULE); 1 ♂, 2 ♀♀, Montejaque, El Pozuelo, Cueva Sima Nueva, 29 Mar. 1986, Escolà leg. (CMCN).

Previous records

SPAIN: Cádiz, Algeciras (Giachino & Vailati 1993); Algeciras, Los Barrios (Blas 1989; Giachino & Vailati 1993); Villaluenga del Rosario (Giachino & Vailati 1993); Villaluenga del Rosario, Cueva Aljibez (= Cueva del Aljibe) (Blas 1976, 1977, 1979; Tinaut 1998; Pérez 2015); Villaluenga del Rosario, Sima Aljibe nº 2, (Ribera 1970). — Málaga, Cortés de la Frontera, Cueva del Berrueco (Jeannel 1922, 1936; Ribera 1970; Blas 1976, 1979; Giachino & Vailati 1993; Tinaut 1998); Cortés de la Frontera, Cueva de las Motillas (Ribera 1970; Blas 1977, 1979, 1989; Giachino & Vailati 1993; Tinaut 1998; Fresneda *et al.* 2007); Montejaque, El Pozuelo, Cueva Sima Nueva (Blas 1989); Montejaque, El Pozuelo, Cueva del Requejo (Blas 1979, 1989; Tinaut 1998; Pérez 2015); Montejaque, El Pozuelo, Cueva Sivieja (Blas 1989; Tinaut 1998; Pérez 2015).

Redescription

BODY. Length 4.0–4.5 (males) and 3.9–4.7 mm (females), body width 1.4–1.5 (males) and 1.5–1.7 mm (females) (Fig. 4). Body color, pubescence and punctuation similar to that observed in *S. angusticollis*.

ANTENNAE. Reaching the basal 4th part of elytra; the antennomeres 1st and 2nd are almost equal in length, also equal in length are the 4th, 5th and 7th ones being the 3rd ones clearly longer than the 2nd one and the 8th nearly twice as long as wide (Table 1).

PRONOTUM. Slightly transverse, maximum width at middle third part; the angles converge, smoothly from the middle area to the base in a straight line; posterior angles obtuse and rounded at vertex; sculpture and granularity well defined (Fig. 12).

ELYTRA. Elliptical and elongated, maximum length/width ratio = 1.92–2.10 (males) and 1.86–2.04 mm (females), with overall shape of the species group and sculpture of “C” type (*sensu* Giachino & Vailati 1993).

Male (Fig. 24)

Features of the genital segment and aedeagus are similar to those described for *S. angusticollis*.

Female

The antennae are similar to those of the male, but the antennomeres are more transverse; 2nd, 4th, 5th and 7th antennomeres having similar length (Table 1). Pronotum less elongated; the overall shape and the ratio of width/length ratio similar to that described for males (Fig. 13). Elytra elliptical and elongated with apical parts notched and serrated. 7th and 8th uroventrites, and genitalia typical of the species group.

Remarks

Speonemadus breuili is re-established as a valid species due to the clear morphological characters that differentiate it from *S. angusticollis*, which was synonymized by Blas (1989). This classification was subsequently followed by several authors (Giachino & Vailati 1993; Perreau 2000; Salgado *et al.* 2008). The main character used to re-evaluate its specific status is the shape of the male protibial keel, which is shorter and with a more rounded ridge, but also because in *S. breuili* the 8th antennomere is less transverse, the elytra are proportionally shorter, and the female pronotum is more hexagonal and clearly transverse. In addition, *Speonemadus vernerii* is established as a synonym of *S. breuili* and not of *S. angusticollis* (Blas 1989), due to the absence of relevant differences compared to *S. breuili*.

Apart from the morphological differences pointed out, there is an obvious geographical isolation. *Speonemadus breuili* colonizes the southernmost caves in Spanish Andalusia, the provinces of Cadiz and Málaga, away from the distribution area of *S. angusticollis*.

Biology and Ecology

Speonemadus breuili is commonly found in the subterranean ecosystem, as are the other species of the group. Inside the caves, it is found mainly in parts rich in organic matter and with a high humidity.

Distribution

Speonemadus breuili is the southernmost species of the *escalerai*-group in the Iberian Peninsula, found in the provinces of Cadiz and Málaga. The limit of its northern distribution is established by the mountain ridge of Ronda. It is distributed in the Sierra de Grazalema and related foothills, while the distribution of *S. bolivari* is linked to the Sierra de Nieves and its foothills. Both mountain ranges are separated geographically by a wide valley of sedimentary material (Fig. 32).

Speonemadus bolivari (Jeannel, 1922)

Anemadus (*Speonemadus*) *bolivari* Jeannel, 1922: 48, 59.

Speonemadus bolivari – Jeannel 1936: 220.

Type locality

“Cueva de la Doña Trinidad, term. mun. de Ardales, partido de Campillos, provincia de Málaga” (Jeannel 1922).

Material examined

SPAIN: Granada: 10 ♂♂, 10 ♀♀, Íllora, Sierra de Parapanda, Cerro de la Mesa, Sima San Rafael, 9 Mar. 2013, GEG leg. (CPB; CJMS); many ♂♂ and ♀♀, Piñar, Cueva de Pagarrecio, 15 Dec. 2012 and 10 Mar. 2013, GEG leg. (CFL, CPB, CJMS, CZULE). — Málaga: 1 ♂, 1 ♀, Ardales, Cueva de Ardales, 17 Oct. 2006, Barranco and Ruíz-Avilés leg. (CFL); 6 ♂♂, 8 ♀♀, Ardales, Cueva de Doña Trinidad, 17 Jan. 2007, Barranco and Ruíz-Avilés leg. (CPB, CJMS); many ♂♂ and ♀♀, Antequera, Cueva de los Higuerones IX, karst en yesos de Gobantes-Meliones, 28 Nov. 2009 and 30 Sep. 2010, GES-SEM leg. (CFL, CPB, CJMS); 4 ♂♂, Benaoján, Sierra de Grazalema, Cueva de la Pileta, 17 Jan. 2007, Barranco leg. (CJMS); 1 ♂, Benalmádena, Cueva de los Botijos, 31 Jul. 1977, Abad leg. (CFL); 1 ♀, Tolox, Sima Raja Helada, 28 Sep. 2009; 1 ♂♂ and 3 ♀♀, same locality, 25 Jul. 2008, GES-SEM leg. (CPB, CJMS).

Previous records

SPAIN: Málaga: Ardales, Cueva de Doña Trinidad (Jeannel 1922, 1936; Coiffait 1954; Ribera 1970; Blas 1976, 1977, 1979, 1989; Tinaut 1998; Giachino & Vailati 1993; Barranco 2005; Fresneda *et al.* 2007; Pérez 2015); Antequera; Complejo del Romeral, (Fresneda 2008, Fresneda *et al.* 2011); Antequera, karst en yesos de Gobantes-Meliones, Cueva del Yeso (Fresneda 2008); Benaoján, Cueva de la Pileta (Blas 1989; Giachino & Vailati 1993; Tinaut 1998; Fresneda *et al.* 2007); 1 ♀ Ronda, Sima del Hoyo Jaralón, 16 May 1922 (Blas 1979, 1989; Giachino & Vailati 1993; Tinaut 1998; Pérez 2015); Ronda, Sierra de las Nieves, Cueva del Rejete (Coiffait 1954; Ribera 1970; Blas 1976, 1977, 1979, 1989; Giachino & Vailati 1993; Tinaut 1998; Pérez 2015); Ronda, Sumidero del Rejete (Blas 1976, 1989); Sierra de Ronda, Sima E Las Palomas (Blas 1979, 1989; Tinaut 1998). — Granada: “Loja, 4.1909, Exp. del Museo, coll. Muséum d’Histoire Naturelle, Paris” (MNHN) (Szymczakowski 1970).

Redescription

BODY. Length 3.9–4.5 (males) and 4.1–4.5 mm (females), body width 1.3–1.4 mm (males) and 1.4–1.6 mm (females). Body shape very long and slender (Fig. 3). The Integument light brown, slightly darker on the head. Pubescence fairly long, golden and slightly raised. Head retractable with well-developed eyes; pubescence adpressed on its forehead and slightly raised on the clypeus.

ANTENNAE. Long, slender, light brown and extended beyond the basal fourth of elytra; 3rd antennomere slightly longer than the 2nd one; 6th one shorter than 4th and 5th ones, and the latter one as long as the 7th one; 8th almost 1.5 × longer than wide (Table 1).

PRONOTUM. Slightly transverse, maximum width/length ratio = 1.23–1.39 (males) and 1.28–1.36 mm (females); with a maximum width towards the middle; basal impressions are not hardly noticeable; side edges regularly arched forward, almost straight and towards the posterior angles that are obtuse and rounded in the vertex (Fig. 10); pronotal base as wide as elytral base; sculpture has a coarse granularity with obvious microsculpture.

ELYTRA. Elliptical and elongated with rounded apical areas, maximum length/width ratio = 1.95–2.04 (males) and 1.88–1.98 mm (females); elytral disc is slightly convex, and briefly depressed along suture at half of basal part. Sutural stria and discal striae well marked.

Male

Genital segment very similar to the other species of the *escalarai*-group and following the model described for *Speonemadus algarvensis* sp. nov. Aedeagus long, 1.1 mm; basal lamina of median lobe well developed and more than half of the median lobe length; ventral blade of tegmen short, inconsistent and forms the widest part of the aedeagus. In dorsal view, median lobe is bottle-shaped, with converging sides towards the base and narrowed distally; apex tapers and ends in a triangular tip with the sides slightly beaded dorsally (Fig. 23). Parameres robust, only curved forwards; apical parts obliquely truncated on the inner side, where four setae are inserted, three thin, subequal, and a larger one, as well as a thick and well sclerotized small tooth. Inner sac with two longitudinal chains formed by small sclerotized parts and surrounded by two longer chains of fine and sharp spines that come together in the apical region, but do not form a typical sclerotized tooth as in other species.

LEGS. Quite long; the protibial keel is elevated in the anterior middle third, showing a single, well marked, projection angle (Fig. 18); first three protarsomeres dilated, being the first almost as wide as the apical tip of the protibia; mesotibia strongly arched and metatibia straight.

Female

Antennae slightly shorter and more robust than in the male, reaching third basal part of elytra; 2nd antennomere is slightly longer than the 3rd one and 5th one longer than 4th and 6th ones; the 8th being clearly longer than wide (Table 1). Pronotum less transverse, but appears longer (Fig. 11). Elytra elliptical and elongated with notched and serrated apical areas. The sexual dimorphism is clear for all species of this group, as well as the structures in uroventrites 7th and 8th, and spermatheca model.

Biology and ecology

Subterranean species, found in deep areas of scattered caves, under stones or on calcite mantles. Groups of adults and larvae have been found in small accumulations of organic matter, such as bat guano.

Distribution

Speonemadus bolivari is endemic to several karst caves located in a narrow strip within the province of Málaga, between the Serrania de Ronda, at the western limit, and the karst areas at its border with the province of Granada, such as the Romeral complex, at its eastern limit. The three distribution records for the Granada province are located to the north and east of the massif of the Sierra Nevada (Fig. 32).

Speonemadus escalarai (Uhagón, 1898)

Anemadus escalarae Uhagón, 1898: 118.

Anemadus (Speonemadus) escalerae – Jeannel 1922: 58.

Speonemadus escalerae zariquieyi – Jeannel 1936: 221.

Speonemadus escalerae – Jeannel 1936: 221.

The specific epithet proposed by Uhagón (1898) in the description was *escalerae*. However, the spelling *escalerae* has mostly been used in the entomological literature; since its use is prevalent, attributed to the original author, according to the ICZN (2016: Article 33.3.1), we propose to continue to use *escalerae*.

Type locality

“Cuevas de la Zarza, del Seguret y del Encomat, cerca de Bocairente” (Uhagón 1898).

Material examined

SPAIN: Alicante: 3 ♂♂, 2 ♀♀, Xixona, Cova-Avenc de Barratxina, 25 May 1976, Comas and Escolà leg. (CMCN); 5 ♂♂, 7 ♀♀, Xixona, Peñas Roset, 6 Apr. 2005, Ortuño leg. (CZULE). — Valencia: 3 ♂♂, 1 ♀, Bocairent, Cova Sarsa, Zaragoza leg. (CMCN); 1 ♀, Enguera, Sima de la Carrasquilla, 8 Mar. 1993, Montagud leg. (CZULE).

Previous records

SPAIN: Alicante: Albaida, Castalla, Cova Melxor (Blas 1977, 1979, 1989; Zaragoza & Sendra 1988); Banyeres, Avenc de Vinalogó (Blas 1977, 1979, 1989; Zaragoza & Sendra 1988); Onil, Cova-Avenc de la Foieta (= Cova de la Foieta, Cueva-Sima de la Foieta) (Jeannel 1936; Blas 1979); Onil, Cova de Galiano (Zaragoza & Sendra 1988); Onil, Cova de Garbina (Jeannel 1936; Blas 1979); Onil, Cova Porrasses (Blas 1977, 1979, 1989; Zaragoza & Sendra 1988); Xixona, Cova-Avenc de Barratxina (Blas 1977, 1979, 1989; Zaragoza & Sendra 1988). MURCIA, Jumilla, Sierra del Carche, MSS (Blas 1989; Giachino & Vailati 1993; Fresneda *et al.* 2007); Jumilla, Cueva Los Cachorros (Blas 1989); Jumilla, Sima los Cachorros, (Fresneda *et al.* 2007); Jumilla, Cueva Los Tiestos (Blas 1989). — Valencia: Bocairent (Blas 1979); Bocairent, Cueva del Encomat (Uhagón 1898; Jeannel 1922, 1936; Blas 1977, 1979); Bocairent, Cueva del Seguret (Uhagón 1898; Jeannel 1922, 1936; Blas 1977, 1979, 1989; Giachino & Vailati 1993); Bocairent, Cueva de la Zarza (Uhagón 1898; Jeannel 1922, 1936; Blas 1977, 1979, 1989; Giachino & Vailati 1993); Bocairent, Cova Sarsa, (Blas 1979, 1989).

Redescription

BODY. Length 4.5–5.0 mm (males) and 4.4–4.9 mm (females); body width 1.3–1.6 mm (males) and 1.3–1.5 mm (females). Body shape long and slender (Fig. 5). Integument reddish brown; pubescence fairly long, golden and lying. Head structure similar to other species of the group.

ANTENNAE. Long and slender, when oriented back reaching sixth basal part of elytra; 3rd antennomere slightly longer than 2nd one; 2nd, 4th, 5th and 7th ones are similar in length and longer than the 6th one; 8th is 1.5 × longer than wide (Table 1).

PRONOTUM. Slightly transverse, maximum width / length ratio = 1.19–1.30 (males) and 1.13–1.20 (females); hexagonal in dorsal view, with maximum width in middle; sides arcuate and almost linear converging towards the base (Fig. 14); posterior angles obtuse with rounded apex. Base of pronotum almost as wide as base of elytra, gently curved sideways and finely beaded. Median granularity sculpture.

ELYTRA. Elliptical and very elongated, maximum length/width ratio = 2.06–2.18 (males) and 1.96–2.06 (female), with rounded apical areas; elytral disc slightly convex and depressed along suture in its half basal part; elytral suture well-marked with thin transverse striae, distant and perpendicular to suture.

Male

Aedeagus and structures of inner sac are similar to those described for *S. bolivari*, although larger in shape, length 1.4–1.5 mm (measured to the apex of the parameres); in dorsal view very similar to all the species of the group but in close slimmer apical area (Fig. 25). Parameres also similar to *S. bolivari*, but with more pronounced steeper area of outer margin in third distal part.

GENITAL SEGMENT STRUCTURE. Similar to that described for *Speonemadus algarvensis* sp. nov.

LEGS. Relatively long and slender; protibia widened in apical area and with a long keel running through the two basal thirds of the margin, showing two sharp protrusions, separated by a slight depression, anterior is sharp and much higher and the second is fuzzy (Fig. 20); first three protarsomeres are dilated, the first being slightly narrower than the anterior tip of protibia; mesotibiae arched and metatibiae slightly arched.

Female

Antennae long, reaching the basal third of elytra, with antennomeres generally slightly longer and transverse (Table 1). Pronotum not so transverse; in dorsal view subrectangular, with side margins almost straight before maximum width; which is situated towards the third part of basal area (Fig. 15). Elytra elliptical and elongate, with notched and serrated apical areas. Sexual dimorphism very clear in pronotum, protibiae and apical part of elytra. Females are generally less robust and with less transverse pronotum than males. The uroventrites 7th and 8th, and spermatheca follows the overall model for the group.

Note

The great variability of this species led to the description of the subspecies *zariquieyi* Jeannel, 1936, later synonymized by Blas (1977), who observed that the differences correspond to intermediate forms and, moreover, the proximity of the different caves does not represent any real evidence of geographic isolation.

Biology and Ecology

Speonemadus escalerae is a subterranean species and, therefore, common in caves. It is mostly found in areas with small accumulations of bat guano, but also under stones or stalagmitic floors and in deep parts of caves (Blas 1989). Blas (1989), Giachino & Vailati (1993) and Fresneda *et al.* (2007) also pointed out its presence in the Superficial Subterranean Habitat (MSS) (*sensu* Giachino & Vailati 2010) in the karst area of Murcia.

Distribution

This species is distributed in the southeast Iberian Peninsula and colonizes caves of the provinces of Alicante, Murcia and Valencia in Spain (Fig. 32).

Discussion

Speciation and biogeography of the *S. escalerae*-group

The genus *Speonemadus* is distributed in the Western Mediterranean area. It is known from Algeria, Spain, Italy, Morocco, Portugal, Tunisia and the south of France, including the Mediterranean islands of Sicily and the Balearics.

Giachino & Vailati (1993) stated that the four species groups, “*vandalitiae*”, “*transversostratus*”, “*escalerae*” and “*clathratus*”, diverged from from the original primitive lineage of the first group.

The synapomorphies of the *escalerai*-group are: male protibia with keels, females with the apex of the elytra notched and serrated (Giachino & Vailati 1993). The five species of this group are endemic to the Iberia Peninsula.

Scarce molecular data are reported for some species of *Speonemadus* (Fresneda *et al.* 2011): for *S. angusticollis* and *S. bolivari*, both of the *escalerai*-group, for *S. clathratus*, a widespread Iberian endemic, and for *S. maroccanus*, an ibero-Maghrebian species distributed in Morocco and in northeast Spain, the provinces of Cádiz, Granada and Málaga (Jeannel 1936; Coiffait 1954; Blas 1976, 1977, 1979, 1981, 1985, 1989; Bellés 1987; Fresneda *et al.* 2007, 2011; Giachino & Vailati 1993; Tinaut 1998; Perreau 2000; Löbl & Smetana 2004; Salgado *et al.* 2008). In the phylogenetic analysis given by Fresneda *et al.* (2011, fig. 74), *S. angusticollis* and *S. bolivari* appear in the same clade, while *S. clathratus* is closer to the previously mentioned species than to *S. maroccanus*. This observation, together with the similarity and consistency of the morphological characters, including very similar aedeagi, led us to think that the diversification of the species of the *escalerai*-group was recent and probably related to the climatic changes of the Pleistocene. In this climate change scenario, an ancestor capable of inhabiting different habitats became isolated underground, through the progressive environmental aridity at the surface in the southern Mediterranean region, therefore leading to a reduction of gene flow and the existence of allopatry in isolated populations in the climatic shelter provided by the subterranean spaces.

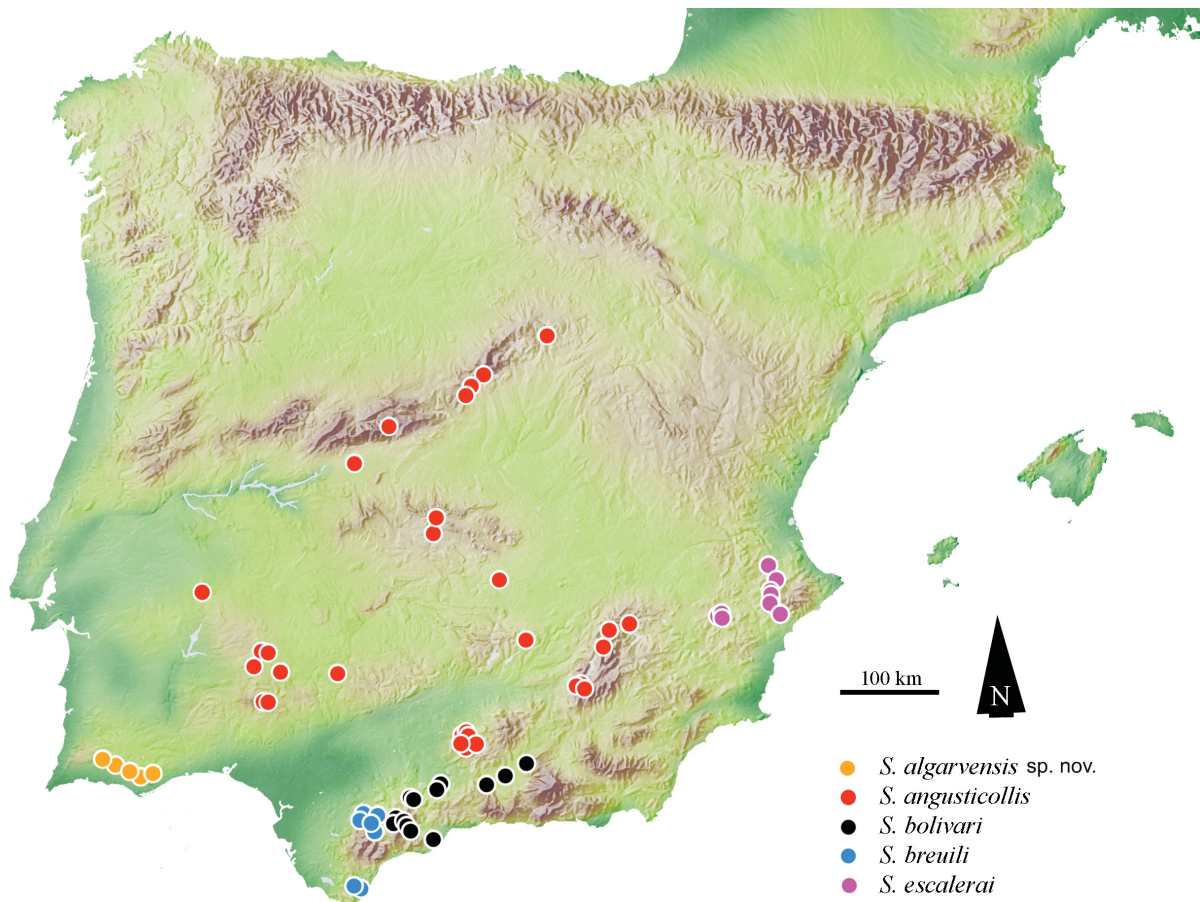


Fig. 32. Distribution of *Speonemadus* of the *escalerai*-group: *S. algarvensis* sp. nov., *S. angusticollis* (Kraatz, 1870), *S. bolivari* (Jeannel, 1922), *S. breuili* (Jeannel, 1922) and *S. escalerai* (Uhagón, 1898).

The species of the *escalerai*-group and related species have a Betic-Rif distribution, where its origin might be located. There is some parallelism with the southern distribution of the *Trechus fulvus*-group (Carabidae), where multiple independent colonizations of the subterranean environment have been proposed based on the existence of troglomorphic species in clades that also include epigeal species (Faille *et al.* 2014; Reboleira *et al.* 2009, 2010a).

The karst of the Algarve, in southern Portugal, is now considered a hotspot for a subterranean-adapted fauna (Reboleira 2012), with a considerable increase in the number of species described over the last decade. Most of them are clearly relicts.

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