**R e s e a r c h   a r t i c l e**

# The mostly cavernicolous millipede genus *Stygiiulus* Verhoeff, 1929, stat. nov.: taxonomy, distribution and phylogenetic relationships (Diplopoda, Julida, Julidae)

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**Abstract.** The blind and mostly endogean julid genus *Stygiiulus* Verhoeff, 1929 stat. nov. is reviewed to include ten species: *S. ausugi* (Manfredi, 1953) comb. nov., *S. fimbriatus* (Strasser, 1971) comb. et stat. nov., *S. gentianae* (Strasser, 1971) comb. et stat. nov., *S. illyricus* (Verhoeff, 1929) comb. nov., *S. insularis* (Strasser, 1938) comb. nov., *S. maximus* (Verhoeff, 1929) comb. nov., *S. montellensis* (Verhoeff, 1930) comb. nov., *S. rotundatus* (Strasser, 1962) comb. et stat. nov., *S. seewaldi* (Strasser, 1967) comb. nov., and *S. tobias* (Berlese, 1886) comb. nov. The distinctiveness of the genus from *Typhloiulus* is proven by both morphological and molecular data. The monotypic genus *Alpityphlus* Strasser, 1967 is here treated as a junior subjective synonym of *Stygiiulus* syn. nov. *Stygiiulus fimbriatus* comb. et stat. nov. and *S. gentianae* comb. et stat. nov., originally described as subspecies of *S. ausugi* comb. nov., are here erected to full species, while the subspecies *S. illyricus stygis* (Verhoeff, 1933) comb. et syn. nov. is considered to be a junior subjective synonym of the typical *S. illyricus* comb. nov. Lectotypes are formally designated for *S. gentianae* comb. et stat. nov. and *S. rotundatus* comb. et stat. nov., to stabilize the nomenclature of the two species under Article 74.1 of the ICZN. The phylogeny of the genus, its distribution patterns, and the modified mouthparts in some of its species are discussed.

## Introduction

Millipedes live primarily in the leaf litter and the superficial soil layer, with the great majority of them being confined to forested areas of various types. However, the deep subterranean domain (including caves) is another habitat that gives shelter to numerous diplopods, some of which are adapted to living under its specific conditions. Most of the larger millipede orders contain considerable number of species, genera, and even whole families that are, or mostly contain, troglobionts (Golovatch 2009; Liu *et al.* 2017).

In the predominantly Palaearctic order Julida, proportionally the most troglobionts are found in the families Blaniulidae and Trichoblaniulidae (Kime & Enghoff 2017). However, the most speciose family by far, Julidae, is relatively scarce in obligate cavernicoles, with most tribes and genera including only a small number of such species. The large genus *Typhloiulus* Latzel, 1884 (see Latzel 1884) is a notable exception, as it comprises only a few species known from superficial or shallow subterranean habitats, while the rest are recorded exclusively from caves. This along with the still insufficiently studied taxonomy and the highly unresolved phylogeny of the genus have lead to an increased interest in it in recent years (Vagalinski *et al.* 2015; Makarov *et al.* 2017; Antić *et al.* 2017, 2018). Some of these studies indicated that *Typhloiulus* is likely non-monophyletic. This is also reflected by the current taxonomy of the genus which includes several distinct subgenera, some of which probably deserve the status of separate genera. Here we revise one of these subgenera – the circum-Alpine *Stygiiulus* Verhoeff, 1929.

Until now, the subgenus *Stygiiulus* was considered to comprise four unquestionable species: *Typhloiulus illyricus* Verhoeff, 1929 (the type species, see Verhoeff 1929), *T. ausugi* Manfredi, 1953, *T. montellensis* Verhoeff, 1930, and *T. maximus* (Verhoeff, 1929) (see Strasser 1962). Vagalinski *et al.* (2015) suggested that *T. tobias* (Berlese, 1886), albeit somewhat deviating from the above-listed species, might be another member of *Stygiiulus*, and Antić *et al.* (2017, 2018) made the same assumption regarding *T. seewaldi* (Strasser, 1967) originally described in a separate genus, *Alpityphlus* Strasser, 1967 (see Strasser 1967), and *T. insularis* Strasser, 1938. In the present paper we confirm the taxonomy of the three latter species under *Stygiiulus* stat. nov. and add three more that have hitherto been treated as subspecies of *T. ausugi* and *T. montellensis*. In addition, we elevate *Stygiiulus* stat. nov. to full generic rank based on both morphological and genetic data.

## Material and methods

### Material preservation and deposition

Most specimens are preserved in 70% ethanol, except for one sample of *Stygiiulus fimbriatus* comb. et stat. nov., collected in 2019 in 95% ethanol and used subsequently for genetic analyses.

The material used for the present study is deposited in CBSS (Croatian Biospeleological Society, Zagreb, Croatia), IBER (Institute of Biodiversity and Ecosystem Research at the Bulgarian Academy of Sciences, Sofia, Bulgaria), IZB (Institute of Zoology, University of Belgrade – Faculty of Biology, Belgrade, Serbia), NMNHS (National Museum of Natural History, Sofia, Bulgaria), MHNG (Muséum d'histoire naturelle, Geneva, Switzerland), and NHMD (Natural History Museum of Denmark, Copenhagen, Denmark (formerly ZMUC – Zoological Museum, University of Copenhagen).

**Morphological study and imaging**

Specimens were examined with a Nikon SMZ 745T and an МБС 10 binocular stereo microscopes (IZB and IBER, respectively). Permanent microscopic slides (MHNG) and temporary glycerine microscope preparations with taxonomically important structures dissected and mounted in the course of the present study were observed with a Carl Zeiss Axioscope 40 microscope (IZB) and a Zeiss Axio Imager 2 microscope (IBER). Drawings of gonopods, penes, male leg-pair 1, and vulvae were obtained using tracing paper placed on a computer monitor displaying pictures of those structures made with a Canon PowerShot A80 digital camera connected to the Carl Zeiss Axioscope 40 microscope and stacked with Zerene Stacker (IZB) or with a ProgRes C7 digital camera connected to a Zeiss Axio Imager 2 microscope and stacked with Helicon Focus 6 (IBER). Pictures of the specimens and relevant habitus structures were taken using a Nikon DS-Fi2 camera with a Nikon DS-L3 camera controller attached to a Nikon SMZ 1270 binocular stereo microscope (IZB). Measurements were performed using a Carl Zeiss Stemi 2000-c binocular stereomicroscope with an AxioCam MRc camera (IZB) and an ocular grid mounted on one of the eyepieces of the МБС 10 binocular stereo microscope (IBER). For Scanning electron microscopy (SEM) the examined morphological structures were air-dried, mounted on glass or metal pads, and sputter-coated with gold for imaging in JEOL JSM-5510 (Chemical Faculty, Sofia University, Sofia, Bulgaria) or with carbon for imaging in JEOL JSM-6010 PLUS/LA (University of Mining and Geology "St. Ivan Rilski", Sofia, Bulgaria).

The distribution maps were created using Google Earth Pro (vers. 7.3.4.8248) and Adobe Photoshop CS6. The final images were processed with Adobe Photoshop CS6.

**Descriptive abbreviations**

BRF   =     body ring formula
H      =     vertical diameter at mid-body
L      =     body length measured at ozopore level

Abbreviations referring to gonopodal, vulval and oral structures are explained both in the text and in the figure captions.

**Molecular analyses**

Total DNA from *Stygiiulus fimbriatus* comb. et stat. nov. was extracted via DNeasy Blood & Tissue Kit (Qiagen, Inc.) according to manufacturers' instructions. The obtained product was quantified by NanoDrop2000 (Thermo Scientific) and diluted to a standard concentration of 25–50 ng/μl. In order to amplify fragments of the nuclear 28S rDNA and the mitochondrial 16S rDNA, polymerase chain reaction was performed using HotStarTaq Plus Master Mix (Qiagen, Inc.). The primers used for 28S rDNA were 28S rDNA-FW 5'-CCCGTCTTGAAACACGGACCAA-3' and 28S rDNA-RE 5'-CCACAGCGCCAGTTCTGCTTAC-3'. The reaction was performed at 94°C for 5 min followed by 35 cycles of denaturation at 94°C for 1 min, annealing at 55°C for 30 sec, and extension at 72°C for 1 min (Muraji & Tachikawa 2000). The final cycle was completed with 10 min of extension at 72°C. For 16S rDNA we used LR-J-12961 5'-TTTAATCCAACATCGAGG-3' (Cognato & Vogler 2001) and LR-N-13398 5'-CGCCTGTTTAACAAAAACAT-3' (Simon *et al.* 1994). The reaction was performed at 94°C for 5 min followed by 5 cycles of denaturation at 94°C for 1.5 min, annealing at 44°C for 1 min and extension at 72°C for 1.5 min, and 30 cycles at 94°C for 1.5 min, 48°C for 1 min and 72°C for 1.5 min (Kutty *et al.* 2007). The final cycle was completed with 10 min of extension at 72°C. The presence of amplicons with an appropriate length was visualized on 2% agarose gel stained with GelRed (Biotium, Inc.) using 3 μl of the reaction. Amplified fragments were then sequenced at Macrogen Europe B.V. (Amsterdam, the Netherlands).

**Genetic data analyses**

Trimming, assembly and visual preparation of the newly obtained sequences were performed in CodonCode Aligner version 8.0.2 (CodonCode, Dedham, MA, USA). DNA sequences from the mitochondrial 16S rRNA and the nuclear 28S rRNA of closely related taxa and outgroups were downloaded from GenBank (Supplementary file 1). Sequence alignments were performed in MEGA X (Kumar *et al.* 2018) in two separate datasets. Unique sequences were selected with DAMBE 7.0.39 (Xia 2018). Best substitution models for matrices were selected using PartitionFinder ver. 2.1.1 (Lanfear *et al.* 2017) on the CIPRES Science Gateway server (Miller *et al.* 2011). Phylogenetic analyses were run on the two datasets (16S rRNA and 28S rRNA) and on a concatenated 16S rRNA+28S rRNA matrix. Maximum likelihood (ML) analyses were performed with RAxML ver. 8.2.12 (Stamatakis 2014) on the CIPRES Science Gateway using 1000 bootstrap resampling to obtain node support. Bayesian inference analyses (BI) were carried out with Mr Bayes 3.2.5 (Ronquist *et al.* 2012) with four simulations of Markov chains and $4 \times 10^6$ generations, sampling one of every 100 trees. The MCMC parameters were monitored in Tracer ver. 1.7.1 (Rambaut *et al.* 2018). The first 25% of trees were removed as burnin.

# Results

## *Taxonomy*

<div align="center">

Class Diplopoda de Blainville in Gervais, 1844
Order Julida Brandt, 1833
Family Julidae Leach, 1814

Genus ***Stygiiulus*** Verhoeff, 1929 stat. nov.

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*Stygiiulus* Verhoeff, 1929: 20 (as subgenus of *Typhloiulus* Latzel, 1884).
*Alpityphlus* Strasser, 1967: 146, **syn. nov.**

**Type species**

*Typhloiulus (Stygiiulus) illyricus* Verhoeff, 1929 (by monotypy)

**Diagnosis**

A genus of blind Julidae characterized by a flagellum-bearing promere, a true mesomere, and an opisthomere with a well-developed velum. Differing from other blind leptoiulinine/typhloiulinine genera by the following combination of characters: promere with an internal and an external lobe on caudal face, both without setae; opisthomere rather slender, devoid of any distinct processes on caudal and lateral side, and possessing a lamellar, marginally often (but not always) serrated or ciliate velum and an apically bifid solenomere (one or both solenomeral branches vestigial in some species), with the exception of (some variations of) *S. tobias* (Berlese, 1886) comb. nov. in which the solenomere apically possesses a minute third branch behind the main two; and hypoproct either blunt or rounded, tightly fitting under paraprocts in both sexes.

**Characterization**

– Small (L from 10 mm) to large (L up to 70 mm) Julidae.
– Colouration pallid to light brown-grey.
– Ommatidia absent.
– Ozopores set considerably (rarely closely) behind pro-metazonal suture.
– Epiproct present, varying from short to very long, mostly straight.
– Hypoproct rounded or subtriangular, not or only insignificantly protruding behind rear contour of paraprocts, ventrally setose.
– Male mandibular stipites not expanded.

– Male walking legs ventrally with a well-developed adhesive pad on tibia at least in more frontal leg-pairs, some species also with a less pronounced pad on postfemur.
– Male pleurotergum 7 with expanded ventral margin forming a rather weakly pronounced lobe in its caudal section.
– Penis (not observed in *S. seewaldi* comb. nov.) long and slender, with short and stout apical lobes and fine, narrow terminal lamellae.

## Gonopods

– Slender, solenomere more or less exceeding both pro- and mesomere in height.
– Promere roughly oar-shaped, with more or less well-developed internal and external lobe, these not bearing setae.
– Mesomere usually subequal to (rarely significantly shorter than) promere.
– Opisthomere simple, rather elongate, lacking paracoxal or other processes in its proximal or middle part, some species with a characteristic posterior hump at mid-distal level; subapically on frontal side with well-developed lamellar velum with often serrated or fringed margin; solenomere apically divided in two (rarely three) small branches – an anterior and a posterior one – with their tips often bearing several minute thread-like filaments; some species with one or both branches very weakly pronounced, difficult to detect.
– Basal spine at flagellum channel, with some exceptions (see below), usually absent.

## Vulva (not observed in *S. seewaldi* comb. nov.)

– Operculum higher than bursa.
– Median cleft of bursa shallow.
– Receptaculum seminis consisting of two narrow and short (in relation to size of vulva) tubes (except for *S. tobias* comb. nov. in which both tubes are rather long), sometimes forming distinct ampullas at bottom.

*Stygiiulus ausugi* (Manfredi, 1953) comb. nov.
Figs 10A, 11A, 13

*Typhloiulus ausugi* Manfredi, 1953b: 136–138, figs 1–2.

*Typhloiulus* (*Stygiiulus*) *ausugi* – Strasser 1962: 11, 12, 18, 37, 38, figs 1–2, 8, 11h, 15, 41–44.
*Typhloiulus* (*Stygiiulus*) *ausugi ausugi* – Strasser 1971a: 13.
*Typhloiulus ausugi ausugi* – Minelli 1985: 9.
*Typhloiulus ausugi* – Vagalinski *et al.* 2015: 336–337.

## Diagnosis

One of the three species of *Stygiiulus* stat. nov. with modified mouthparts, the other two being *S. fimbriatus* comb. et stat. nov. and *S. gentianae* comb. et stat. nov. Differs from both mainly by the complete absence of posterior hump on opisthomere, the very large velum with minute fringes on posterodistal margin, and the anterior and posterior solenomeral branches both being very short, hardly distinguishable.

## Material examined

ITALY – **Trentino (Autonomous Province of Trento)** • 1 ♂; topotype; Altopiano dei Sette Comuni, Grigno, Grotta [Cave] della Bigonda (243 VT/TN); 450 m a.s.l.; 10 Mar. 1996; G. Peretto and E. Piva leg.; H. Enghoff det. 2013; NHMD • 1 ♀; Grigno, Grotta [Cave] del Calgeron (new record), a side branch of the waterfall; Dec. 1973; Ischia leg.; H. Enghoff det. 1984; A. Minelli ded. 1985; NHMD.

**Descriptive notes**

ANTENNAE. 2–2.1 times as long as head and 1.7–1.75 times as long as H in males, and 1.7–1.8 times and ca 1.4 times, respectively, in females; antennomere 5 ca twice as long as broad; antennomeres 2, 3 and 4 subequal in length, ca 1.2 times as long as 5, and 1.7–1.8 times as long as 6; 6 visibly broader than 5, giving a clavate appearance of the antenna.

MOUTHPARTS. With strong hydrophilous modifications (sensu Enghoff 1985): labrum edentate or with three minute, vestigial teeth. Gnathochilarium short and distally markedly broad, stipites with conspicuously large palps. Gnathal lobes of mandibles with the external and the internal tooth strongly reduced, both being distinct but very small and pointed, deeply hidden in the buccal cavity; molar plate much smaller than the normal julid condition; pectinate lamellae five instead of the usual four, consisting of very fine and densely set teeth.

TARSUS OF MID-BODY LEGS. Ca 2.5 times as long as tibia and ca 5 times as long as apical claw. Mid-body legs ca 1.7 times as long as H in males and ca 1.4 times in females.

FEMALE SEXUAL CHARACTERS. Legs 1 and 2 slightly shorter but not thicker than following legs. Vulva (Fig. 11A) symmetric; bursa very broad, strongly compressed in the sagittal plane; each valve of bursa with one vertical row of setae; operculum (op) distally bulging, with a distinct apical concavity, exceeding bursa by nearly ⅓ of total height of vulva, with just several setae each side. Receptaculum seminis consisting of two small tubes: a very fine, somewhat bent, mesal one (mt) ending in a small ovoid ampulla (ma), and a significantly broader, mostly straight, lateral one (lt), not forming ampulla at bottom.

**Distribution**

Prior to this study, the species was known only from its type locality – the Grotta della Bigonda – on the northern border of the central part of the Venetian Prealps. The new locality of this species – the Grotta del Calgeron – is located in the same area, some 20 km south of the type locality (Fig. 13, blue circles).

**Remarks**

Strasser (1971a) described two subspecies of *ausugi*, viz., *fimbriatus* and *gentianae*. Considering the gonopod conformations of the two latter forms, both of which differ significantly from *S. ausugi* comb. nov. and are instead much more similar to *S. illyricus* comb. nov., *S. maximus* comb. nov., *S. montellensis* comb. nov., and *S. rotundatus* comb. et stat. nov., it becomes obvious that Strasser (1971a) treated the modified mouthparts as a taxonomic feature of primary importance, being unaware of the adaptive nature of such modifications, as revealed later by Enghoff (1985). Thus we here elevate *fimbriatus* and *gentianae* to the species level and describe both of them in detail below.

In the Grotta della Bigonda, this species lives in sympatry with *S. tobias* comb. nov.

*Stygiiulus fimbriatus* (Strasser, 1971) comb. et stat. nov.
Figs 1–3, 13

*Typhloiulus ausugi fimbriatus* Strasser, 1971a: 13–14, fig. 14.

*Typhloiulus ausugi fimbriatus* – Minelli 1985: 10. — Vagalinski *et al.* 2015: 336–337.

**Diagnosis**

A species of *Stygiiulus* stat. nov. with modified mouthparts. Differs from its most similar congener, *S. gentianae* comb. et stat. nov., by gonopod details, viz. both promere and mesomere being apically bent
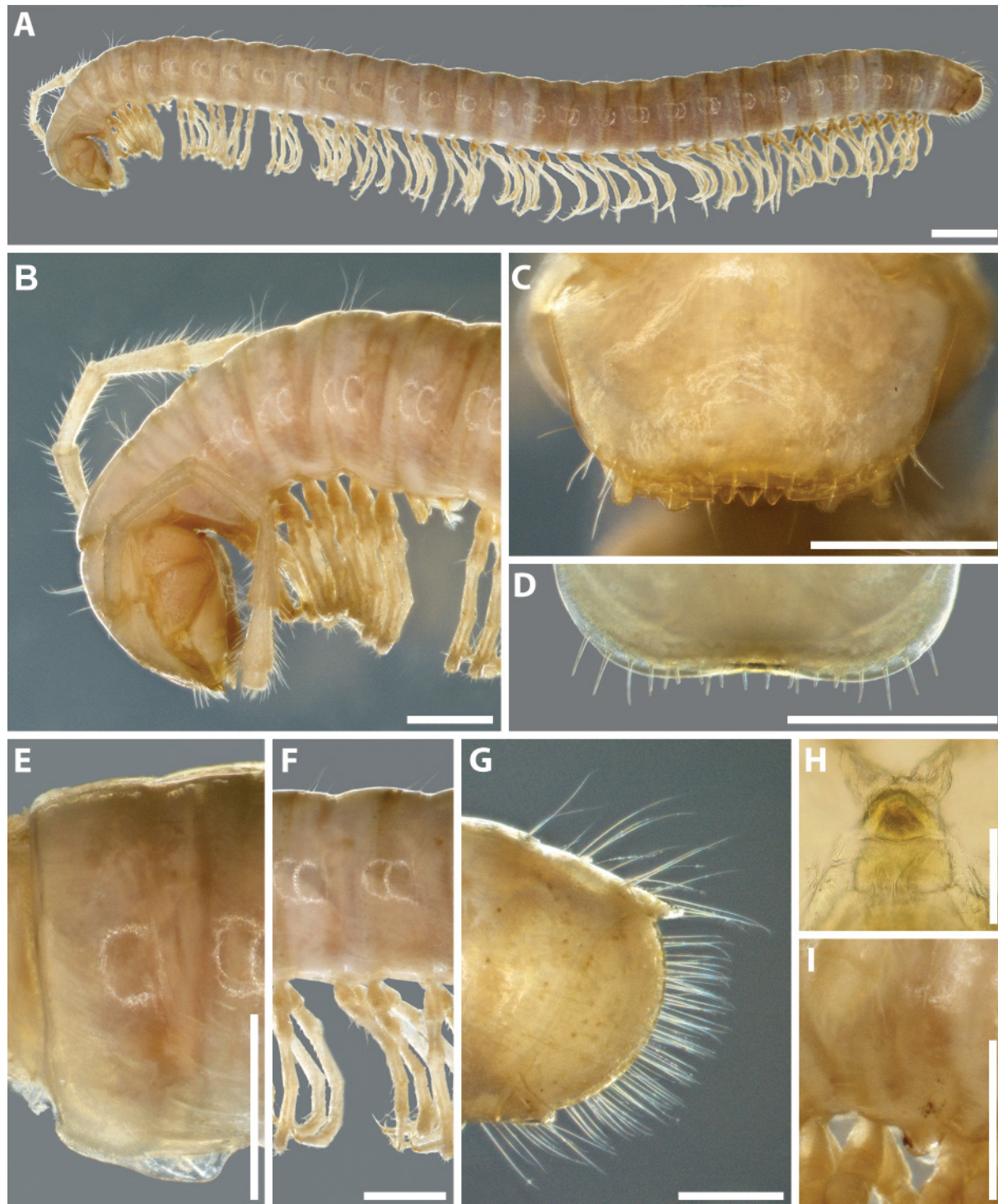
**Fig. 1.** *Stygiiulus fimbriatus* (Strasser, 1971) comb. et stat. nov., ♂♂ (A–H) and ♀ (I) from Foran di Landri Cave (IZB). **A**. Habitus, lateral view. **B**. Anterior part of body, lateral view. **C**. Labrum, fronto-dorsal view. **D**. Labrum, dorsal view. **E**. Pleurotergum 7, lateral view. **F**. Mid-body rings, lateral view. **G**. Telson, lateral view. **H**. Posterior node of hypopharynx, fronto-ventral view. **I**. Lobe of body ring 3, lateral view. Scale bars: A = 1 mm; B–G, I = 0.5 mm; H = 0.1 mm.

frontad rather than turned towards one another, velum being marginally serrated all along rather than having a smooth anterior margin; by the more pronounced posterior part of pleurotergal flange 7 in males; by the vulval operculum being concave rather than convex, exceeding bursa by ca ¼ rather than ⅖ of total height of vulva; by the presence of a small, roundish anterior lobe on ventral margin of body ring 3 in females, vs ventral margin of body ring 3 in females being almost entirely subtriangular in *S. gentianae* comb. et stat. nov., and by the somewhat longer epiproct.

## Material examined

### Holotype
ITALY • ♂; slide preparation plus ethanol sample; Friuli-Venezia Giulia, San Pietro al Natisone, Grotta [cave] di San Giovanni d'Antro; slide no. 1003: gonopods, antennae, leg-pairs 1, 2, 3, 7, penis, gnathochilarium, flanges of pleurotergum 7; ethanol sample: broken in six pieces; MHNG-ARTO-26720.

### Other material
ITALY • 3 ♂♂, 1 ♀; Friuli-Venezia Giulia, Prestento di Torreano, Foran di Landri Cave (11 / 46FR); 10 Jul. 2019; G. Canciani and M. Colautti leg.; IBER • 4 ♂♂, 2 ♀♀; same collection data as for preceding; IZB • 1 ♂; same collection data as for preceding; NHMD.

## Comment

Since the original description was based upon one male which was not designated by Strasser (1971a) as holotype, we here consider that male as a holotype fixed by monotypy, in order to stabilize the nomenclature of the species under Article 73.1.2 of the ICZN.

## Redescription

SIZE AND NUMBER OF BODY RINGS. Non-type ♂♂ with BRF 26–31+0–1+T, L = 14–20 mm, H = 1.1–1.25 mm; non-type ♀♀ with BRF 28–32+0–1+T, L = 16–21 mm, H = 1.3–1.6 mm.

COLOURATION (Fig. 1A–B, E–G). Generally brown-beige; metazonae with a narrow transverse dark brown band before their last third, the band gradually narrowing ventrally.

EXTERNAL STRUCTURES. Head with 2 vertigial, 2+2 supralabral and 16–18 labral setae. Antennae (Fig. 1B) 2.3 times as long as head and 2.3–2.4 times as long as H in males, and 2 times and 1.85–1.9 times, respectively, in females; antennomere 5 3.12–3.15 times as long as broad; antennomeres 2–5 subequal in length, 1.3–1.6 times as long as 6. Antennomeres V and VI each with a terminal corolla of large sensilla basiconica bacilliformia; antennomere VII with a terminal corolla of small sensilla basiconica bacilliformia.

MOUTHPARTS (Figs 1C–D, H, 2A–B). With moderate hydrophilous modifications (sensu Enghoff 1985): Labrum either edentate (Fig. 1D) or with three well-developed labral teeth (Fig. 1C). Gnathochilarium (Fig. 2A) rather short and distally markedly broad, with the 3 long distal setae on each stipes usual for the family, stipites medially each with 4–10 short setae arranged longitudinally, stipital palps conspicuously large; promentum large (pm), completely separating lingual lamellae, the latter each with 2–3 proximal and 1 distal seta. Gnathal lobes of mandibles (Fig. 2B) with the external (et) and the internal tooth (it) slightly to moderately reduced; molar plate (mp) relatively small (but larger compared to that in *S. ausugi* comb. nov.); the four pectinate lamellae (pl) consisting of slender and very densely set teeth. Hypopharynx distally densely ciliate, posterior node reduced, with roundish posterior margin (Fig. 1H).

COLLUM. Entirely smooth, its frontolateral margin bent outwards. Body rings considerably vaulted. Prozonae smooth. Metazonae with well-developed striation only ventrally, dorsally and laterally with faint and short striae only in anterior parts; setae ca 20% of H (Fig. 1F), arranged in moderately dense
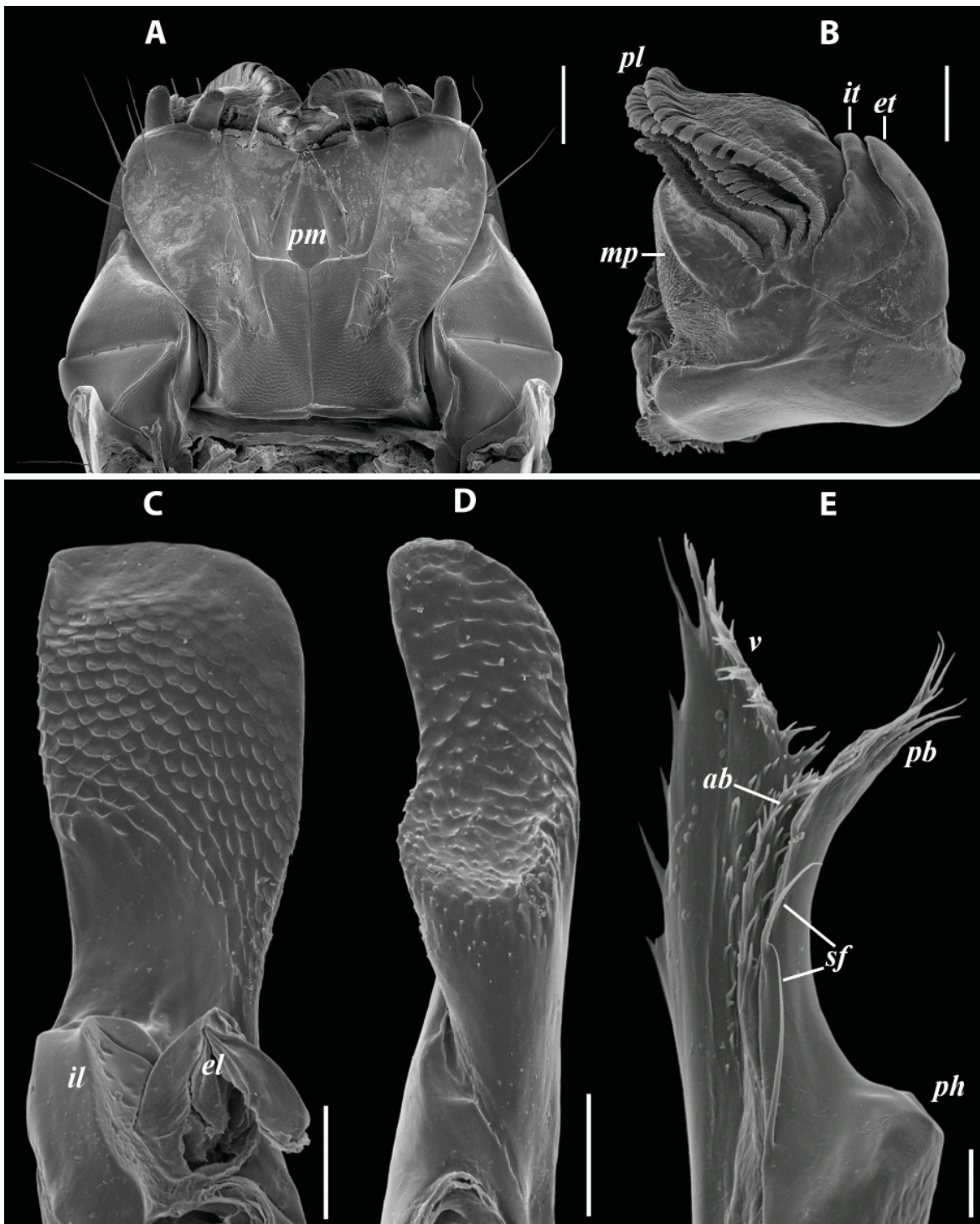
**Fig. 2.** *Stygiiulus fimbriatus* (Strasser, 1971) comb. et stat. nov., ♂ from from Foran di Landri Cave (IBER). **A**. Gnathochilarium, ventral view. **B**. Gnathal lobe of left mandible, ventral view. **C**. Left promere, caudal view. **D**. Left mesomere, oral view. **E**. Distal part of left opisthomere, mesal view. Abbreviations: ab = anterior branch of solenomere; el = external lobe; et = external tooth; il = internal lobe; it = internal tooth; mp = mollar plate; pb = posterior branch of solenomere; ph = posterior hump; pl = pectinate lamellae; pm = promentum; sf = setiform filaments; v = velum. Scale bars: A = 0.2 mm; B = 0.1 mm; C–D = 0.05 mm; E = 0.02 mm.

whorl. Ozopores very small, placed behind pro-metazonal suture at ca ⅖ of metazonal length measured from front to back. Tarsus of mid-body legs 2.2–2.4 times as long as tibia and 2.8–3.7 times as long as apical claw; accessory claw absent. Mid-body legs 1.5–1.6 times as long as H in males, 1.4 times in females.

Telson (Fig. 1G). Epiproct short and stout, straight all along, ending with a short hyaline tip turned more or less dorsad, barely protruding behind caudal contour of paraprocts. Hypoproct broadly rounded, tightly fitting under paraprocts, with rather evenly setose ventral face. Paraprocts densely covered with long setae, without distinct rows of shorter setae along caudal margins.

Male sexual characters. Leg-pair 1 (Fig. 3A) rather slender hooks oriented towards one another; with three complete and another one or two faintly indicated segments; with apically densely microdentate tibial outgrowths, and without or with barely visible tarsal remnants. Legs of more anterior body rings with an adhesive pad on tibia, most pronounced in leg-pair 2, gradually diminishing in caudal direction, completely disappearing around mid-body; tibia and femora without modifications. Pleurotergum 7 (Fig. 1E) caudo-ventrally forming small rounded lobes directed caudad. Penis (Fig. 3B) long, in situ visible behind coxae 2, slender hourglass shaped: broadest at base, narrowing until the middle, then slightly widening again, ending with short, diverging, apical lobes bearing fine, blunt, terminal lamellae.

Gonopods (Figs 1B, 2C–E, 3C). In situ obliquely protruding from gonopodal sinus with their distal parts (Fig. 1B). Promere (Fig. 2C, p in Fig. 3C) somewhat higher than mesomere, both being significantly surpassed by the opisthomere. Promere stout, oar-shaped (broadest apically), forming a near right-angled meso-apical corner and a broadly rounded latero-apical corner; apical margin bent somewhat frontad; caudal face distally densely microsquamose, basally with an internal and an external lobe, both being short and robust, partly fused to one another. Mesomere (Fig. 2D, m in Fig. 3C) narrow spoon-like, with the apex turned meso-frontad; caudal face distally deeply concave and sparsely microsquamose. Opisthomere (Figs 2E, 3C) markedly slender, with a distinct, obtuse posterior hump (ph); velum (v) pointing distad, both its frontal and caudal margin apically deeply serrated; solenomere with a slender posterior branch (pb) bent caudad, ending with several long ciliae, anterior branch (ab) vestigial, barely protruding, mostly concealed between the velum and the posterior solenomeral branch, densely ciliate; with 2 or 3 fine distal setiform filaments (sf), and sometimes with a variously developed basal spine (bs) at flagellum channel (fc).

Female sexual characters. Leg-pairs 1 and 2 visibly shorter, 1 also thicker, than following legs. Ventral margin of body ring 3 with roundish anterior lobe (Fig. 1I). Vulva (Fig. 3D) somewhat compressed in the sagittal plane, mostly symmetric: lateral side of operculum higher and apically more pointed than mesal one; each valve of bursa with one vertical row of setae; operculum (op) broad and thick, with a concave apical margin, exceeding bursa by ca ¼ of total height of vulva, medio-laterally with two longitudinal rows of setae each side. Receptaculum seminis consisting of two short and narrow, somewhat folded tubes – a lateral (lt) and a mesal one (mt), both insignificantly widening towards bottom, not forming distinct ampullae.

**Distribution**

Known only from two caves in the Julian Alps in Italy, near the border with Slovenia (Fig. 13, yellow circles).

**Remark**

The new locality of *S. fimbriatus* comb. et stat. nov., Cave Foran di Landri, is an active cave with a stream running through it year-round, flowing out of the entrance, after passing through a series of syphons
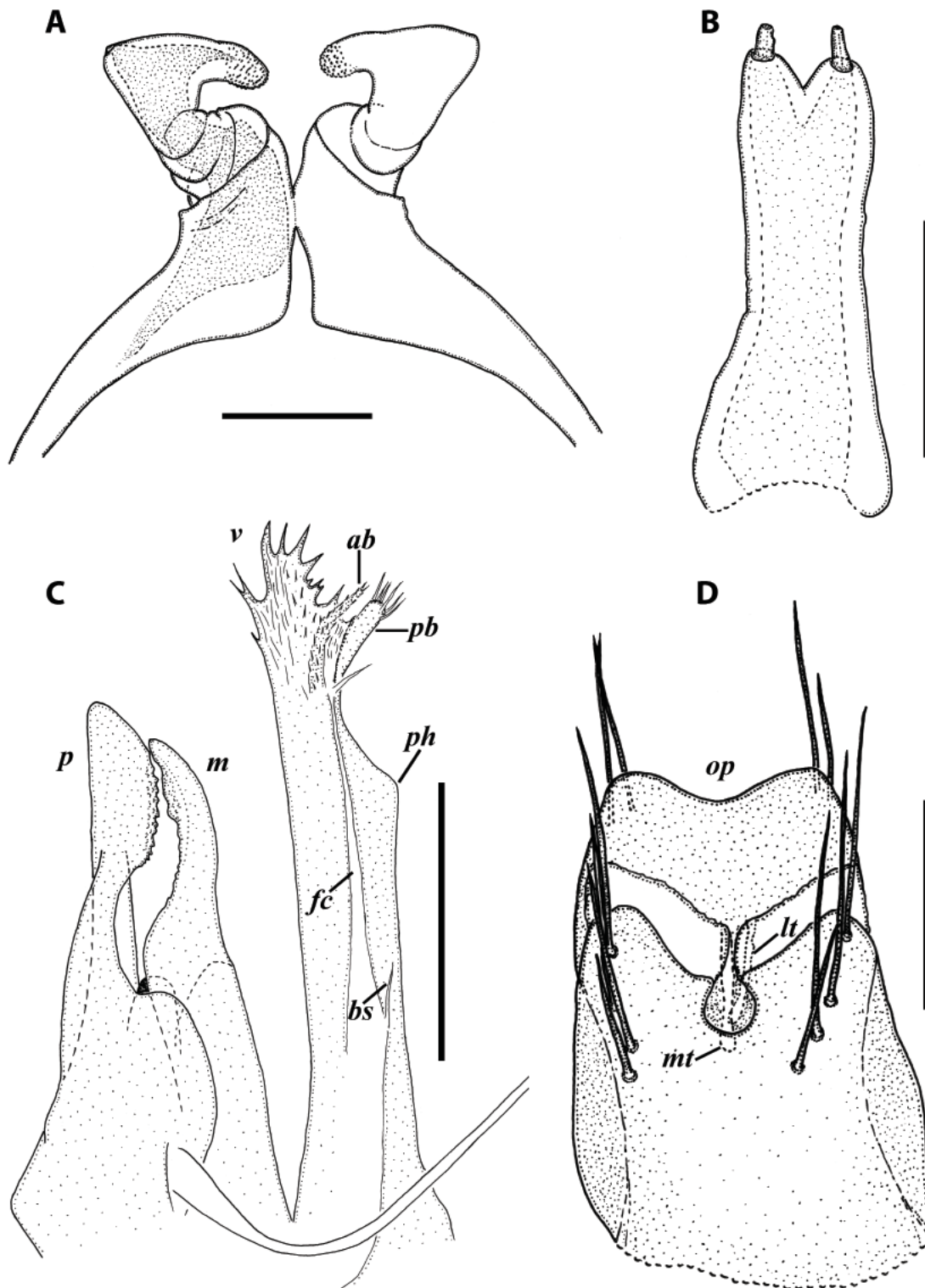
**Fig. 3.** *Stygiiulus fimbriatus* (Strasser, 1971) comb. et stat. nov., holotype ♂ (A, B) (MHNG), ♂ (C) (IZB) and ♀ (D) (IBER) from Foran di Landri Cave. **A**. Leg-pair 1, caudal view. **B**. Penis, oral/caudal view. **C**. Left gonopods, mesal view. **D**. Left vulva, caudal, somewhat mesal view. Abbreviations: ab = anterior branch of solenomere; bs = basal spine; fc = flagellum channel; lt = lateral tube; m = mesomere; mt = median tube; op = operculum; p = promere; pb = posterior branch of solenomere; ph = posterior hump; v = velum. Scale bars = 0.2 mm.

(four discovered so far). All examined specimens were found right beyond the first two syphons, ca 40 meters from the entrance. This part of the cave includes a number of ponds, and it probably becomes completely flooded during rainy periods (Canciani 2019). Part of the individuals was observed moving on the surface of the ponds – a behaviour most likely associated with a filtrating rather than chewing feeding mode, in which small organic particles adhere to the fine and densely set teeth of the pectinate lamellae and to the cilia of the hypopharynx.

The cave of San Giovanni d'Antro (the type locality) is of the same type as Foran di Landri, and Strasser (1971a) noted that it was occasionally flooded.

### *Stygiiulus gentianae* (Strasser, 1971) comb. et stat. nov.
Figs 4–6, 13

*Typhloiulus ausugi gentianae* Strasser, 1971a: 13–14, fig. 15.

*Typhloiulus ausugi gentianae* – Minelli 1985: 10. — Vagalinski *et al.* 2015: 336–337.

## Material examined

**Lectotype** (designated here)
ITALY • ♂; Veneto, Bosco del Cansiglio [Cansiglio Forest], Bus [cave] de la Genziana; specimen unbroken; MHNG-ARTO-26721.

**Paralectotypes**
ITALY • 1 ♀; same collection data as for lectotype; specimen unbroken; MHNG-ARTO-26722 • 1 ♂ slide preparation; same collection data as for lectotype; labrum, mandibles, gnathochilarium, antennae, penis, flanges of pleurotergum 7; MHNG-ARTO-26723 • 1 ♂ slide preparation; same collection data as for lectotype; gonopods; MHNG-ARTO-26724.

**Other material**
ITALY • 1 topotype ♀; Veneto, province of Treviso, Bosco del Cansiglio [Cansiglio Forest], Fregona, q. 1020, Bus [cave] de la Genziana (1000 V/TV); 3 Oct. 1985; E. Piva leg. and ded.; NHMD • 1 topotype ♂, 2 topotype ♀♀; same locality as for preceding; 22. Oct. 1994; E. Piva leg.; H. Enghoff det. 2013; NHMD • 2 ♂♂, 1 ♀; Friuli-Venezia Giulia, Cansiglio Cavallo, Barcis (PN), Grotta [cave] della Vecchia Diga (786 / 327FR); 484 m a.s.l.; 30 Jun. 1996; G. Peretto and E. Piva leg.; H. Enghoff det. 2013; NHMD • 2 ♂♂, 1 ♀; Friuli-Venezia Giulia, province of Pordenone, Montereale Valcellina (PN), Inghiottitoio [karstic pot-hole] della Val di Pai (1027 / 469FR); 30 Aug. 1984; Comotti leg.; R. Pisoni ded. 1989; NHMD.

## Comment

Since the original description was based upon three males and two females, none of which was designated by Strasser (1971a) as holotype, we here designate the only intact male specimen as lectotype, in order to stabilize the nomenclature of the species under Article 74.1 of the ICZN.

## Diagnosis

A species of *Stygiiulus* stat. nov. with modified mouthparts. Differs from its most similar congener, *S. fimbriatus* comb. et stat. nov., by gonopod details, viz. promere and opisthomere being turned towards one another rather than apically both bent frontad, velum with a smooth rather than entirely serrated anterior margin; by the weakly rather than strongly pronounced posterior part of pleurotergal flange 7 in males; by the vulval operculum being convex rather than concave, exceeding bursa by ca $\frac{2}{5}$ rather than with $\frac{1}{4}$ of total height of vulva; by the entirely subtriangular ventral margin of body ring 3 in females, rather than ventral margin with a small, roundish anterior lobe; and by the somewhat shorter epiproct.
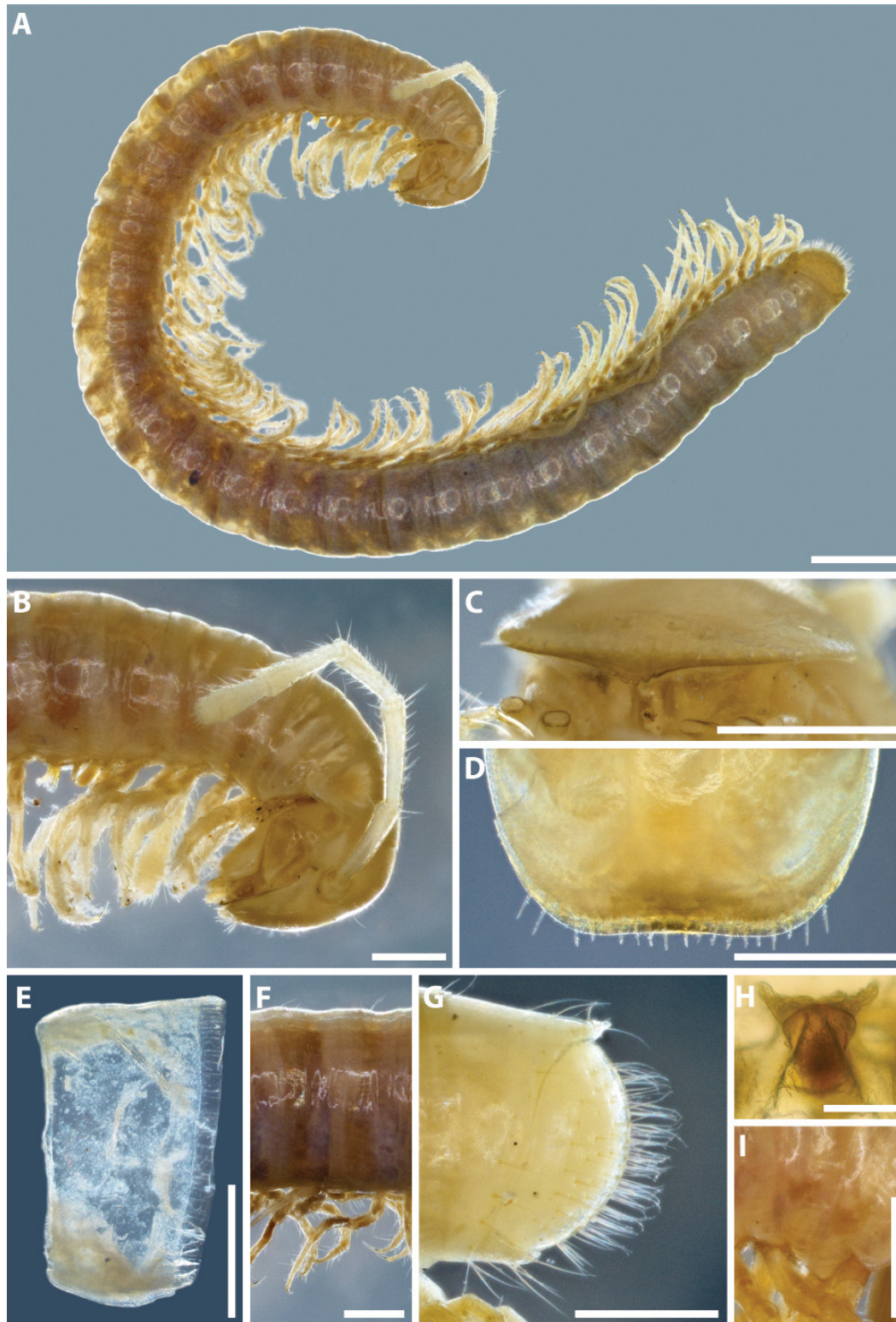
**Fig. 4.** *Stygiiulus gentianae* (Strasser, 1971) comb. et stat. nov., ♂ (A–C, E, G) from Grotta [cave] della Vecchia Diga, ♂ topotype (D, H) and ♀ topotype (F, I) (NHMD). **A**. Habitus, lateral view. **B**. Anterior part of body, lateral view. **C**. Labrum, frontal view. **D**. Labrum, dorsal view. **E**. Pleurotergum 7, lateral view. **F**. Mid-body rings, lateral view. **G**. Telson, lateral view. **H**. Posterior node of hypopharynx, fronto-ventral view. **I**. Lobe of body ring 3, lateral view. Scale bars: A = 1 mm; B–G, I = 0.5 mm; H = 0.1 mm.

**Redescription**

SIZE AND NUMBER OF BODY RINGS. Lectotype ♂ with BRF 36+0+T, L = 18 mm, H = 1.3 mm, paralectotype ♀ with BRF 33+0+T, L = 16.5 mm, H = 1.2 mm; topotype ♂ with BRF 31+0+T, L = 20.5 mm, H = 1.4 mm; topotype ♀♀ with BRF 31–35+0–1+T, L = 19–22 mm, H = 1.4–1.7 mm; males from Val di Pai with BRF 30–32+1+T, L = 13 mm, H = 1.05–1.1 mm; female from Val di Pai with BRF 30+1+T, L = 17 mm, H = 1.3 mm; males from Vecchia Diga with BRF 29–31+0+T, L = 18–19 mm, H = 1.15–1.2 mm, female from Vecchia Diga with BRF 27+1+T, L = 18.5 mm, h = 1.3 mm. In general, males with BRF 29–36+0–1+T, L = 13–20.5 mm, H = 1.05–1.3 mm; females with BRF 27–36+0–1+T, L = 16.5–22 mm, H = 1.2–1.7 mm.

COLOURATION (Fig. 4A–B, F–G). Completely pallid, probably as a result of the long alcohol conservation (considering the presence of some colour pattern in the highly similar *S. fimbriatus* comb. et stat. nov.).

EXTERNAL STRUCTURES. Head with 2 vertigial, 2+2 supralabral and 16–23 labral setae. Antennae (Fig. 4B) 2.5 times as long as head and 2.4–2.5 times as long as H in males, and 2.1–2.2 times and 1.8–2.1 times, respectively, in females; antennomere 5 2.8 times as long as broad. Antennomeres V and VI each with a terminal corolla of large sensilla basiconica bacilliformia; antennomere VII with a terminal corolla of small sensilla basiconica bacilliformia.

MOUTHPARTS (Fig. 4C–D, H). Generally similar to those of *S. fimbriatus* comb. et stat. nov., including individuals with edentate labrum (Fig. 4D), as well as individuals with three small but distinct labral teeth (Fig. 4C). Gnathochilarial stipites each with a row of 2–5 rather than up to 10 setae. Posterior node of hypopharynx (Fig. 4C) reduced, with somewhat squarish posterior part.

COLLUM. Collum as in *S. fimbriatus* comb. et stat. nov., but with the frontolateral margin only slightly bent outwards. Metazonal striation faint and sparse even on ventral side; setation somewhat shorter than in *fimbriatus* – around 10% of H. Tarsus of mid-body legs 2.1–2.3 times as long as tibia.

TELSON (Fig. 4G). Epiproct very short, not protruding behind caudal contour of paraprocts), ending with a minute hyaline tip turned more or less dorsad. Hypoproct more narrowly rounded compared to the former species, blunt subtriangular in some specimens (regardless of sex).

All remaining external somatic characters as in *S. fimbriatus* comb. et stat. nov.

MALE SEXUAL CHARACTERS. Male leg-pair 1 (Fig. 5A) similar to the condition in *S. fimbriatus* comb. et stat. nov., differing in having a proportionately smaller tibial part, apically more sparsely microdentate/microtuberculate. Male walking legs with more pronounced tibial pads than in *S. fimbriatus* comb. et stat. nov., these being still visible behind mid-body. Penis (Fig. 5B) as in the former species, but with longer and more tapering terminal lamellae.

GONOPODS (Figs 5C, 6). Very similar to those of *S. fimbriatus* comb. et stat. nov., differing from the latter species mainly by the pro- (p) and mesomere (m) being gradually bent towards one another, rather than both apically turned frontad, and by the smooth rather than ciliate anterior margin of velum (v); also promere in *S. gentianae* comb. et stat. nov. relatively broader, with the external lobe (el) significantly higher than, rather than subequal to, the internal one (il); posterior branch of solenomere (pb) somewhat more robust, anterior branch of solenomere (ab) and posterior hump of opisthomere (ph) of same size and shape as in *S. fimbriatus* comb. et stat. nov.

FEMALE SEXUAL CHARACTERS. Leg-pairs 1 and 2 shorter, 1 also slightly thicker, than following legs. Ventral margin of body ring 3 subtriangular (Fig. 4I). Vulva (Fig. 5D) mostly symmetric, somewhat compressed in the sagittal plane; operculum (op) very large, with a convex apical margin forming several rounded
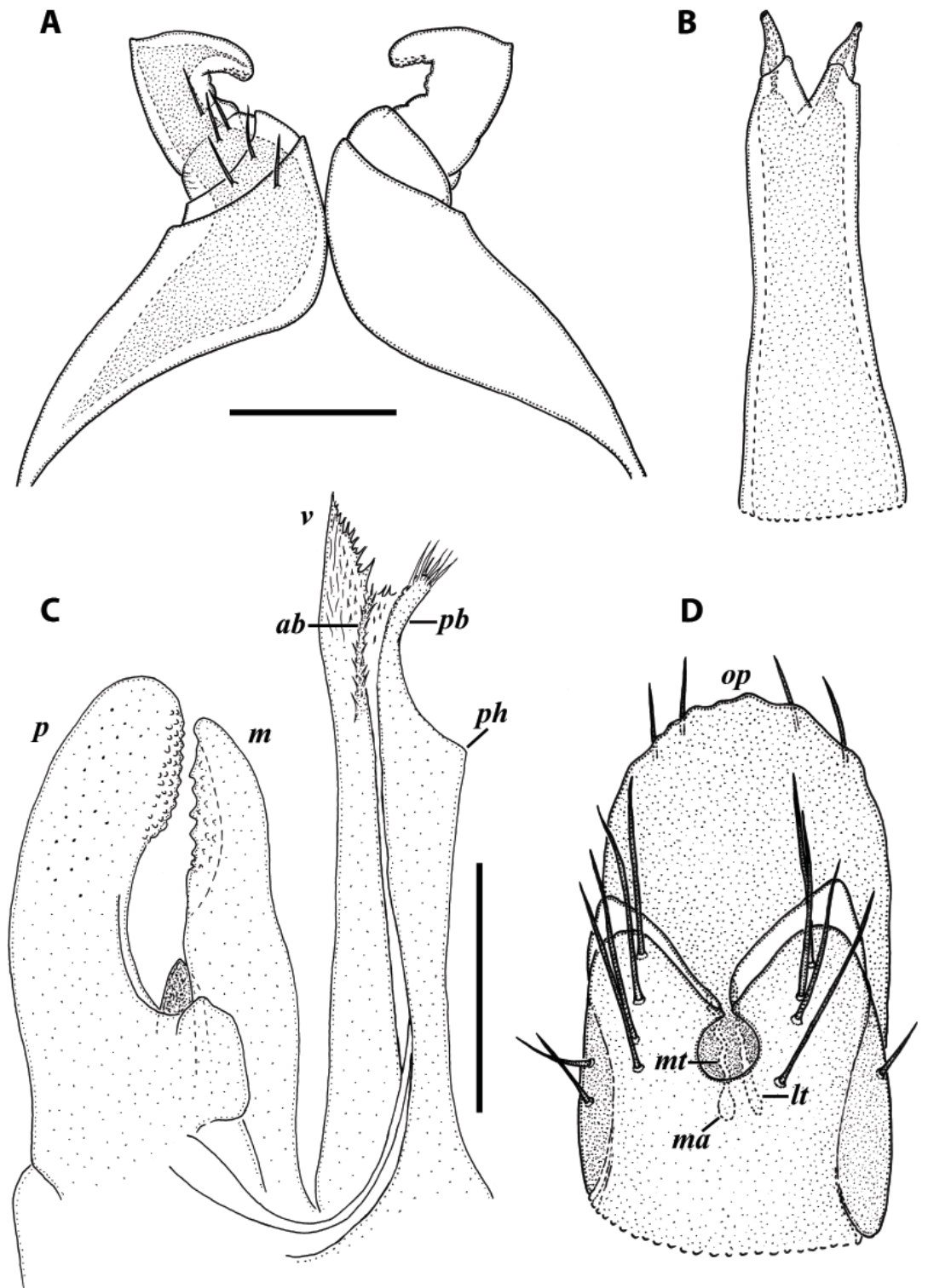
**Fig. 5.** *Stygiiulus gentianae* (Strasser, 1971) comb. et stat. nov., ♂ paralectotype (A–B) (MHNG), topotype ♂ (C) (NHMD) and topotype ♀ (D) (NHMD). **A**. Leg-pair 1, oral view. **B**. Penis, oral/caudal view. **C**. Left gonopods, mesal view. **D**. Left vulva, caudal, somewhat mesal view. Abbreviations: ab = anterior branch of solenomere; lt = lateral tube; m = mesomere; ma = median ampulla; mt = median tube; op = operculum; p = promere; pb = posterior branch of solenomere; ph = posterior hump; v = velum. Scale bars: A, C–D = 0.2 mm; B = 0.1 mm.

bumps, exceeding bursa by nearly ⅖ of total height of vulva; setation on both bursa and operculum in a similar pattern as in *S. fimbriatus* comb. et stat. nov., but with 1–2 setae on side sclerites in addition. Receptaculum seminis represented by two short and narrow tubes: a mesal one (mt) leading to an ovoid ampulla (ma), and a lateral one (lt) ending without distinct ampulla at bottom.

**Distribution**

Known from several caves in the easternmost part of the Venetian Prealps mountain range (Fig. 13, red circles).

**Remark**

Strasser (1971a) wrote that this species was found on wet vertical walls (common place for many troglobitic arthropods with mouthpart modifications).

*Stygiiulus illyricus* (Verhoeff, 1929) comb. nov.
Figs 10B, 11B, 13

*Typhloiulus* (*Stygiiulus*) *illyricus* Verhoeff, 1929: 20–23, fig. 1.



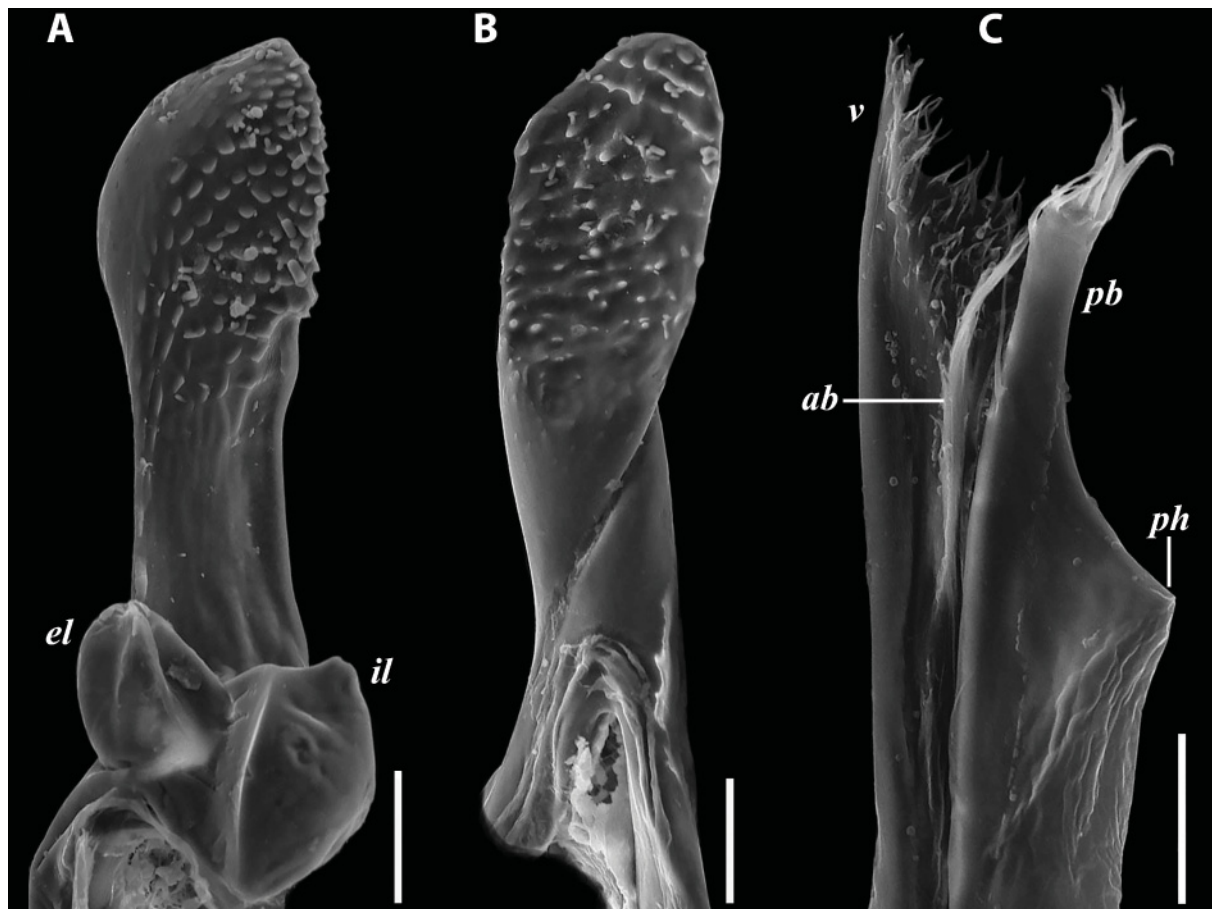**Fig. 6.** *Stygiiulus gentianae* (Strasser, 1971) comb. et stat. nov., ♂ from Grotta [cave] della Vecchia Diga (NHMD). **A**. Right promere, caudal view. **B**. Right mesomere, oral view. **C**. Distal part of left opisthomere, mesal view. Abbreviations: ab = anterior branch of solenomere; el = external lobe; il = internal lobe; pb = posterior branch of solenomere; ph = posterior hump; v = velum. Scale bars = 0.05 mm.

*Typhloiulus* (*Stygiiulus*) *illyricus* – Manfredi 1932: 81. — Strasser 1962: 20, 35–36, figs 11i, 36–37.
*Typhloiulus illyricus* – Verhoeff 1930: 17. — Antić *et al.* 2018: 263, fig. 3.
*Typhloiulus illyricus stygis* – Verhoeff 1933: 15–17, figs 28–29, **syn. nov.**
*Typhloiulus illyricus* var. *obscurus* – Verhoeff 1933: 17.
*Typhloiulus illyricus* var. *obscura* – Wolf 1934–38: 515.

## Material examined

SLOVENIA • 2 topotype juvs; Ocizla, Beško-Ocizeljski System (= Ocizeljska Jama Pit); 19 Apr. 2012; T. Delić leg.; D. Antić det. 2018; IZB • 1 ♂, 1 ♀; Dane, Divača, Mejame Pit (= Med jamah, Medjama); 22 Apr. 2014; M. Zagmajster leg.; D. Antić det. 2018; IZB. CROATIA • 1 ♂, 1 ♀; Istria, Ročko polje, Roč, Rabakova Cave; 30 Jun. 2013; D. Šuperina leg.; D. Antić det. 2018; IZB • 1 ♀; same collection data as for preceding; 16 Apr. 2013; IZB.

## Diagnosis

A species of *Stygiiulus* with normal mouthparts. Distinguishable from congeners by the combination of certain gonopodal characters (Fig. 10B), viz., a mostly straight promere, a mesomere with the apex bent frontad, and an opisthomere with a small but distinct posterior hump, a broad and deeply serrated velum, and a vestigial posterior solenomeral branch, this being completely fused to the velum.

## Descriptive notes

Antennae. 2.2 times as long as head and ca 1.8 times as long as H in males, and 1.7 times and ca 1.5–1.55 times, respectively, in females; antennomere 5 ca 2.4 times as long as broad; antennomeres 2–5 subequal in length, ca 1.3–1.4 times as long as 6.

Tarsus of mid-body legs. Ca 2.4 times as long as tibia and ca 2 times as long as apical claw. Mid-body legs ca 1.1 times as long as H in both sexes.

Female sexual characters. Leg-pairs 1 and 2 considerably shorter than, but as thick as, following legs. Vulva (Fig. 11B) slightly compressed in the sagittal plane, mostly symmetric; median cleft deeper than in most congeners; each valve of bursa with several, mostly vertically arranged setae, 1–2 setae on side sclerites; operculum (op) distally markedly thickened, with a concave apical margin, exceeding bursa by slightly more than ¼ of total height of vulva, medio-laterally with two longitudinal rows of setae each side, with a bunch of setae on each latero-apical corner. Receptaculum seminis consisting of a fine, slightly bent, mesal tube (mt) ending in a small piriform ampulla (ma), and a somewhat shorter lateral tube (lt) ending in an ampulla (la) of similar shape and size as the former one.

## Distribution

Known exclusively from caves and pits in the Istrian Peninsula in Croatia and the northwestern Dinarides in Slovenia (Fig. 13, green squares).

## Remark

From Rabakova Cave, Verhoeff (1933) described the subspecies *illyricus stygis*, mentioning the possibility that the observed differences between the single male his description was based upon and the typical *illyricu*s were due to periodomorphosis, but he nevertheless opted to give a formal name to the new morph. Indeed, the gonopods he drew seem to be underdeveloped (see Verhoeff 1933: 20, fig. 28). Fortunately, we examined here one adult male from Rabakova Cave, whose gonopods appeared completely identical to the gonopods of the typical *illyricus*. We were even luckier to find that one of the juveniles from the type locality of the typical *illyricus* was a subadult male with unmodified first pair of legs. The gonopods of this subadult male are very similar to Verhoeff's (1933) drawing of the gonopods of the subspecies *stygis*.

Based on these observations, it is clear that Verhoeff's *stygis* was actually a non-adult male or "Junior-Männchen" [junior male] – a term coined by Strasser (1971b), referring to typhloiulinine males with almost fully developed gonopods, but with non-modified first pair of legs and other, less conspicuous, underdeveloped external somatic structures (see also Vagalinski *et al.* 2015). We thus consider here *S. illyricus stygis* syn. nov. as a junior subjective synonym of the typical *S. illyricus* comb. nov.

### *Stygiiulus insularis* (Strasser, 1938) comb. nov.
Figs 10C, 11C, 13

*Typhloiulus insularis* Strasser, 1938: 399–402, fig. 10.

*Typhloiulus insularis* – Vagalinski *et al.* 2015: 340. — Antić *et al.* 2018: 263–264; figs 5–6, 18c.

**Material examined**

CROATIA • 1 topotype ♂; Island of Cres, Beli, Petričevići, Čampari Pit; 8 Apr. 2001; R. Ozimec and B. Jalžić leg.; IZB • 1 topotype ♀; same collection data as for preceding; 20 Oct. 2000; CBSS.

**Diagnosis**

A species of *Stygiiulus* stat. nov. with normal mouthparts. Distinguishable from congeners by its smaller body (L = 10–16 mm) and shorter legs in relation to H, by the ozopores being placed on or right behind the pro-metazonal suture instead of at considerable distance behind it, and in several aspects of gonopod structures (Fig. 10C), viz., ridge- rather than knob-like internal lobe of the promere, spoon-shaped mesomere, rather robust opisthomere without a posterior hump (the latter shared with *S. seewaldii* comb. nov.), long basal spine at flagellum channel (sometimes present in *S. rotundatus* comb. et stat. nov. and *S. fimbriatus* comb. et stat. nov.), and the presence of a distinct distal outgrowth (do) on velum (seen also in *S. seewaldi* comb. nov. and *S. tobias* comb. nov.).

**Descriptive notes**

Antennae. 1.6 times as long as head and 1.65 as long as H in the male, and 1.35 and 1.3 times, respectively, in the female; antennomere 5 ca 1.6 as long as broad; antennomeres 2 and 5 subequal in length, ca 1.3 times as long as 3 and 4, and 1.5 times as long as 6.

Tarsus of mid-body legs. Ca 2.7 times as long as tibia and ca 3.7 times as long as apical claw. Mid-body legs 1.25 times as long as H in the the male and 0.7 times in the female.

Female sexual characters. Leg-pairs 1 and 2 visibly longer and thicker than following legs. Vulva (Fig. 11C) of nearly equal width in both the sagittal and the transverse planes, mostly symmetric; bursa with a narrow median cleft; each valve distally with a vertical row of 2–4 setae; operculum (op) proximally broad, distally abruptly narrowing, ending with a more or less straight apical margin, exceeding bursa by ca ⅛ of total height of vulva, disto-laterally with one vertical row of setae each side. Receptaculum seminis consisting of a very short and narrow, somewhat bent, median tube (mt) leading to a minute piriform ampulla (ma), and a slightly longer, mostly straight, lateral tube (lt) ending in a minute spherical ampulla (la).

**Distribution**

Known only from its type locality, the Čampari Pit on the island of Cres in Croatia (Fig. 13, red square).

**Remarks**

Strasser's (1938) description of *S. insularis* comb. nov. was based upon four females only. Due to the absence of male specimens, this species has remained enigmatic for 80 years, until Antić *et al.* (2018) described the

first male and, according to the gonopod structure, hypothesized this species could belong to *Stygiiulus* stat. nov. Here we follow that assumption, which is further supported by the vulval structure, and formally transfer *insularis* to the genus *Stygiiulus* stat. nov. However, this species is obviously different externally compared to other *Stygiiulus* stat. nov. members, and is characterized by a smaller body and proportionatelly shorter antennae, as well as by a more anterior position of the ozopores. And while these external differences (or some of them) may be connected with its currently unknown ecology rather than with its phylogenetic affinities, certain gonopod characters, viz., the aforementioned spoon-like shape of the mesomere and the robustness of the opisthomere, plus a ridge- rather than knob-like internal lobe of the promere leave some doubts about the exact systematic position of *insularis*. But since the general gonopod conformation in this species is much more similar to other *Stygiiulus* stat. nov. than to any other typhloiulinine/blind leptoiulinine genus, we have opted here to formally place this interesting taxon in the aforementioned genus. Nevertheless, we are aware that in the future this tiny species could find its place in another (new) genus.

The Čampari Pit is also the type locality of another julid species, the pachyiulinine *Chersoiulus ciliatus* Strasser, 1938. Both *S. insularis* comb. nov. and *C. ciliatus* are strict endemics of this pit and are listed as critically endangered species (CR) in the Red Book of the Croatian cave dwelling fauna (Ozimec *et al.* 2009).

## *Stygiiulus maximus* (Verhoeff, 1929) comb. nov.
Fig. 10D

*Mesoporoiulus maximu*s Verhoeff, 1929: 19–20, fig. 2.

*Typhloiulus* (*Stygiiulus*) *maximus* – Verhoeff 1930: 9, 12–13, figs 1–2. — Manfredi 1932: 81.
*Typhloiulus* (*Mesoporoiulus*) *maximus* – Pretner & Strasser 1931: 87.
*Typhloiulus maximus* var. *longicauda* Strasser, 1962: 59–60, fig. 71.
*Typhloiulus maximus* var. *maximus* – Strasser 1962: 59, fig. 72.
*Typhloiulus maximus* – Attems 1949: 145. — Strasser 1971a: 14. — Vagalinski *et al.* 2015: 342–343.

not *Typhloiulus tobias* – Attems 1927: 250–251, figs 352–354.

### Diagnosis
A species of *Stygiiulus* stat. nov. with normal mouthparts. Distinguishable from congeners by the combination of certain gonopodal characters (Fig. 10D), viz., a mostly straight pro- and mesomere, and an opisthomere with a faint and blunt posterior hump, a marginally broad (not tapering) and deeply serrated velum, and a solenomere with both the anterior and the posterior solenomeral branch being well developed and clearly discernible.

### Distribution
This species has the widest distribution of all representatives of the genus *Stygiiulus* stat. nov. Known from numerous caves, as well as epigean habitats, ranging from the Julian Alps in the east, across the southern parts of the Carnic Alps Range, through the Venetian Prealps, all the way to the Piave River in the west (Fig. 13, pink squares).

### Remark
Attems (1927: 250, 251, figs 352–354) gave a short description and drawings of what he thought was already described as *S. tobias* comb. nov. from Monte Cavallo (Lombardy). Just two/three years later, Verhoeff (1930) described another blind julid, *S. maximus* comb. nov., from a cave in the same area. What is evident from the gonopod drawings of both Attems and Verhoeff alone – that is that Attems' (1927) record actually refers to *S. maximus* comb. nov. – was already confirmed by Strasser (1962: 60) based on re-examination of the specimens from Monte Cavallo.

## *Stygiiulus montellensis* (Verhoeff, 1930) comb. nov.
Figs 7, 13

*Typhloiulus* (*Stygiiulus*) *montellensis* Verhoeff, 1930: 14–16, figs 4–5.

*Typhloiulus* (*Stygiiulus*) *montellensis* – Manfredi 1932: 81. — Strasser 1962: 57–58, figs 5, 11j, 66–67.
*Typhloiulus montellensis* – Wolf 1934–38: 516. — Vagalinski *et al.* 2015: 343.
*Typhloiulus montebellensis* (sic!) – Attems 1949: 145.
*Typhloiulus* (*Stygiiulus*) *montellensis montellensis* – Paoletti 1978: 108.
*Typhloiulus montellensis montellensis* – Minelli 1985: 10.

### Diagnosis

A species of *Stygiiulus* stat. nov. with normal mouthparts. Differs from its most similar congener, *S. rotundatus* comb. et stat. nov., by the distal part of mesomere (Fig. 7B, m in Fig. 7A) being clavate, ending with a broad, flat apex, vs the same being fronto-caudally compressed, ending with a rounded apex in the latter species; and by the vulval operculum being broader and with a smooth and gently concave apical margin, vs the same being relatively narrow, with an uneven, coarsed/undulating apical margin in *S. rotundatus* comb. et stat. nov.

### Material examined

ITALY • 3 ♂♂, 4 ♀♀; Veneto, province of Treviso, Susegana, Grotta [cave] Crede-a (2098 V/TV); 175 m a.s.l.; 20 Feb. 1993; E. Piva leg.; NHMD • 2 ♂♂, 1 ♀, 1 juv.; Veneto, province of Treviso, Massiccio del Grappa Mtn, Cavaso del Tomba, Speoncia [cave] del Diaol (1811 V/TV); 45°50'49" N, 11°54'26.4" E; 275 m a.s.l.; 17 Oct. 1999; E. Piva leg.; NHMD.

### Descrptive notes

Antennae. 1.85–2.2 times as long as head and 1.5–2.1 times as long as H in males, and 2–2.1 and 1.3–1.5 times, respectively, in females; antennomere 5 2–2.3 times as long as broad; antennomeres 2 and 3 subequal in length, 1.1–1.2 times as long as 4 and 5, and 1.2–1.4 times as long as 6. Tarsus of mid-body legs 2–2.3 times as long as tibia and 3–4 times as long as apical claw. Mid-body legs from equal to, to 1.4 times as long as, H in males, and 0.9–1.1 times in females.

Female sexual characters. Legs 1 and 2 slightly shorter but not thicker than following legs. Vulva (Fig. 7C) symmetric, somewhat compressed in the sagittal plane; bursa with a rather broad cleft, each valve distally with several setae in a vertical row; operculum (op) large, subquadrangular, with a slightly convex, smooth apical margin, exceeding bursa by ca ⅓ of total height of vulva, distally with several setae each side. Receptaculum seminis represented by a relatively long, narrow, slightly bent, mesal tube (mt) leading to a minute piriform ampulla (ma), and an even finer, shorter, twisted, lateral tube (lt) forming an ovoid ampulla (la) at bottom.

### Distribution

Known from several caves as well as epigean habitats in a small area on the southern side of the Venetian Prealps' foothill, north of Treviso. All but one record come from the right side of the Piave River (Fig. 13, yellow squares).

## *Stygiiulus rotundatus* (Strasser, 1962) comb. et stat. nov.
Figs 8–9, 13

*Typhloiulus* (*Stygiiulus*) *montellensis rotundatus* Strasser, 1962: 57–58, figs 68–69.

*Typhloiulus montellensis rotundatus* – Minelli 1985: 10. — Vagalinski *et al.* 2015: 343.

**Diagnosis**

A species of *Stygiiulus* stat. nov. with normal mouthparts. Differs from its most similar congener, *S. montellensis* comb. nov. by the distal part of mesomere being fronto-caudally compressed, ending with a rounded apex, vs the same being clavate, ending with a broad and flat apex in the latter species; and by the vulval operculum being relatively narrow, with an uneven, coarsed/undulating apical margin, vs the same being broader and with a smooth and gently concave apical margin in *S. montellensis* comb. nov.

**Material examined**

   **Lectotype** (designated here)
ITALY • ♂ 20-41-71 slide preparation; Veneto, province of Treviso, Refrontolo, Busa di Fave [Bus de le Fave Cave]; 7 May 1959; gonopods, flanges of pleurotergum 7; MHNG-ARTO-27001.
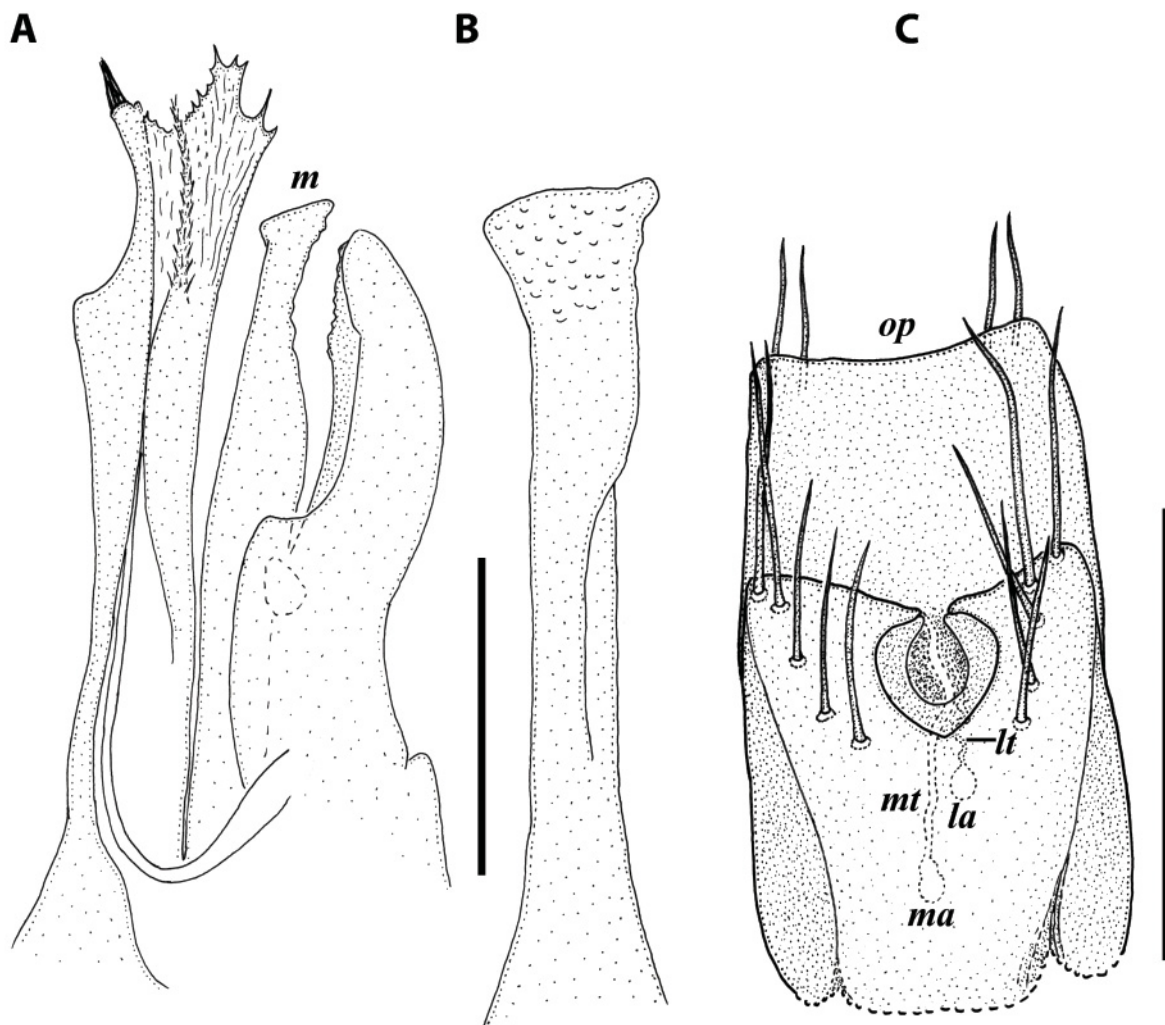


**Fig. 7.** *Stygiiulus montellensis* (Verhoeff, 1930) comb. nov., ♂ from Grotta [cave] Crede-a (NHMD). **A**. Right gonopods, mesal view. **B**. Right mesomere, oral view. **C**. Left vulva, caudal, slightly mesal view. Abbreviations: la = lateral ampulla; lt = lateral tube; m = mesomere; ma = median ampulla; mt = median tube; op = operculum. Scale bars: A–B = 0.2 mm; C = 0.3 mm.

**Paralectotypes**
ITALY • 1 ♂ 28-43-74 slide preparation; same collection data as for lectotype; gonopods, antenna, legs 1, 2, 3, 7, mouthparts, flanges of pleurotergum 7; MHNG-ARTO-27002 • 1 ♂ 19.5-41-63 slide preparation; same collection data as for lectotype; gonopods, flanges of pleurotergum 7; MHNG-ARTO-27003.

**Other material**
ITALY • 1 ♂; Veneto, province of Treviso, San Pietro di Feletto, Grotta [cave] di Foltran (1251 V/TV); 8 Aug. 1961; Paoletti leg.; specimen unbroken; MHNG • 1 ♂ 23-43-75 slide preparation; same collection data as for preceding; 8 Aug. 1971; gonopods, antenna, flanges of pleurotergum 7; MHNG-ARTO-27004 • 1 ♂ 17-38-61 slide preparation; same locality; date unknown; gonopods, antenna, flanges of pleurotergum 7; MHNG-ARTO-27005 • 1 ♂ 26-46-81 slide preparation; Veneto, province of Treviso, Farra di Soligo, Grotta [cave] di Collagù (1225 V/TV); 30 Oct. 1966; gonopods, antennae, gnathochilarium, legs 1 and 2 plus penis, flanges of pleurotergum 7; MHNG 901/5 • 2 ♂♂, 3 ♀♀; Veneto, province of Treviso, San Pietro di Feletto, La Bora Cave (1252 V/TV); 110 m a.s.l.; 9 Mar. 2008; D. Bianco and E. Piva leg.; H. Enghoff det. 2013; NHMD.

**Comment**

The original description of Strasser (1962) does not contain information on the number of type specimens and a holotype has not been designated. However, it can be inferred from text that the type locality is the cave Bus de le Fave near the village of Refrontolo, province of Treviso, and the material the description is based upon was collected on 7th May and 10th June 1959. The label data of three of the examined MHNG slides contain the same toponym and date. Since the position of the right gonopods in slide "♂ 20-41-71" is most similar to the aspect shown in Strasser's (1962: fig. 68) description, we here designate that same slide as lectotype, in order to stabilize the nomenclature of the species under Article 74.1 of the ICZN.

**Redescription**

Size and number of body rings. ♂♂ with BRF 42–49+1+T, l=17–28 mm, H = 1.3–1.4 mm; ♀ with BRF 50+0+T, L = 27.5–33.5 mm, H = 1.54–1.92 mm.

Colouration (Fig. 8). Mostly light grey, apparently further faded from the alcohol conservation, with a brownish transverse band at posterior parts of metazonae; head, telson and legs brown.

External structures. 2+2 supralabral setae (one ♀ with 5), spread in more or less equal distances from one another, and 12–16 labral setae. Antennae (Fig. 8B) 2–2.4 times as long as head and ca 1.5 as long as H in males, and ca 2 times and 1.3 times, respectively, in females; antennomere 5 2.5 times as long as broad; antennomeres 3–5 subequal in length, somewhat shorter than 2 and ca 1.3 times longer than 6.

Mouthparts. Of normal julid type. Labrum tridentate. Lingual lamellae each with 2–3 basal, 1 median and 1 distal seta in a longitudinal row. Promentum markedly elongated, separating the lamellae in about their proximal ½. Gnathochilarial stipites each with a group of several short setae medially, just under lingual lamellae.

Collum. Completely smooth. Prozonae smooth. Metazonae with well-developed striation only ventrally, dorsally and laterally with short and shallow striae; length of setae from 9% (in mid-body and hind body rings) to 25% (in anterior-most rings) of H.

Ozopores. Placed behind pro-metazonal suture at ca ⅖ (in more anterior rings) to almost ½ (in more posterior rings) of metazonal length measured from front to back. Tarsus of mid-body legs 1.9–2.2 times

as long as tibia and 2.7–3.6 times as long as apical claw. Mid-body legs 1–1.2 times as long as H in males, and ca 0.85 times in females.

TELSON (Fig. 8E). Epiproct stout, wedge-like, more or less straight, ending with a short and blunt hyaline tip directed completely distad or slightly dorsad, not reaching level of longest paraproctal setae. Hypoproct from narrowly rounded to blunt triangular, not protruding past rear contour of paraprocts in



**Fig. 8.** *Stygiiulus rotundatus* (Strasser, 1962) comb. et stat. nov., ♀ (A) and ♂ (B–E) from La Bora Cave (NHMD). **A**. Habitus, lateral view. **B**. Anterior part of body, lateral, slightly ventral view. **C**. Pleurotergum 7, lateral view. **D**. Mid-body rings, lateral view. **E**. Telson, lateral view. Scale bars: A = 1 mm; B–E = 0.5 mm.

both sexes, bearing 5–10 submarginal and a pair of median parabasal setae. Paraprocts moderately to densely covered with long setae, without distinct rows of shorter setae along caudal margins.

MALE SEXUAL CHARACTERS. Leg-pair 1 (9A) rather compact, three-segmented hooks oriented towards one another, with relatively small, apically microdentate/micropapillate tibial outgrowths, without tarsal remnants. Leg-pairs 2 and 3 somewhat ticker than following legs. Tibial adhesive pads well developed until about mid-body, first several leg-pairs with a less strongly pronounced postfemoral pad in addition. Pleurotergum 7 (Fig. 8C) with considerably expanded ventral margins forming broad and rounded lobes. Penis (Fig. 9B) long, in situ visible behind coxae 2, basally broad, abruptly narrowing until ⅓ of its length, then running parallel-sided, before barely widening distally, ending with short, diverging apical lobes bearing small, pointed, terminal lamellae turned completely laterad.

GONOPODS (Fig. 9C–D). In situ completely concealed in gonopodal sinus and between lobes of pleurotergum 7. Mesomere slightly exceeding promere, both being considerably shorter than opisthomere. Promere (p in Fig. 9C) slender oar-shaped, bent somewhat caudad, forming a narrowly rounded meso-apical corner; caudal face distally not too densely microsquamose/macropapillate, basally with a strongly pronounced, ridge-like internal lobe and a smaller, leaf-like external lobe. Mesomere (Fig 9D, m in Fig. 9C) narrow spade-like, with a flattened or broadly rounded apex directed distad; caudal face distally deeply concave and sparsely micropapillate. Opisthomere (Fig. 9C) relatively slender, with a strongly pronounced posterior hump (ph); velum (v) very broad, with a smooth frontal and a deeply serrated apical margin; solenomere with a rather stout, apically ciliate posterior branch (pb) and a very fine and pointed anterior branch (ab), shortly ciliate all along.

FEMALE SEXUAL CHARACTERS. Leg-pairs 1 and 2 somewhat thicker and slightly longer than following legs. Vulva (Fig. 9E) mostly symmetric: only mesal valve of bursa somewhat broader than lateral one; bursa slightly compressed on sides, with a relatively broad and shallow median cleft; each valve distally with one vertical row of several setae, side sclerites each with a pair of setae; operculum (op) somewhat narrowing distad, with an uneven, undulating apical margin exceeding bursa by ca ⅓ of total height of vulva, distally with a group of several setae each side. Receptaculum seminis consisting of two very short and narrow, somewhat folded tubes: a mesal (mt) and a lateral one (lt), both ending in two ovoid ampullae, the lateral one (la) being considerably larger than the mesal one (ma).

## Distribution

Known from several caves in a small area on the southern side of the Venetian Prealps' foothill, north of Treviso. All records come from the left side of the Piave River (Fig. 13, blue squares).

*Stygiiulus seewaldi* (Strasser, 1967) comb. nov.
Figs 10E, 13

*Alpityphlus seewaldi* Strasser, 1967: 146–150, figs 4–9.

*Typhloiulus seewaldi* – Fritsch 1998: 149–150, 16. — Vagalinski *et al.* 2015: 346.

## Diagnosis

A species of *Stygiiulus* stat. nov. with normal mouthparts. Easily distinguishable from congeners by its specific gonopod conformation (Fig. 10E) including a narrow, pointed velum considerably exceeding the solenomere and bearing a small, pointed, distal outgrowth (do) (the latter structure present also in *S. insularis* comb. nov. and in (some specimens of) *S. tobias* comb. nov.), in combination with the complete absence of a posterior hump on the opisthomere. Also outstanding by the small and rounded internal lobe of the promere, which is positioned close to promeral base.
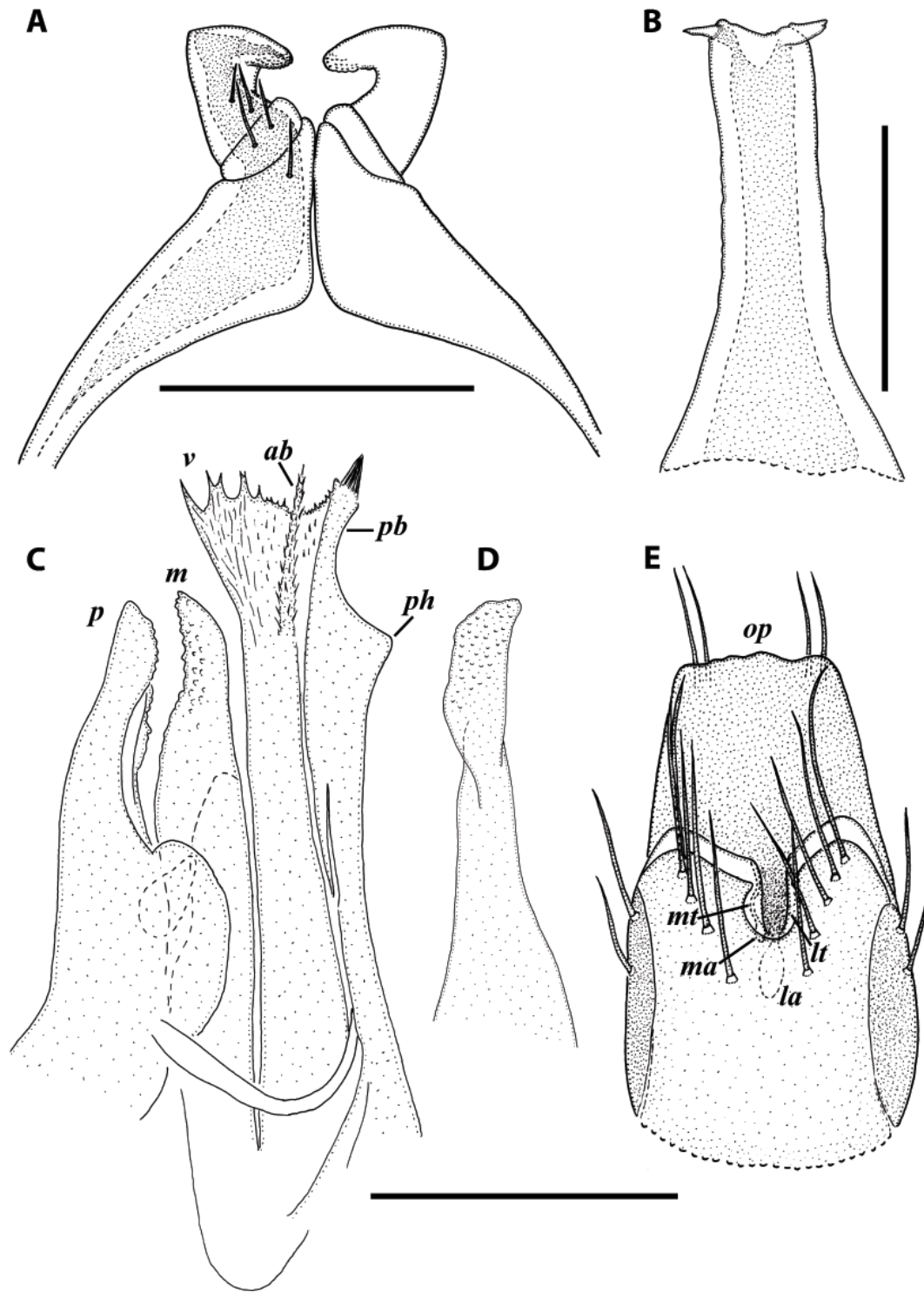
**Fig. 9.** *Stygiiulus rotundatus* (Strasser, 1962) comb. et stat. nov., paralectotype ♂ (A) (MHNG), ♂ from Grotta [cave] di Collagù (B) (MHNG) and ♂ (C–D) and ♀ (E) from La Bora Cave (NHMD). **A**. Leg-pair 1, oral view. **B**. Penis, oral/caudal view. **C**. Right gonopods, mesal view (inverted). **D**. Left mesomere, oral view. **E**. Left vulva, caudal, somewhat mesal view. Abbreviations: ab = anterior branch of solenomere; la = lateral ampulla; lt = lateral tube; m = mesomere; ma = median ampulla; mt = median tube; op = operculum; p = promere; pb = posterior branch of solenomere; ph = posterior hump; v = velum. Scale bars: A = 0.4 mm; B = 0.2 mm; C–E = 0.3 mm.

**Distribution**

Germany, Upper Bavaria, Berchtesgadener Land, Untersberg Massif, Cave Hollerloch (the type locality); Austria, Dachstein Mts, tunnel Warmwasserstollen near Lake Hallstatt and Obere Brangrabenhöhle Cave (Fritsch 1998) (Fig. 13, orange squares).

**Remark**

Fritsch (1998) listed this species under the genus *Typhloiulus*, relying on J.-P. Mauriès' opinion expressed in a letter to him. According to Mauriès who studied material of *seewaldi*, the erection of the genus *Alpityphlus* by Strasser (1967) was unfounded, the species being a member of *Stygiiulus*, at that time a subgenus of *Typhloiulus*. A similar view was expressed by Antić *et al.* (2017, 2018), but without a formal transfer to *Stygiiulus*. Based on the detailed original drawings we fully agree on that view, hence the new name combination is formalized here.

<div align="center">

***Stygiiulus tobias*** (Berlese, 1886) comb. nov.
Figs 10F, 11D, 13

</div>

*Julus* (*Typhloiulus*) *Tobias* Berlese, 1886: 98–99, tab. XIII, figs 20–23.

*Typhloiulus* (*Iulus, Mesoporoiulus*) *Tobia* (*tobias*) – Manfredi 1932: 81.
*Typhloiulus tobias* – Wolf 1934–38: 516. — Vagalinski *et al.* 2015: 345–346.
*Typhloiulis* (sic!) *tobias* – Boldori 1936: 113.
*Typhloiulus Tobia* (sic!) – Boldori 1937: 11.
*Typhloiulus* (*Mesoporoiulus*) *tobias* – Verhoeff 1930: 16–17, fig. 3. — Strasser 1962: 38–39, figs 11f, 45–46.
*Typhloiulus Tobias* – Conci 1951: 44.
*Typhloiulus tobias* var. *fuscus* Manfredi, 1953a: 139.
? *Typhloiulus tobias pygmaeus* Manfredi, 1953b: 100.
*Typhloiulus tobias fuscus* – Manfredi 1953b: 101.

**Diagnosis**

A species of *Stygiiulus* stat. nov. with normal mouthparts. Clearly distinguishable from congeners by the very distinctive structure of the opisthomere (Fig. 10F) including a right- to acute-angled posterior hump pointing distad, a large, (sometimes) bipartite velum (with a posteriorly positioned distal outgrowth (do), this being much less prominent than in *S. insularis* comb. nov. and *S. seewaldi* comb. nov.), with the main part being mostly smooth (barely serrated), and a solenomere distally forming a stout anterior and a much more slender posterior branch, both apically finely ciliate; some specimens with a minute third thumb-like branch basally to the posterior branch. In addition, this species (except for its dubious subspecies *T. t. pygmaeus*, see below) differs from all other *Stygiiulus* stat. nov. species by the presence of a very long and upwards curved epiproct.

**Material examined**

ITALY • 2 ♂♂, 1 ♀; Veneto, Altopiano dei Sette Comuni, Vastagna (VI), Grotta [cave] del Subiolo (135 V/VI); 169 m a.s.l.; 4 Mar. 1990; G. Peretto and E. Piva leg.; H. Enghoff det. 2013; NHMD.

**Descriptive notes**

ANTENNAE. 2.2–2.4 times as long as head and 1.65–1.7 as long as H in males, and 1.9–2 and 1.3–1.4 times, respectively, in females; antennomere 5 2.6–2.9 times as long as broad; antennomeres 2, 3 and 5 subequal in length, slightly longer than 4, and 1.4–1.5 times as long as 6.
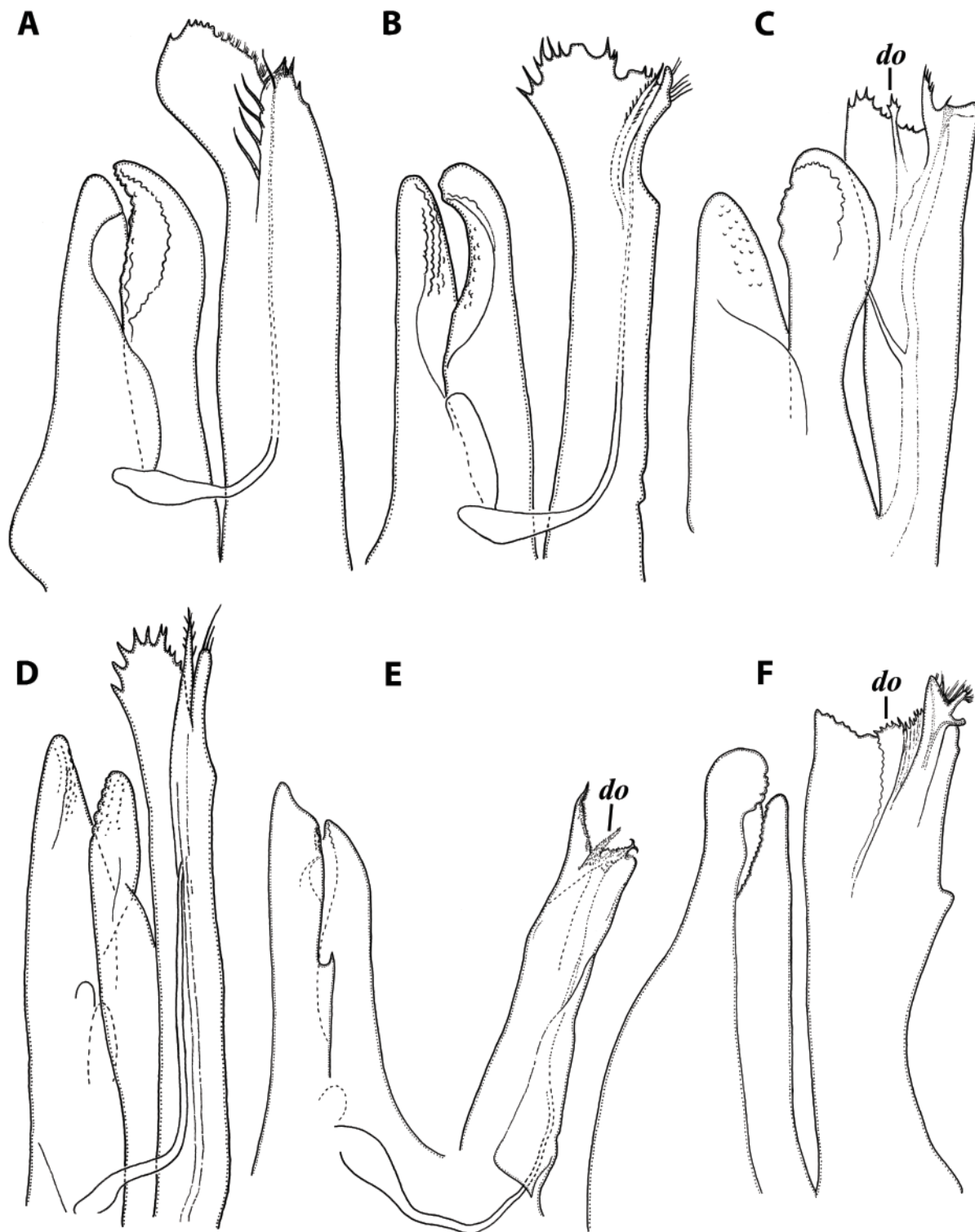
**Fig. 10.** Left gonopods of species of *Stygiiulus* stat. nov., mesal views. **A**. *S. ausugi* (Manfredi, 1953) comb. nov., topotype ♂ (NHMD). **B**. *S. illyricus* (Verhoeff, 1929) comb. nov., redrawn from Verhoeff (1929). **C**. *S. insularis* (Strasser, 1938) comb. nov., redrawn from Antić *et al.* (2018). **D**. *S. maximus* (Verhoeff, 1929) comb. nov., redrawn from Verhoeff (1930). **E**. *S. seewaldi* (Strasser, 1967) comb. nov., redrawn and modified from Strasser (1967). **F**. *S. tobias* (Berlese, 1886) comb. nov., ♂ from Grotta [Cave] del Subiolo (NHMD). Abbreviations: do = distal outgrowth of velum. Drawn not to scale.

Tᴀʀsᴜs ᴏꜰ ᴍɪᴅ-ʙᴏᴅʏ ʟᴇɢs. 1.8–1.9 times as long as tibia and 2.8–4.3 times as long as apical claw. Mid-body legs ca 1.25 times as long as H in males, and equal in length in females.

Fᴇᴍᴀʟᴇ sᴇxᴜᴀʟ ᴄʜᴀʀᴀᴄᴛᴇʀs. Leg-pairs 1 and 2 considerably thicker and shorter than following legs. Vulva (Fig. 11D) nearly symmetric; bursa slightly compressed in the sagittal plane; each valve distally with one vertical row of several setae; a similar row present on each side sclerite; operculum (op) very thick, subconical, i.e., tapering to a distinct blunt apex, exceeding bursa by ca ⅕ of total height of vulva, distally with a dense bunch of setae each side. Receptaculum seminis consisting of two long and narrow, closely adjacent tubes of equal length – a twisted lateral one (lt) leading to a small piriform ampulla (la), and a mostly straight mesal one (mt) ending in a somewhat larger ovoid ampulla (ma).

## Distribution

Known from numerous caves and one epigean locality in the central Venetian Prealps, as well as from several caves in Monti Lessini (extreme south of the Venetian Prealps). Also known from two caves on the southern slopes of Dolomiti (Fig. 13, white squares).

## Remarks

In the past, this taxon was treated as a member of *Mesoporoiulus* Verhoeff, 1905. Vagalinski *et al.* (2015) hypothesized it could be a somewhat deviating member of *Stygiiulus*. Here we fully confirm this assumption and formally transfer *tobias* to the genus *Stygiiulus*.

The subspecies *S. t. pygmaeus* (Manfredi, 1953) comb. nov. has already caught the attention of Strasser (1962). On page 60 of the latter work, the author commented on the significant size difference between *pygmaeus* (23 mm of length) and the typical *tobias* (50–67 mm of length), and also emphasized the apparent confusion of Manfredi (1953b) regarding the gonopods of her newly described subspecies, which she stated to match well (along with most other characters) to the descriptions of *tobias* given by both Attems (1927) and Verhoeff (1930). In fact, what Attems (1927) recorded and depicted was *S. maximus* comb. nov. (see Remark under the latter species). The short and straight epiproct in *pygmaeus* (as originally described), unlike the long and upwards curved process in the typical form, adds further uncertainty about the identity of Manfredi's subspecies. We agree with Strasser's (1962) opinion that *pygmaeus* most likely represents a separate species. However, its status can only be resolved after examination of type or topotype material.

The gonopods of the two presently examined males from Grotta del Subiolo differ from Verhoeff's (1930) drawings based on material from Grotta Parolini near Vastagna and/or "Bus de la Bela" near San Donato, prov. Belluno, by a blunt and finely serrated, rather than tapering and ciliate, posterior part of velum, and by an apically tri- instead of bipartite solenomere.

In Grotta della Bigonda, this species lives in sympatry with *S. ausugi* comb. nov.

### *Key to species of* Stygiiulus *stat. nov. based on gonopodal and external somatic characters*
1. Mouthparts modified for a hydrophilous lifestyle ...................................................................... 2
– Mouthparts normal .................................................................................................................... 4

2. Opisthomere completely devoid of a posterior hump and with an anteriorly arched, apically finely fringed velum; both the anterior and the posterior branch of solenomere vestgial .........................
.........................................................................................***S. ausugi*** (Manfredi, 1953) comb. nov.
– Opisthomere with a distinct posterior hump and a rather narrow, marginally deeply serrated velum; solenomere with a well-developed, slender posterior branch ........................................................ 3

57

3. Promere with the apex turned frontad; velum with serrations on both anterior and posterior margins ...................................................................................................................................... ...........................................................................***S. fimbriatus*** (Strasser, 1971) comb. et stat. nov.
– Promere distally somewhat bent caudad; velum with serrations only on anterior margin ................. ...........................................................................***S. gentianae*** (Strasser, 1971) comb. et stat. nov.

4. Opisthomere completely devoid of a posterior hump ................................................................ 5
– Opisthomere with a posterior hump ......................................................................................... 6

5. Opisthomere with slender, pointed velum, considerably outreaching solenomere; ozopores set at considerable distance behind pro-metazonal suture ............ ***S. seewaldi*** (Strasser, 1967) comb. nov.
– Opisthomere with a rather broad velum being subequal to solenomere; ozopores set just next to, or on, pro-metazonal suture .................................................***S. insularis*** (Strasser, 1938) comb. nov.

6. Mesomere bent strongly frontad; velum clearly outreaching solenomere; anterior branch of solenomere vestigial, completely fused to velum ................***S. illyricus*** (Verhoeff, 1929) comb. nov.
– Mesomere more or less straight; velum shorter than, or subequal to, solenomere; anterior branch of solenomere clearly discernible ................................................................................................. 7

7. Velum bipartite, the larger anterior part with mostly smooth margins, the posterior one serrated or ciliate; solenomere apically with a rather robust anterior branch and one or two finer posterior branches ....................................................................................***S. tobias*** (Berlese, 1886) comb. nov.
– Velum unipartite, marginally deeply serrated; anterior and posterior branch of solenomere of similar proportions ............................................................................................................................. 8

8. Promere straight, considerably outreaching mesomere; large species (adults 50–70 cm long) ......... ..............................................................................................***S. maximus*** (Verhoeff, 1929) comb. nov.
– Promere bent caudad, slightly shorter than mesomere; smaller species (adults 16–35 mm long) ... 9

9. Distal part of mesomere clavate, with a broad and flat apex ............................................................. ................................................................................. ***S. montellensis*** (Verhoeff, 1930) comb. nov.
– Distal part of mesomere fronto-caudally compressed, with a narrow, rounded apex ........................ ...........................................................................***S. rotundatus*** (Strasser, 1962) comb. et stat. nov.

### *Additional material of* Leptoiulini/Julini *and* "Typhloiulini" *examined*

Vulvae in Julidae can provide valuable taxonomic characters and, in some cases, even carry phylogenetic signals, as suggested by, e.g., Vagalinski & Lazányi (2018). However, information about vulvae is typically missing from original descriptions including from those referring to julinine (in a broad sense) taxa. Here, in addition to species of *Stygiiulus* stat. nov., we have observed the vulvae in the type species of *Leptoiulus*, *Typhloiulus* s. str., the subgenus *Inversotyphlus* of *Typhloiulus*, and a species of *Serboiulus* in an attempt to find further clues for the systematic position of the study genus, as well as to bring some clarity to the poorly delimited and (partly) overlapping tribes Julini, Leptoiulini and Typhloiulini. Although drawing of any firm conclusions seems to be impossible at this point, certain patterns in the observed vulval structures can be recognized.

*Leptoiulus* **cf.** *trilineatus* (C.L. Koch, 1847)
Fig. 11E

**Material examined**

BULGARIA • 1 ♀; Belasitsa Mtn, *Castanea sativa* forest; 3–10 May 2010; B. Georgiev and H. Delchev leg.; pitfall trap; IBER.

**Descriptive notes**

Vulva (Fig. 11E). Vulva of nearly equal width in both the sagittal and the transverse planes, mostly symmetric; bursa with a deep and rather broad median cleft; evenly setose throughout, without distinct rows; operculum (op) with markedly concave apical margin, exceeding bursa by ca ¼ of total height of vulva, distally with several long setae. Receptaculum seminis consisting of a very long and thin, somewhat bent, mesal tube (mt) ending in a medium-sized, piriform ampula (ma), and a somewhat ticker and mostly straight lateral tube (lt) forming a large, strongly elongate ampulla (la) at bottom.

*Serboiulus spelaeophilus* Gulička, 1967
Fig. 11F

**Material examined**

BULGARIA • 1 ♀ topotype; Belogradchik District, Dolni Lom, Vodni Pech Cave; 25 Feb. 2000; B. Petrov leg.; guano-clay; NMNHS.

**Descriptive notes**

Vulva (Fig. 11F). Strongly compressed in the sagittal plane, mostly symmetric; bursa with a shallow and very narrow median cleft; each valve distolaterally with a few setae; operculum (op) with a deeply concave apical margin, just slightly higher than bursa, distally bearing long setae. Receptaculum seminis consisting of two similarly narrow and twisted tubes – a lateral (lt) and a mesal one (mt), each forming an ovoid ampulla at bottom, the lateral one (la) being somewhat larger than the mesal one (ma).

*Typhloiulus* (*Inversotyphlus*) *lobifer* Attems, 1951
Fig. 11G

**Material examined**

CROATIA • 1 ♀; island of Brač, Škrip, Minjera-Bauxite Mine; 11 Sep. 2015; D. Antić leg.; D. Antić ded. 2021; IBER.

**Descriptive notes**

Vulva (Fig. 11G). Slender, of nearly equal width in both the sagittal and the transverse planes, slightly asymmetric: lateral valve being somewhat higher than mesal one, as well as more densely setose; bursa with a broad and relatively deep median cleft; several, mostly vertically arranged setae on each valve; operculum (op) with narrowly rounded apical margin, exceeding bursa by ca ⅔ of total height of vulva, distally with a dense submarginal row of setae each side. Receptaculum seminis consisting of a long, thin and twisted mesal tube (mt) ending in a lemon-shaped ampula (ma), and a somewhat ticker, nearly straight, lateral tube (lt), not forming an ampula at bottom.

*Typhloiulus* (*Typhloiulus*) *strictus* (Latzel, 1882)
Fig. 11H

**Material examined**

BULGARIA • 1 ♀; Lovech District, Kunino, at the entrance of Samuilitsa 2 Cave; 30 Oct. 2020; B. Vagalinski leg.; under large stones with moss; IBER.

**Descriptive notes**

Vulva (Fig. 11H). Slender, of nearly equal width in both the sagittal and the transverse planes, mostly symmetric; bursa with a rather broad and deep median cleft; each valve with up to ten, mostly vertically arranged setae; several setae in a vertical row on each side sclerite; operculum (op) with broadly rounded,

somewhat coarsed, apical margin, exceeding bursa by nearly ⅓ of total height of vulva, distally with a few long setae each side. Receptaculum seminis consisting of a narrow, partly twisted posterior tube (pt) ending in a medium-sized piriform/lemon-shaped ampula (pa), and a much broader, mostly straight anterior tube (at), not forming an ampulla at bottom.

### *Phylogeny*

A total of 37 taxa (1 outgroup) were included in the analyses. The 28S rRNA dataset included 499 bp and 20 gaps. Of these there were 61 variable and 41 parsimony-informative sites. The 16S rRNA dataset included 488 bp with 69 gaps, 350 variable and 295 parsimony-informative sites. Maximum likelihood and Bayesian inference analyses showed similar topology, but ML did not obtain strong bootstrap support. The two matrices, analyzed separately, resulted in similar topology but did not resolve deeper nodes (trees not shown). The best resolution was shown by the BI tree, inferred from the concatenated 16S rRNA + 28S rRNA dataset (Fig. 12).

Our analyses reproduced the results of previous studies and show agreement with published trees (see Enghoff *et al.* 2011, 2013; Makarov *et al.* 2017). The deep nodes did not receive strong support, although some monophyletic clades were strongly supported. These include the tribes Brachyiulini and Pachyiulini, as well as the clade *Leucogeorgia* + (*Pteridoiulus* + *Heteroiulus*) (see Enghoff *et al.* 2013). Members of the dubious tribe Typhloiulini formed a strongly supported monophyletic clade with the following topology: *Rhodopotyphlus mitovi* + ((*Typhloiulus orpheus* + (*T. lobifer* + *T. gracilis*)) + (*T. bureschi* + *T. georgievi* + (*T. nevoi* + (*Serboiulus deelemani* + *Serboiulus lucifugus*)))). The newly represented species *Stygiiulus fimbriatus* comb. et stat. nov. grouped with *Xestoiulus imbecillus* (Latzel, 1884), the two forming a sister clade to the monophyletic (julinine/leptoiulinine) group: *Ophyiulus pilosus* + (*Pacifiiulus amurensis* + (*Leptoiulus trilineatus* + (*Leptoiulus proximus* + *Julus scandinavius*))).

## Discussion

**The systematic position of *Stygiiulus* stat. nov. and the relations between Leptoiulini and Typhloiulini**

Due to their outstanding morphology, species of *Stygiiulus* stat. nov. have been long recognized as a distinct group within the genus *Typhloiulus*, and together with *Typhloiulus* s. str. are arguably its best defined subgenera (Vagalinski *et al.* 2015). Apart from the slender opisthomere lacking an intermediate lamella and having a large velum and (usually) an apically bifid solenomere, a number of non-gonopodal features, like the penial shape, the upturned or straight rather than downturned epiproct, and the position of the ozopores considerably behind the pro-metazonal suture (in most species) all suggest that *Stygiiulus* stat. nov. is only distantly related to the nominate subgenus. A possible separate generic status of *Stygiiulus* stat. nov. has already been considered by Vagalinski *et al.* (2015) and Antić *et al.* (2018), although a formal status change was not proposed in any of the two papers.

There are also other subgenera or distinct species/species groups within *Typhloiulus* that differ significantly from the nominate subgenus, thus questioning the monophyly of the former. Such are the subgenera *Spelaeoblaniulus* Ceuca, 1956 and *Inversotyphlus* Strasser, 1962 (as revised by Antić *et al.* 2018), or the aberrant species *T. longipes* Strasser, 1973 and *T. parvulus* Antić & Dražina, 2018. The molecular-based phylogeny of Typhloiulini or blind Leptoiulini/Julini in Makarov *et al.* (2017), despite dealing with a limited number of taxa, clearly indicates that *Typhloiulus* is a poly- or paraphyletic genus in its current composition, as species of *T.* s. str. (not all of the analyzed) appear in one clade together with species of the genus *Serboiulus* Strasser, 1962, while *T. lobifer* and *T. gracilis* [listed as *Typhloiulus* aff. *lobifer*] (both belonging to the subgenus *Inversotyphlus*) form a separate clade. *Serboiulus*, on the other hand, is morphologically highly distinct, making the paraphyly of *Typhloiulus* the less plausible possibility than the polyphyly.
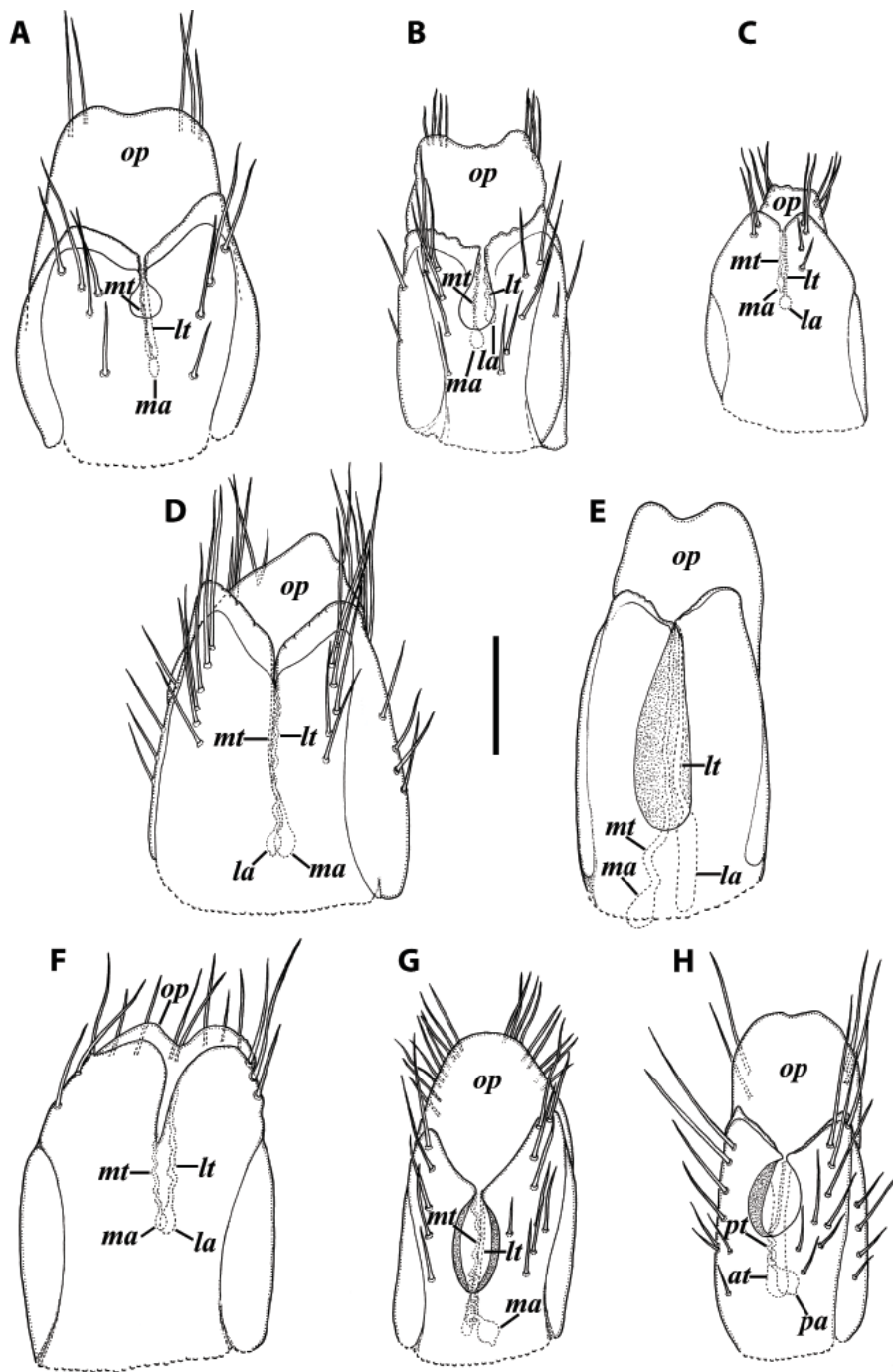
**Fig. 11.** Left vulvae of species of *Stygiiulus* stat. nov. (A–D) and representatives of (other) Julini/ Leptoiulini (E) and Typhloiulini/blind Julini/Leptoiulini in caudal, somewhat mesal views. **A**. *S. ausugi* (Manfredi, 1953) comb. nov., ♀ from Grotta [Cave] del Calgeron (NHMD). **B**. *S. illyricus* (Verhoef, 1929) comb. nov., ♀ from Rabakova Cave (IZB). **C**. *S. insularis* (Strasser, 1938) comb. nov., topotype ♀ (CBSS). **D**. S. *tobias* (Berlese, 1886) comb. nov., ♀ from Grotta [Cave] del Subiolo (NHMD). **E**. *Leptoiulus* cf. *trilineatus* (C.L. Koch, 1847), ♀ from Belasitsa Mtn, Bulgaria. **F**. *Serboiulus spelaeophilus* Gulička, 1967, ♀ from Vodni Pech Cave (NMNHS). **G**. *Typhloiulus* (*Inversotyphlus*) *lobifer* Attems, 1951, ♀ from Minjera-Bauxite Mine (IBER). **H**. *Typhloiulus* (s. str.) *strictus* (Latzel, 1882), ♀ from Kunino (IBER). Abbreviations: at = anterior tube; la = lateral ampulla; lt = lateral tube; ma = median ampulla; mt = median tube; op = operculum; pa = posterior ampulla; pt = posterior tube. Scale bar = 0.2 mm.

Interestingly, according to the currently obtained molecular data of *Stygiiulus fimbriatus* comb. et stat. nov., the species is not only excluded from *Typhloiulus*, but is also placed outside the 'Typhloiulini' (= *Typhloiulus* s. str. plus closely related sub/genera), forming a relatively well-supported clade with *Xestoiulus imbecillus* (Latzel, 1884), the type species of the genus (Fig. 12). Such grouping may initially seem surprising, as *Xestoiulus* Verhoeff, 1893 is traditionally considered as closely related to *Leptoiulus* Verhoeff, 1894, both genera being represented by numerous species, of which all are more or less well pigmented and with ommatidia, thus nothing to do with the strongly troglomorphic appearance of *Stygiiulus* stat. nov. However, careful comparison between the posterior gonopods of *X. imbecillus* and *S. fimbriatus* comb. et stat. nov. reveals a definite structural similarity. Both species are characterized by an apically bifid solenomere, a large velum, and a weakly developed (in *X. imbecillus*) or absent/ vestigial (in *S. fimbriatus* comb. et stat. nov.) phylacum. Furthermore, the very characteristic, pointed, distal outgrowth of the velum, although absent in *S. fimbriatus* comb. et stat. nov., is present (in a more or less similar shape) in *Stygiiulus insularis* comb. nov. and *S. seewaldi* comb. nov., as well as (as a less
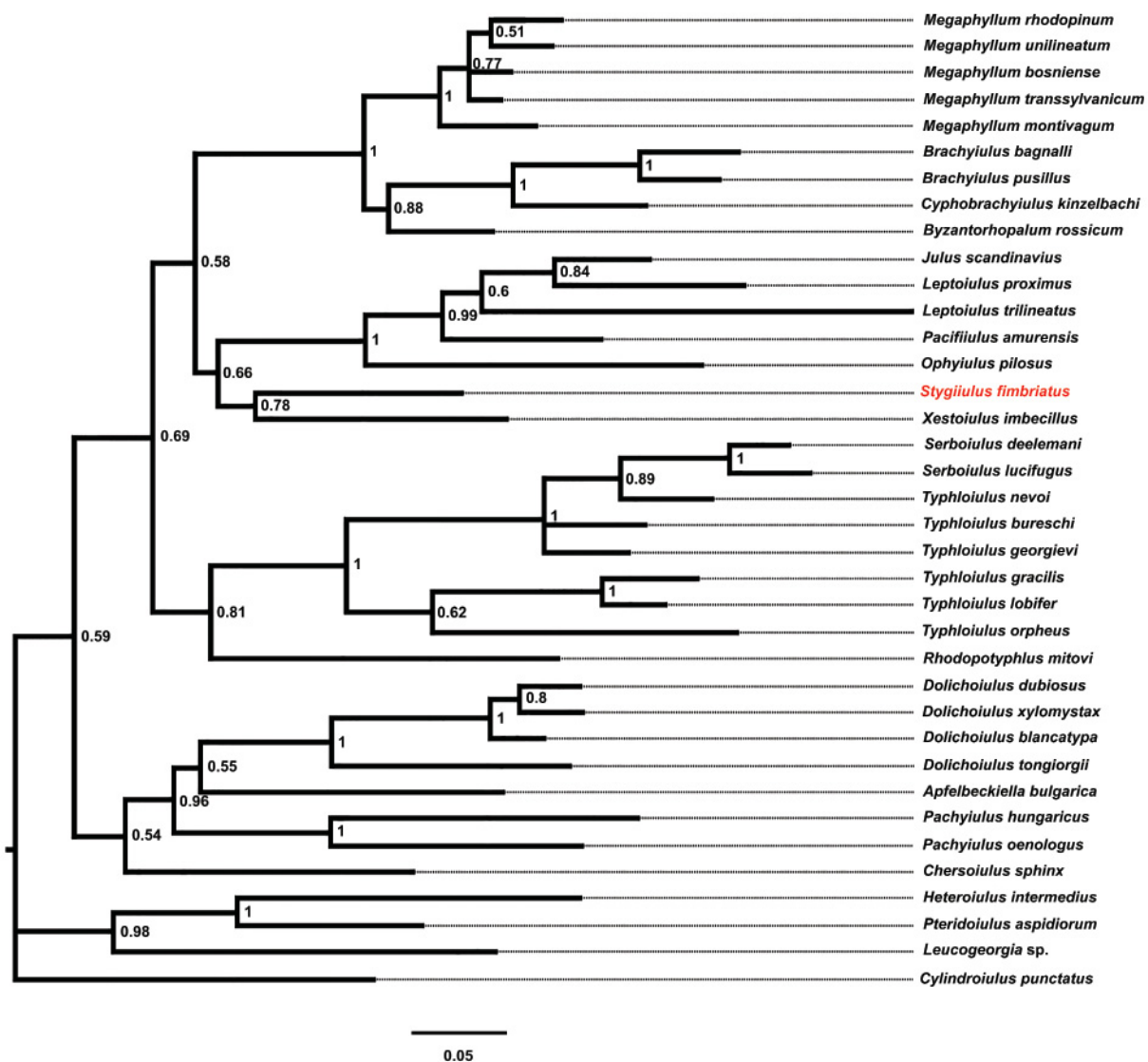


**Fig. 12.** Bayesian inference tree based on concatenated 16S rRNA+28S rRNA dataset from Enghoff *et al.* (2013) and Makarov *et al.* (2017). The single species with newly obtained sequences is shown in red.

conspicuous lamella) in *S. tobias* comb. nov. There is thus little doubt that *Stygiiulus* stat. nov. does not belong to 'Typhloiulini', but presents a separate evolutionary lineage that has adapted to subterranean life independently.

While the two newly obtained gene sequences (16S and 28S rRNA) of *Stygiiulus fimbriatus* comb. et stat. nov. confirm the separate genus status of *Stygiiulus* stat. nov., they raise more questions regarding the taxonomic compositions of the tribes Leptoiulini/Julini and Typhloiulini and the delimitations between the two/three groups. The only reliable morphological character to distinguish between Leptoiulini and Typhloiulini may be the presence vs absence of phylacum on the opisthomere, respectively (if the posterior hump in *Stygiiulus* stat. nov. is indeed a vestigial phylacum). Similarities between the two tribes, on the other hand, are numerous and refer to both gonopodal (promere usually with an internal and an external lobe, and with a distally microdentate/squamose caudal face, with the mesomere having a similarly textured frontodistal part; opisthomere with a velum, often with one or several basal spines at flagellum channel, and never with a basolateral lobe) and external somatic (body and appendages more or less slender, occipital setae present, male mandibular stipites not expanded, metazonal setae present, ozopores placed at some distance behind the suture (with very few exceptions), epiproct well-developed), as well as vulval (compare Fig. 11E to Fig. 11G or H) characters. The remarkably similar penial shape in species of *Leptoiulus*, *Ophyiulus* Berlese, 1884, *Typhloiulus*, and *Serboiulus* (look in Enghoff 1996) add more support to the concept of one large tribe including *Leptoiulus* plus *Typhloiulus* and their related genera. The genus *Julus* Linnaeus, 1758 on the other hand, despite sharing certain similarities with Lepto- and Typhloiulini, is morphologically unique among Julidae with the combination of a very thick gonopodal flagellum, knob-like first pair of male legs, and male coxa 2 with 1–3 processes (Evsyukov *et al.* 2018).
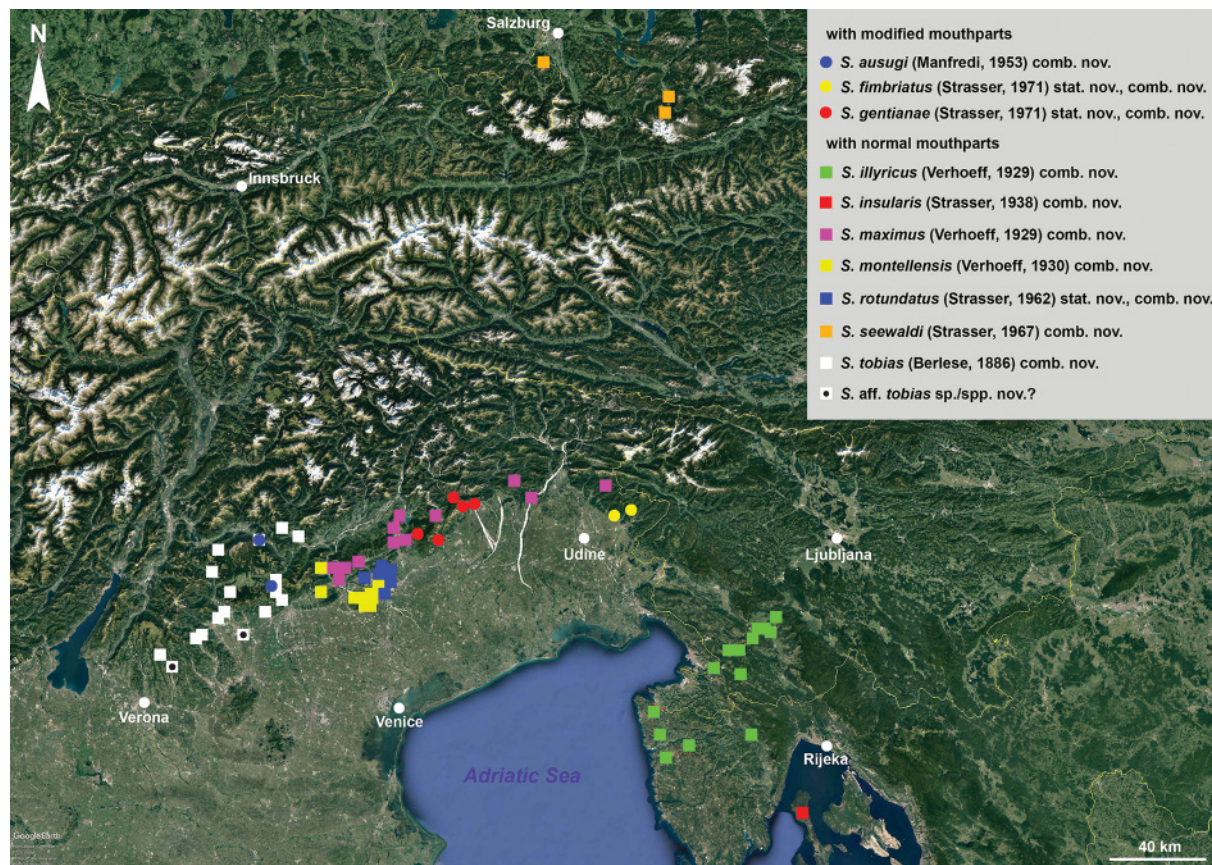


**Fig. 13.** General distribution of the species of the genus *Stygiiulus* stat. nov.

The current molecular evidence, however, points to the existence of two distinct tribes: tribe Julini including *Julus* and several 'leptoiulinine' genera (both with or without ommatidia), and Typhloiulini encompassing *Typhloiulus* and *Serboiulus*. Surprisingly, the two tribes do not even appear to be closely related on most phylogenetic reconstructions: on the single most-parsimonious tree in Enghoff *et al.* (2013) the only analyzed *Typhloiulus* species, *T. orpheus* Vagalinski, Stoev & Enghoff, 2015 [listed as *Typhloiulus* sp. nov.], appears far from Julini, in a common clade with members of Calyptophyllini, Catamicrophyllini and Pachyiulini; while in Makarov *et al.* (2017) *Typhloiulus* and *Serboiulus* appear either in a separate basal branch of a large clade including several julid tribes (on the ML-tree) or in one of six branches of an even larger, unresolved clade (on the BI-tree). Our phylogenetic analysis also does not suggest direct common ancestry of Julini and Typhloiulini (Fig. 12). It should be emphasized that *Rhodopotyphlus mitovi* Vagalinski, 2021 appears as sister group to the typhloiulinine, but not to the julinine/leptoiulinine members included. Considering the supposedly primitive gonopodal conformation of *R. mitovi* (see Vagalinski 2021), its position on the tree indeed implies a division between Julini and Typhloiulini that dates back from the early stages of the evolution of Julidae.

Anyhow, we should bear in mind that the current julid phylogeny is very preliminary, as the number of analyzed taxa is still rather low, and it is based on only two gene fragments: 16S and 28S rRNA. Furthermore, the 28S rRNA fragment gives a rather poor resolution at the genus and tribal levels due to its very high conservatism. It is notable for example that the 28S sequences of *Julus scandinavius* (Latzel, 1884) and *Leptoiulus proximus* (Nemec, 1896) are completely identical. The inclusion of more gene sequences (e.g., COI, 12S rRNA, or ND2) is likely to lead to significant rearrangements of the clades, and perhaps to a more logical (from a morphological aspect) solution for *Julus*, *Leptoiulus*, *Typhloiulus* and their related genera.

### 'Hydrophilous' mouthparts in *Stygiiulus* stat. nov.

As elaborated above, the genus *Stygiiulus* stat. nov. includes blind and, mostly, depigmented julids. Of the ten species currently recognized in the genus, six or seven are confined exclusively to caves, while three or four are known both from caves and epigean habitats. Of those troglobionts, three, viz., *S. ausugi* comb. nov., *S. fimbriatus* comb. et stat. nov., and *S. gentianae* comb. et stat. nov. are characterized by modified mouthparts, elongated head, shorter body, long legs and large tarsal claws, all connected with a presumed hydrophilous way of life and filtering diet. Modifications in hydrophilous cave julids were recently elaborated by Antić & Reip (2020). The proportionately shorter body, elongated legs and strong tarsal claws undoubtedly enable these animals to occasionally submerge in cave water bodies, spend time on their surface, or live on vertical wet walls. On the other hand, the elongated head, the reduction of the labral teeth, as well as the hypertrophy of the pectinate lamellae combined with the reduction of the biting parts of mandibles present adaptations for filtering diet in such habitats (see also Enghoff 1985; Antić *et al.* 2017; Antić & Reip 2020).

Here, we would like to highlight some intraspecific and/or intrapopulational variability of mouthpart modifications in these three hydrophilous species of *Stygiiulus*. One of the most obvious mouthpart modification in hydrophilous julids is the complete absence of the three characteristic labral teeth seen in most family members. However, it was already observed by Antić & Reip (2020) that within two hydrophilous species of *Leucogeorgia* Verhoeff, 1930, besides specimens with edentate labrum, there were such possessing three minute, reduced, median labral teeth (see Antić & Reip 2020: 21, fig. 11c; 23, fig. 12e; 94, fig. 55e). The same condition is observed in *S. ausugi* comb. nov.: Most individuals are characterized by an edentate labrum, but one of the here examined specimens possesses three minute, vestigial, labral teeth. The studied specimens of *S. fimbriatus* comb. et stat. nov. and *S. gentianae* comb. et stat. nov. are even more variable in this respect, having either edentate (Figs 1D, 4D) or normal julid labrum (Figs 1C, 4C), i.e., with three well developed median teeth, these being only insignificantly reduced in some individuals. The two states occur not only intraspecifically but also within the same population.

Interestingly, specimens with distinct labral teeth have mandibles with less strongly reduced biting parts compared to their counterparts with edentate labrum, while the mandibular pectinate lamellae are equally hypertrophied in both groups. This may suggest that apart from modified body proportions, the first step to hydrophilous/amphibious life and filtering diet in cave julids must be the hypertrophization of the pectinate lamellae, while biting parts of mandibles and the labral teeth are reduced at a later stage. Such an assumption is further supported by the fact that apart from the presence of an extra fifth pectinate lamella in *S. ausugi* comb. nov., the lamellae are similarly hypertrophied in all three hydrophilous species of *Stygiiulus* stat. nov., while the mandibular gnathal lobe is strongly reduced and the labral teeth are never well pronounced only in *S. ausugi* comb. nov. However, it is likely that the observed intraspecific variability of mouthparts is at least partly due to lack of stabilizing selection – a common phenomenom concerning organs in the state of reduction, as exemplified by Enghoff (1976) with sexual characters in thelytokous populations of the nemasomatid millipede *Nemasoma varicorne* C.L. Koch, 1847.

By all means, the modifications in hydrophilous and amphibious julids, which are currently known only from caves in Europe and the Caucasus, are a very interesting phenomenon that will be the subject of future extensive research (Antić *et al.* in prep.).

### Distribution patterns of *Stygiiulus* stat. nov.

From the general distribution of *Stygiiulus* stat. nov. (Fig. 13), it is obvious that the core of the genus' range is in the Venetian Prealps where the largest number of species and localities is registered. This region is inhabited by seven out of ten species of this genus, including three (four) species that can be found also outside caves. Of these, only two species, viz., *S. tobias* comb. nov. and *S. maximus* comb. nov., both known from endogean as well as superficious habitats, show a wider distribution, while the rest are narrow local endemics. *Stygiulus tobias* comb. nov. is the westernmost-occurring species of the genus, ranging from the southern through the central Venetian Prealps, to the southern slopes of the Dolomiti. It partially co-occurs in the central Venetian Prealps with the hydrophilous *S. ausugi* comb. nov. known only from two caves. *S. maximus* comb. nov. has the widest distribution range within *Stygiiulus* stat. nov., stretching from the Piave River in the west, through the Venetian Prealps and the Carnic Alps, all the way to the Julian Alps in the east. Another four species are found within the same region. From west to east these are: *S. montellensis* comb. nov., *S. rotundatus* comb. et stat. nov., *S. gentianae* comb. et stat. nov., and *S. fimbriatus* comb. et stat. nov. However, it seems that the actual distribution areas of these species, except perhaps that of *S. gentianae* comb. et stat. nov., do not overlap with the distribution of *S. maximus* comb. nov. All four areas are much smaller compared to that of *S. maximus* comb. nov. Both *S. montellensis* comb. nov. and *S. rotundatus* comb. et stat. nov. are limited to a small area on the southern side of the Venetian Prealps' foothill, north of Treviso, with partial overlap. The hydrophilous *S. gentianae* comb. et stat. nov. and *S. fimbriatus* comb. et stat. nov. are known from several caves in the easternmost part of the Venetian Prealps and two caves in the Italian part of the Julian Alps, respectively.

The remaining three species of the genus *Stygiiulus* stat. nov. are distributed outside the borders of Italy. *S. illyricus* comb. nov. occur south of the Julian Alps, in the Istrian peninsula in Croatia and the northwestern Dinarides in Slovenia, where it is known from a large number of subterranean localities. The southernmost representative of the genus is *S. insularis* comb. nov., a species known only from one pit in the northern part of the Croatian island of Cres. Finally, in addition to these nine species distributed on the south side of the main Alpine ridge, one congener, *S. seewaldi* comb. nov., occur on the other side of the Alps, found in three underground habitats in the Northern Limestone Alps, Germany and Austria. It is interesting to mention that all three "border species" of the genus, viz., *S. tobias* comb. nov. (westernmost), *S. insularis* comb. nov. (south-easternmost) and *S. seewaldi* comb. nov. (northernmost) are characterized by some deviations in their gonopod structure compared to the remaining congeners from the "core group".

It seems that the representatives of the genus *Stygiiulus* stat. nov. today mostly inhabit underground and epigean habitats up to an altitude of about 1500 m a.s.l., but the great majority of records come from altitudes below 1000 m a.s.l., mainly below 700 m a.s.l. Therefore, it is clear why these species inhabit the slopes in a small region south and north of the main Alpine chain. The distribution of the genus is limited in the south by the Po Valley and the flatlands of Veneto and Friuli. In the west *Stygiiulus* stat. nov. is replaced with *Trogloiulus*, while in the southeast it is bordering with the subgenus *Inversotyphlus* of the genus *Typhloiulus*. So apparently there is not much room for discoveries of new species of this genus south of the Alps in the future, with the exception of the northern Dinarides in Slovenia, where there is currently a gap in the distribution of *Stygiiulus* (although it is possible that *Typhloiulus carniolensis* Strasser, 1940, described on the basis of a single female, is actually a member of *Stygiiulus* stat. nov.), as well as in the extreme south of the Istrian peninsula in Croatia, were one juvenile of a blind, cave julid similar to *Stygiiulus* stat. nov. was found (T. Dražina, personal communication). But on the other hand, as for the already questioned *S. tobias pygmaeus* comb. nov., we cannot exclude the presence of more undescribed and undiscovered species in the main distribution area of the genus in Italy. The main gap in the distribution in relation to the core area is in the north, where the genus' range is interrupted by the main chain of the Alps. The question is whether some representatives of *Stygiiulus* stat. nov. have remained overlooked in the canyons and gorges of the high Alps, or this gap can be explained by the extinction of taxa from this area during colder geological periods, leaving *S. seewaldi* comb. nov. isolated from all of its extant congeners.

# Acknowledgements

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## Supplementary file

**Supp. file 1**. Species and accession numbers of sequences used in the analyses.
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