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## Monograph

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# Revision of the spider genus *Stygopholcus* (Araneae, Pholcidae), endemic to the Balkan Peninsula

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**Abstract.** The genus *Stygopholcus* Kratochvíl, 1932 is endemic to the Balkan Peninsula and includes only four nominal species: the epigeal *S. photophilus* Senglet, 1971 in the south (Greece to Albania) and the ‘northern clade’ consisting of three troglophile species ranging from Croatia to Albania: *S. absoloni* (Kulczyński, 1914); *S. skotophilus* Kratochvíl, 1940; and *S. montenegrinus* Kratochvíl, 1940 (original rank re-established). We present redescrptions of all species, including extensive data on ultrastructure, linear morphometrics of large samples, and numerous new localities. We georeference previously published localities as far as possible, correct several published misidentifications, and clarify nomenclatorial problems regarding the authority of *Stygopholcus* and the identity of the type species *S. absoloni*. We suggest that the ‘northern clade’ has a relict distribution, resulting from past and present geologic and climatic factors. Future work on *Stygopholcus* should focus on the southern Dinarides, combining dense sampling with massive use of molecular data.

**Keywords.** Smeringopinae, Balkan Peninsula, cave spider, troglophile, relict.

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## Introduction

Pholcid spiders have their highest species diversity in the tropics and subtropics, with ~93% of all published records (excluding synanthropic species) between 40° S and 40° N (Huber & Chao 2019; B.A. Huber, unpubl. data). Compared to many other spider families such as Linyphiidae Blackwall, 1859, Lycosidae Sundevall, 1833, and Gnaphosidae Banks, 1892 (Marusik & Koponen 2002), Pholcidae C.L. Koch, 1850 do not seem to tolerate low temperatures, with few exceptions (e.g., Bennett 2014; Huber 2011a, 2014). As a result, continental Europe is poor with respect to pholcid spider diversity (Nentwig *et al.* 2020). Apart from several introduced synanthropic species and some widespread Mediterranean species of uncertain geographic origin [*Holocnemus pluchei* (Scopoli, 1763); *Spermophora senoculata* (Dugès, 1836)], the few autochthonous species are largely restricted to three areas: the western Mediterranean (*Spermophorides* Wunderlich, 1992 and *Holocnemus* Simon, 1873), eastern Europe (*Pholcus* Walckenaer, 1805), and the Balkan Peninsula (*Stygopholcus* Kratochvíl, 1932).

Among these, the Balkan Peninsula is the only European region with an endemic pholcid genus, *Stygopholcus*. This is noteworthy but unsurprising. The western part of the peninsula in particular is widely recognized as one of the regions in Europe with the highest species diversity (Griffiths *et al.* 2004), and for many taxa the level of endemism is the highest in Europe (e.g., Gottstein-Matočec *et al.* 2002; Eastwood 2004; Tzedakis 2004; Džukić & Kalezić 2004; Sket *et al.* 2004; Mammola *et al.* 2019; Bregović *et al.* 2019; Lukić *et al.* 2020). Several factors have been proposed to account for this exceptional biological richness, including historical aspects (glacial refugia, land bridges) and present geography (terrain complexity, transition zone), geology (karst, caves), and climate variability (Mediterranean, mountainous, and continental) (Kryštufek & Reed 2004; Reed *et al.* 2004; Džukić & Kalezić 2004; Mihevc *et al.* 2010).

Some spider genera share this exceptional species diversity on the Balkan Peninsula, as for example *Troglohyphantes* Joseph, 1882, *Harpactea* Bristowe, 1939, and *Dysdera* Latreille, 1804 (Deeleman-Reinhold 1978; Deeleman-Reinhold & Deeleman 1988; Deltshv 2004; Komnenov 2009, 2020; Platania *et al.* 2020). By contrast, *Stygopholcus* is not particularly diverse. Three of the four species we recognize below have been known since Kratochvíl's (1940) diligent revision, and the fourth species was added half a century ago by Senglet (1971). *Stygopholcus* spiders are large and conspicuous; in the western Balkan they are among the first animals any biologist will encounter upon entering a cave. Thus, we have no reason to expect that a substantial number of species remain to be discovered. Nevertheless, we deemed this revision necessary for three main reasons.

First, species limits are not always obvious. For example, the similarity between the two species described by Kratochvíl (1940) prompted Senglet (1971) to reduce them to subspecies. Numerous misidentifications in the literature are further testimony to the difficulty in distinguishing some of the species, in particular females. Our revision is based on many more specimens from many more localities than available to previous authors, and we additionally support species limits with morphometric data. In addition, we point out deviating specimens from particular caves or areas that we tentatively assign to known species but that deserve further study.

Second, precise geographic data are a fundamental aspect of taxonomic work, but many previously published collecting sites are difficult to locate. We thus made a major effort to georeference published localities, using a simple scheme to point out uncertainties (see Material and methods).

Third, this revision is part of a series that aims to result in a full cladistic morphological analysis of Smeringopinae. This subfamily contains two sub-Saharan genera (*Smeringopus* Simon, 1890; *Smeringopina* Kraus, 1957; revised in Huber 2012, 2013), the mysterious Seychelles endemic *Cenemus* Saaristo, 2001, and a clade ranging from northern Africa to Central Asia (including *Hoplopholcus*



Kulczyński, 1908, revised in Huber 2020; *Crossopriza* Simon, 1893; *Holocnemus* Simon, 1873; and *Stygopholcus*). To support a future comprehensive analysis of the entire subfamily, we did not limit our attention to characters useful for species delimitation but also focused on characters supposed to be useful for reconstructing the phylogeny of the subfamily (in particular SEM characters). We briefly discuss intergeneric relationships, but a more complete analysis will only be possible when the remaining two genera are revised (*Crossopriza* Simon, 1893 and *Holocnemus* Simon, 1873; revision in progress).

## Material and methods

Taxonomic descriptions follow the style of recent publications on Smeringopinae (e.g., Huber 2020; based on Huber 2000). Measurements were done on a dissecting microscope with an ocular grid and are in mm unless stated otherwise; eye measurements are  $\pm 5 \mu\text{m}$ . Photographs were made with a Nikon Coolpix 995 digital camera (2048  $\times$  1536 pixels) mounted on a Nikon SMZ 18 stereo microscope or a Leitz Dialux 20 compound microscope. CombineZP (<https://combinezp.software.informer.com/>) was used for stacking photos. Drawings are partly based on photos that were traced on a light table and later improved under a dissecting microscope, or they were directly drawn with a Leitz Dialux 20 compound microscope using a drawing tube. Cleared epigyna were stained with chlorazol black. For SEM photos, specimens were dried in hexamethyldisilazane (HMDS) (Brown 1993), and photographed with a Zeiss Sigma 300 VP scanning electron microscope. SEM data are presented within the descriptions but are usually not based on the specific specimen described. The number of decimals in coordinates is supposed to give a rough indication about the accuracy of the locality data: four decimals means that the collecting site (or cave entrance) is within about 10 m of the indicated spot; three decimals: within  $\sim 100$  m; two decimals: within  $\sim 1$  km; one decimal: within  $\sim 10$  km. Coordinates for some caves were taken from the GeoRef portal (<http://www.georef.hr/>) and Bioportal – Katastar speleoloških objekata RH (<http://www.bioportal.hr/gis/>), hosted by the Institute for Environment and Nature of Croatia. Distribution maps were generated with ArcMap ver. 10.0.

Original cave names are used as much as possible, i.e., the Serbo-Croatian *pećina*, the Croatian *špilja*, and the Greek *spilaio* are mostly used instead of ‘Cave’; the Serbo-Croatian *jama* means pit, the Serbo-Croatian *ponor* means sinkhole.

## Institutional abbreviations

This study is based on the examination of more than 800 adult specimens from approximately 200 localities, deposited in the following collections:

AMNH	= American Museum of Natural History, New York, USA
CBSS	= Croatian Biospeleological Society, Zagreb, Croatia
CMK	= Collection M. Komnenov, Skopje, Macedonia
HISR	= Hellenic Institute of Speleological Research, Irakleion, Greece
IZUB	= Institute of Zoology, University of Belgrade, Belgrade, Serbia
MCVR	= Museo Civico di Storia Naturale, Verona, Italy
MHNG	= Muséum d’histoire naturelle, Genève, Switzerland
MIZW	= Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland
MMUE	= Manchester Museum, University of Manchester, Oxford, USA
MNHN	= Muséum national d’histoire naturelle, Paris, France
NHMC	= Natural History Museum of Crete, University of Crete, Irakleion, Greece
NHMW	= Naturhistorisches Museum Wien, Vienna, Austria
NMNHS	= National Museum of Natural History, Sofia, Bulgaria
NMNL	= National Museum of Natural History Naturalis, Leiden, Netherlands
NMP	= National Museum, Prague, Czech Republic

- ROC = Collection Roman Ozimec, Zagreb, Croatia  
SMF = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany  
ZCSL = Zoological collection of SubBio Lab, University of Ljubljana, Ljubljana, Slovenia  
ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany  
ZMB = Museum für Naturkunde, Berlin, Germany

### Morphological abbreviations used in the text

- ALE = anterior lateral eyes  
ALS = anterior lateral spinnerets  
AME = anterior median eyes  
a.s.l. = above sea level  
L/d = length/diameter  
PME = posterior median eyes  
PMS = posterior median spinnerets

Abbreviations used in figures only are explained in the figure legends.

## Results

Class Arachnida Lamarck, 1801  
Order Araneae Clerck, 1757  
Family Pholcidae C.L. Koch, 1850

Genus *Stygopholcus* Kratochvíl, 1932

*Stygopholcus* Kratochvíl, 1932: 2–3 (type species: *Holocnemus absoloni* Kulczyński, 1914; see below).

*Stygopholcus* – Absolon & Kratochvíl 1932: 75. — Kratochvíl 1934: 182; 1940: 8; 1978: 27 — Senglet 1971: 354; 2001: 58, 65. — Brignoli 1971: 257; 1976: 561.

### Authority of *Stygopholcus*

There has long been disagreement about the publication that has made the genus name *Stygopholcus* validly available. Some cataloguers such as Roewer (1942) and Brignoli (1983) considered the original description to be in Kratochvíl (1940), while Bonnet (1958) cited Absolon & Kratochvíl (1932) as the source for the name. Platnick (1993) first opted for Kratochvíl (1940), later (Platnick 2000) for Absolon & Kratochvíl (1932). The World Spider Catalog (2020) adopted Platnick's later view. A third option, namely Kratochvíl (1932), was offered by Kratochvíl himself (Kratochvíl 1940), and adopted by Senglet (1971).

The name *Stygopholcus* is first mentioned in two papers in 1932: in one of these, Absolon & Kratochvíl (1932) explicitly refer to the other publication (Kratochvíl 1932) as the source of the name:

“Mit dem Namen *Stygopholcus* n. g. hat J. Kratochvíl (siehe “Sur quelques Araignées de Slavonie central”, Bulletin de l'Institut national agronomique, Sign. C. 23, Brno 1932) die Art *Holocnemus* (*Hoplopholcus*) *absoloni* Kulcz. als selbständige Gattung abgetrennt.” [“With the name *Stygopholcus* n. g., J. Kratochvíl (see “Sur quelques Araignées de Slavonie central”, Bulletin de l'Institut national agronomique, Sign. C. 23, Brno 1932) has moved the species *Holocnemus* (*Hoplopholcus*) *absoloni* Kulcz. to constitute a separate genus”].

Other than this statement, Absolon & Kratochvíl (1932) just say a few words about the habitat of *S. absoloni*. Absolon & Kratochvíl (1932) thus fail to satisfy a requirement of ICZN (1999) Article

13.1.1 for names published after 1930 to be available: "... be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon." The fact that Absolon & Kratochvíl (1932) contains a bibliographic reference to such a published statement could be construed as satisfying ICZN Article 13.1.2. We do not know which 1932 paper was published first. However, if Kratochvíl (1932) was published first, it has priority for that reason; if it was published second, it has priority because Absolon & Kratochvíl (1932) refer to a statement that was not yet published at the time.

Confusingly, the paper to which Absolon & Kratochvíl (1932) refer was originally also not intended to be the source of the name. Kratochvíl (1932) referred to "*Stygopholcus* n. g. in lit., ježž popíši na jiném místě" ["*Stygopholcus* n.g. in lit., that I will describe elsewhere"], suggesting that the genus name was intended to be made available in an upcoming publication (possibly Kratochvíl 1934). However, Kratochvíl (1932) provides "characters that are purported to differentiate the taxon", satisfying ICZN Article 13.1.1; and he explicitly names "*H. absoloni* Kulcz." as the only species to be included in the genus, satisfying the requirements of ICZN Article 13.3 regarding the fixation of a type species. From a formal perspective, Kratochvíl's (1932) intentions (of making the name available later) are as irrelevant as the confusion between genus rank (in the Czech text) and subgenus rank (in the French summary), and the minimalist nature of his diagnosis: he mentions that (1) the female sternum process present in *Holocnemus pluchei* is absent in *Stygopholcus*; (2) the abdomen shape differs between *Holocnemus* and *Stygopholcus*; (3) the female palp of *Stygopholcus* resembles that of *Pholcus* rather than that of *Holocnemus pluchei* (which is enlarged); and (4) *Stygopholcus* has cheliceral stridulation like *Holocnemus* (in contrast to *Pholcus*).

We conclude that *Stygopholcus* was made available by Kratochvíl (1932).

#### **Identity of *Stygopholcus absoloni* (Kulczyński, 1914)**

In the original description of "*Holocnemus (Hoplopholcus) Absolonii*", Kulczyński (1914) mentions two caves near Trebinje by name: "Mares et feminae lecta sunt prope Trebinje in speluncis: Ilijina pećina ... et Zovica jama..." ["*males and females were collected in caves near Trebinje: Ilijina cave ... and Zovica pit ...*"]. He then notes that according to Absolon ("Teste Cel. C. Absolon"), this species has been found in many other caves in southeastern Herzegovina (southern region of modern Bosnia and Herzegovina). This strongly suggests that he had only seen the specimens from the two caves near Trebinje. Any specimens he had from these caves, and only these specimens, constitute the type series (syntypes).

In Kulczyński's (1914) long original text, the morphology is described in considerable detail but complex shapes are notoriously difficult to understand from text alone. However, he was obviously aware of differences among the specimens available to him, starting a paragraph with "Maris palpi variant paululo formâ, etiam mandibularum armatura paulo mutabilis" ["*the male palps vary slightly in shape, and also the armature of the chelicerae is slightly variable*"]. He clearly interpreted this as intraspecific variation, but without specifying to which variant(s) his four figures referred.

When Kratochvíl (1940) made a first careful and detailed revision of *Stygopholcus*, he realized that Kulczyński's (1914) figures represented the two variants, which Kratochvíl interpreted (correctly) as different species. He considered Kulczyński's (1914) fig. 25 to represent one species, figs 24, and 26–27 the other species. This view was accepted by subsequent cataloguers and authors, also by Senglet (1971, 2001), the only author other than Kratochvíl who studied *Stygopholcus* in some detail. Since Kulczyński's (1914) figures of the male palps are in different views, we checked Kratochvíl's (1940) distinction of the two putative species by orienting palps of both species in exactly the same positions as in Kulczyński's (1914) figures. There is no doubt that Kratochvíl (1940) was right in this respect.

Kratochvíl's (1940) error was that he felt either entitled or obliged (or both) to designate new types from a new type locality for *S. absoloni*, choosing a cave ~35 km NW of Trebinje, "Grabova peć kod Grabova dola". We can only speculate about his motivation, but it seems reasonable to assume that he had been postponing his detailed revision of the genus for many years (at least since 1932), hoping to eventually be able to see Kulczyński's type series. This hope was frustrated, as indicated in a footnote (Kratochvíl 1940: 16) where he explicitly stated that the specimens from Ilijina pećina and Zovica jama were not accessible to him. Unfortunately, among his rich new material there were no specimens from any of these two caves.

We made a major effort to locate Kulczyński's types, but found only one vial, deposited in the Museum & Institute of Zoology, PAS, in Warsaw, Poland. The supposed types of *S. absoloni* deposited in Prague and listed in Růžička *et al.* (2005) are Kratochvíl's erroneous 'types' from "Grabova peć kod Grabova dola". Kulczyński's true type vial contains a label in his own handwriting, but the only locality information on this label is "Trebinje". A second, very detailed label says "Ilijina pećina", but other information on this label leaves no doubt that it was added much later. Fortunately, Kulczyński's original catalogue (in Warsaw) offers a clear hint about the origin of the specimens in the vial. It says "Jaskinie koło Trebinje" ["caves near Trebinje"], suggesting that Kulczyński joined the specimens from Ilijina pećina and Zovica jama.

This type vial contains only three specimens, one male and two females. This is clearly only part of Kulczyński's material, because he obviously had at least two males available. However, both variants/species are represented in this vial. Circumstantial evidence suggests that one female is from Ilijina pećina (it corresponds to more recently collected females from this cave). This forces us to conclude that the other specimens (one male and one female) are from Zovica jama.

This is clearly a case where a lectotype should be designated for *S. absoloni* in order to provide stability and avoid further confusion about the basics (ICZN Recommendation 74G). However, it is not obvious which specimen would best serve as a lectotype. Selecting the male specimen has one major disadvantage: it makes Zovica jama the type locality, a cave that we were not able to locate, and that was even unknown to local cavers in Trebinje we met in 2014. On the other hand, Ilijina pećina is well known and easily accessible, providing a precise type locality. Selecting the female from Ilijina pećina would thus seem to better satisfy ICZN Recommendation 74E (Verification of locality).

At the same time, selecting the male specimen as lectotype has also advantages. Most importantly, it preserves the prevailing usage of the name. This male is the same variant/species as Kratochvíl's (1940) *S. absoloni* 'types' from "Grabova peć kod Grabova dola", and it also corresponds to what Senglet (1971) interpreted as *S. absoloni*. Thus, selecting the male satisfies ICZN Recommendation 74A (Agreement with previous restriction). A second (minor) advantage is the fact that species in *Stygopholcus* are slightly easier to distinguish by males than by females (as in most Pholcidae).

Thus, we decided to select the male as lectotype, mainly for two reasons: it seems to better serve stability, one of the major guiding principles of the Code. Second, it is possible that the exact location of Zovica jama will eventually be determined, weakening the argument against selecting the male.

### Diagnosis

*Stygopholcus* includes relatively large (total body length: ~5–6), long-legged spiders with oval abdomen (Figs 1–5). Males of *Stygopholcus* are easily distinguished from all other Smeringopinae by modified (club-shaped) hairs frontally on chelicerae (Figs 19, 51); also by unique transparent or weakly sclerotized dorsal bulbal process (arrows in Figs 17, 117) and by distinct brushes of hair-shaped retrolateral



membranous processes at tip of procurus (Figs 29, 67, 99, 137). Males and females differ from other Smeringopinae by tarsal organs of legs with undulating rim (Figs 38, 75, 97, 142).



**Figs 1–5.** *Stygopholcus* Kratochvíl, 1932; live specimens. 1. *S. absoloni* (Kulczyński, 1914); male from Vjetrenica, Bosnia and Herzegovina. 2. *S. skotophilus* Kratochvíl, 1940; male from Pavlova pećina, Bosnia and Herzegovina. 3. *S. montenegrinus* Kratochvíl, 1940; male and female with egg-sac from Studenačka pećina, Montenegro. 4–5. *S. photophilus* Senglet, 1971; male and female from Episkopi, Crete. Photos: BAH.



## Description

### Male

**BODY.** Total body length ~5–6; carapace width ~1.5–2.5. Carapace with deep central pit and pair of shallow furrows diverging from posterior side of pit toward posterior rim (Figs 39, 61, 91, 107); ocular area slightly raised, eye triads relatively close together (distance PME–PME similar to PME diameter), each secondary eye (especially PME) accompanied by indistinct elevation (arrows in Fig. 61; “pseudo-eyes”; cf. Huber 2009), AME relatively large (usually ~40–50% of PME small diameter). Clypeus high, unmodified or with indistinct modified area medially (arrow in Fig. 129). Abdomen oval, never elevated or pointed above spinnerets (Figs 1–5). Male gonopore with 4–8 epiandrous spigots (Figs 62, 92, 143), ALS with only two spigots each: one large widened spigot and one pointed spigot (Figs 69, 135); PMS with two spigots each (cf. female, Fig. 42); PLS without spigots.

**COLOR.** In general ochre-yellow to brown, with distinct dark pattern in *S. photophilus*, without or with reduced dark pattern in other (troglophile) species. Carapace mostly pale, with darker ocular area and posterior triangle (Figs 1–2, 4); sternum either dark brown to black (*S. photophilus*), or light brown, with darker brown radial marks (other species). Legs in *S. photophilus* with dark rings on femora (subdistally) and tibiae (proximally and subdistally) and with short dark longitudinal lines dorsally on femora (Figs 127–128); in other species monochromous, without dark rings and longitudinal lines. Abdomen in *S. photophilus* with distinct dorsal and ventral patterns; in other species with fewer dorsal and lateral dark marks restricted to posterior part and without or with indistinct ventral pattern.

**CHELICERAE.** Chelicerae with 1–4 modified (cone-shaped to club-shaped) hairs on each distal cheliceral apophysis and ~10–40 club-shaped hairs on frontal face (Figs 19, 27–28, 51, 63–64, 93–94, 119, 130, 132); in *S. photophilus* with strongly sculptured median edge (Fig. 131); with stridulatory ridges (Figs 35, 71, 95, 133), distances between ridges ~6–9  $\mu\text{m}$  in ‘northern clade’, ~3  $\mu\text{m}$  in *S. photophilus*.

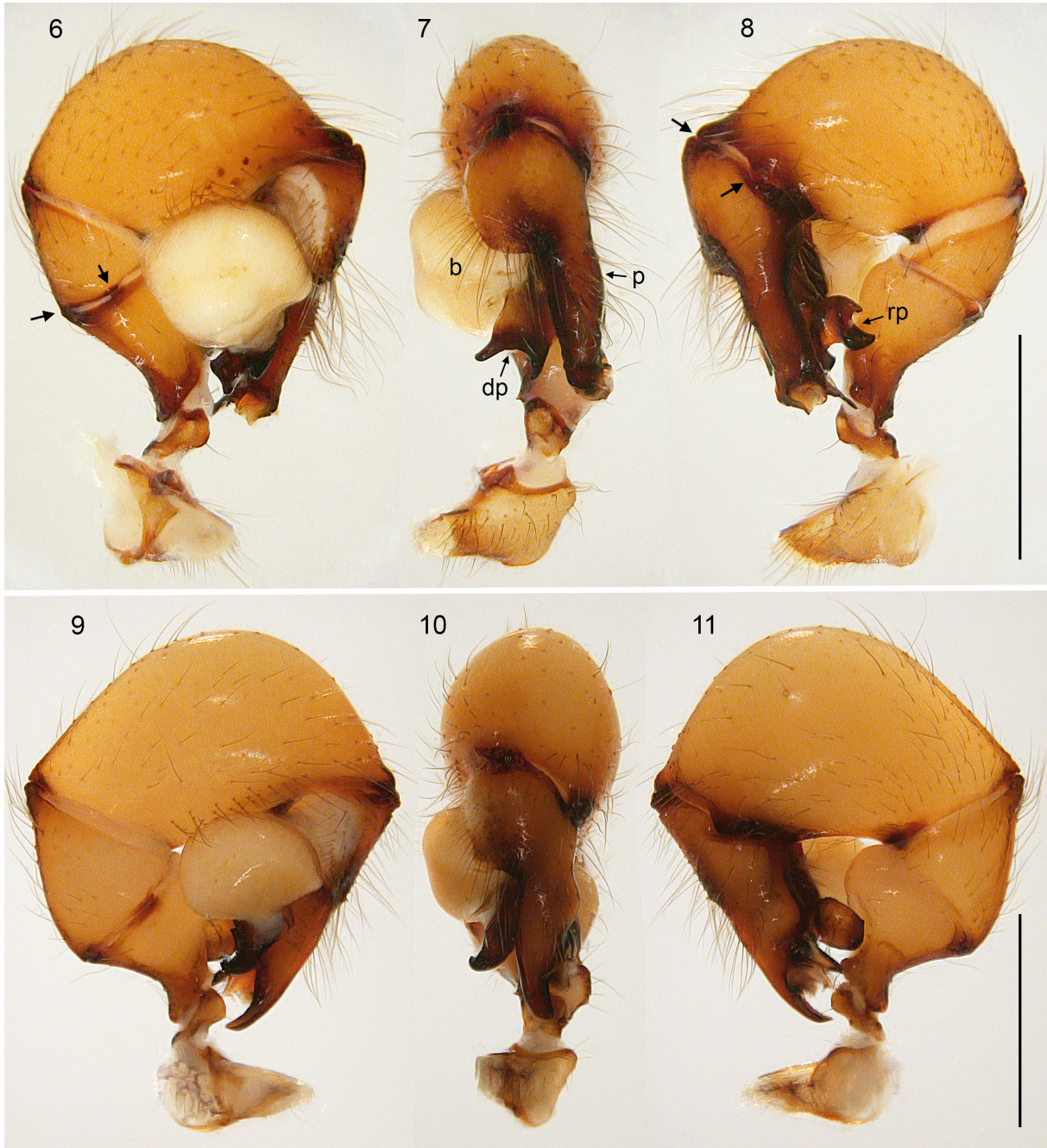
**PALPS.** In general as in Figs 6–11; coxa with rounded retrolateral hump; trochanter barely modified; femur widening distally, slightly curved towards dorsal, with proximal retrolateral process, indistinct transversal dark line on retrolateral side, and stridulatory pick (modified hair) on prolateral side (Figs 65, 103); femur-patella joints shifted toward prolateral side (arrows in Fig. 6); tibia-tarsus joints shifted toward retrolateral side (arrows in Fig. 8); palpal tarsus without dorsal macrotrichia, palpal tarsal organ exposed (Figs 30, 104); procurus dorsally with approximately five (*S. photophilus*) to ten (other species) weakly to strongly curved hairs; procurus without ventral ‘knee’, distally with strong ventral spine, with dorsal and prolateral processes of variable size, and distinctive brushes of hair-shaped retrolateral membranous processes (Figs 29, 67, 99, 137); genital bulb with basal sclerite connecting to tarsus (bs in Figs 15, 118), with small and weakly sclerotized (*S. photophilus*) or transparent (other species) dorsal process (arrows in Figs 17, 117), and main sclerite consisting of retrolateral and dorsal processes (rp and dp in Figs 15–18, 118); sperm duct opening directly on genital bulb at basis of dorsal process (arrow in Fig. 32).

**LEGS.** Legs long and relatively thin, leg 1 length ~35–60, tibia 1 length ~10–15, tibia 2 longer than tibia 4 (1.1–1.2 $\times$ ). Tibia 1 L/d ~60–75. Femur 1 usually with spines ventrally in one row (*S. photophilus*) or two rows (other species) (Fig. 73), in very small males rarely without spines; spines proximally gradually transforming into regular setae; spines never present on femur 2 or on tibia 1; legs without curved hairs; with few short vertical hairs; retrolateral trichobothrium in proximal position (at 2–4% of tibia length in tibia 1), prolateral trichobothrium absent on tibia 1, present on other tibiae. Tarsal pseudosegments very indistinct, never regular rings but rather indistinct irregular platelets. Tarsus 4 with two rows of prolatero-ventral comb-hairs (Figs 34, 74; see also Huber & Fleckenstein 2008: fig. 13). Tarsal organs of legs capsulate, with weakly (*S. photophilus*) to strongly (other species) undulating rim (Figs 75, 97).



**Female**

In general very similar to male; chelicerae with less distinct or without stridulatory files (Figs 36, 72, 96, 134); legs slightly shorter than in male, without spines. All tarsal organs capsulate (i.e., also on palps; Figs 37, 109, 141). Representatives of the ‘northern clade’ with pair of indistinct processes posteriorly



**Figs 6–11.** *Stygopholcus* Kratochvíl, 1932; left male pedipalps, prolateral, dorsal, and retrolateral views. 6–8. *S. skotophilus* Kratochvíl, 1940; from Ilijina pećina, Bosnia and Herzegovina (ZFMK (Ar 22198)). 9–11. *S. photophilus* Senglet, 1971; from Episkopi, Crete (ZFMK (Ar 22205)). Abbreviations: b = genital bulb; dp = dorsal process (of genital bulb); p = procursus; rp = retrolateral process (of genital bulb). Arrows point at joints shifted toward prolateral (femur-patella) and retrolateral (tibia-tarsus). Scale bars: 1 mm.



on carapace (arrows in Figs 39, 107) acting against pair of poorly visible plates on abdomen. Epigynum usually consisting of large, simple anterior plate and short but wide posterior plate (Figs 23, 55, 85, 123); in *S. photophilus* with pair of bulging areas in front of anterior plate (arrows in Fig. 144). Internal genitalia (Figs 145–156) with sclerotized arc that consists of dorsal and ventral parts (da and va in Figs 153, 156) and is variably visible in uncleared specimens; uterus externus with median ventral pouch, usually clearly visible as round or oval structure in untreated specimens (e.g., Figs 55–60); with pair of sclerites originating from posterior margin and either slightly converging anteriorly or parallel (arrows in Figs 25, 125), indistinct in *S. skotophilus*; pore plates large, flat, with homogeneously distributed pores (Figs 22, 54, 84, 122).

### Relationships

*Stygopholcus* is morphologically very similar and geographically very close to *Hoplopholcus* (Huber 2020). This led to a debate between A. Senglet and P. Brignoli in the 1970s and 80s, on whether the two genera should be synonymized or not (Senglet 1971; Brignoli 1971, 1976, 1983). In the end, Senglet (2001) presented a series of morphological differences, and since version 2.5 of the World Spider Catalog (Platnick 2002) *Stygopholcus* has been listed as a valid genus.

The most recent molecular phylogeny of Pholcidae (Eberle *et al.* 2018) has suggested that *Stygopholcus* and *Hoplopholcus* are not even sister taxa, placing *Stygopholcus* closer to *Crossopriza* than to *Hoplopholcus* (with a ‘reasonable’ bootstrap support of 87). Morphological characters that support a sister-group relationship between *Stygopholcus* and *Crossopriza* are the female stridulatory apparatus between prosoma and abdomen and the dark lines on the legs. However, a convincing morphological analysis will require a detailed study of *Crossopriza* (a revision is in preparation) and of *Holocnemus*. The type species of *Holocnemus* (*H. pluchei*) was not included in the molecular analysis of Eberle *et al.* (2018), and the two species of *Holocnemus* that were included (*H. caudatus* and *H. hispanicus*) may in fact be misplaced in *Holocnemus* and belong to *Crossopriza* (B.A. Huber, unpubl. data).

The monophyly of *Stygopholcus* is strongly supported by molecular data (maximum bootstrap support; Eberle *et al.* 2018) and by several putative synapomorphies: (1) male chelicerae with club-shaped hairs on frontal face (Figs 19, 51); (2) unique undulating rim of leg tarsal organs (Figs 38, 75, 97, 142); (3) transparent to weakly sclerotized process dorsally on genital bulb (arrows in Figs 17, 117).

Within *Stygopholcus*, there is strong evidence that *S. photophilus* is sister to all other species (the ‘northern clade’). Both a six genes approach (Eberle *et al.* 2018) and a study using hundreds of universal single-copy orthologs (L. Dietz *et al.*, unpublished data) consistently recovered this relationship, and numerous morphological characters are shared by all species except *S. photophilus*. Some of these are likely to be synapomorphies: (1) spines on male femur 1 arranged in two rows rather than in just one (Fig. 73); (2) dorsal bulbal process with two separate tips (Figs 17–18, 49–50, 81–82); (3) troglophile mode of life and corresponding pale coloration (Figs 1–2).

Within the ‘northern clade’, there is equally strong support for the relationship *absoloni* + (*skotophilus* + *montenegrinus*). Several morphological characters shared by *S. skotophilus* and *S. montenegrinus* support this view, even though it is not clear yet if all of these shared similarities are synapomorphies: (1) procurus straight (rather than weakly curved toward femur as in *S. absoloni*) (Fig. 44); (2) distance between tips of dorsal bulbal process (bulbal measure D; Fig. 17) > 0.24 (< 0.24 in *S. absoloni*) (Fig. 159); (3) size of bulb (bulbal measure E; Fig. 15) > 0.80 (< 0.78 in *S. absoloni*) (Fig. 160).

### Natural history

*Stygopholcus photophilus* can be classified as an epigeal species. It tolerates direct sunlight, is often found in exposed webs among the vegetation, and enters caves only occasionally. Compared to epigeal

relatives in the genera *Holocnemus*, *Hoplopholcus*, and *Crossopriza*, it does not show any obvious troglomorphy. By contrast, all other congeners are slightly troglomorphic. While eye size and leg length do not seem to indicate troglomorphy, their general coloration is paler and they have fewer dark marks on the abdomen and legs. This reflects their strong preference for dark sheltered spaces like caves, deep fissures and cracks, and spaces under rocks in forests. Most records of these species are from caves, but this is probably due to the fact that access to caves is usually much easier for collectors than access to other shallow subterranean habitats.

According to Kratochvíl (1940), cave-dwelling *Stygopholcus* prefer dry caves, or dry areas of caves that include humid sections. We do not have quantitative data on this, but our impression was that *Stygopholcus* requires high humidity; specimens were occasionally found even on dripping wet rocks. They seem to prefer the twilight area, avoiding both direct sunlight at the cave entrance and complete darkness. As already noted by Kratochvíl (1940), individual specimens are occasionally found in deeper parts of caves. As usual in Pholcidae in general, they avoid caves or cave sections with strong air flow (Kratochvíl 1940).

Beyond basic habitat information, little is known about the biology of *Stygopholcus* spiders. Adult specimens of representatives of the northern clade were found throughout the year (20 of 186 collecting events between December and February); we have no records of *S. photophilus* from January and February. Our limited observations (MK, unpublished data) suggest that representatives of the northern clade produce egg-sacs between May and August. In a cave near Podgorica in Montenegro, the last author observed a mating of *S. montenegrinus* where the female kept holding on to her egg-sac while mating. Senglet (2001) observed mating in *S. photophilus* and studied genital mechanics by freeze-fixing mating pairs. He described rhythmic palpal movements during copulation, sperm uptake with a single thread held between legs 3, and was able to ascribe specific functions to individual genitalic structures.

### Composition

The genus includes four named species and this number is unlikely to change substantially in the future. However, some specimens assigned tentatively to *S. absoloni*, *S. skotophilus*, and *S. montenegrinus*, respectively, may represent separate species. A convincing resolution of species limits will probably require both a denser sampling and a massive use of molecular data.

### Distribution

The genus is restricted to the Mediterranean part of the Balkan Peninsula, ranging from southern Croatia to Crete (Fig. 167). The epigeal *S. photophilus* has a wide distribution, ranging from southern Albania to Crete. The three troglophile species of the ‘northern clade’, *S. absoloni*, *S. skotophilus*, and *S. montenegrinus*, range from southern Croatia to northern Albania (Fig. 168). They seem to be relicts that have survived further north by adapting to subterranean conditions (see Discussion).

### Identification key

1. Distinct dark marks on entire abdomen, also dorsally in anterior half (Figs 4–5); leg femora and tibiae with dark rings; procurus distally with strongly projecting dorsal sclerite (ds in Figs 113, 137, 138); spines on male femur 1 in only one row; tibia 1 > 1.40 × longer than tibia 2 in males (Fig. 165), > 1.45 × in females (Fig. 166); strong transversal ridges on anterior part of epigynum (Figs 121, 144); epigynum width/length usually < 1.75 (Fig. 163) ..... *S. photophilus* Senglet, 1971
- Dark marks on abdomen dorsally restricted to posterior half (Figs 1–2); leg femora and tibiae without dark rings; dorsal sclerite distally on procurus distinct but not projecting (ds in Figs 13, 44); spines on male femur 1 in two rows; tibia 1 < 1.40 × longer than tibia 2 in males (Fig. 165), < 1.45 × in

- females (Fig. 166); epigynum with weak transversal ridges (e.g., Figs 23, 55); epigynum width/length usually  $> 1.75$  (Fig. 163) ..... ‘northern clade’ – 2
2. Prolateral sclerite distally on procurus large, heavily sclerotized, and triangular (arrow in Fig. 14), procurus slightly curved towards femur (Fig. 13), procurus short ( $< 1.3$ ; Fig. 161), bulb measure D small ( $< 0.23$ ; Fig. 159); posterior sclerites in female internal genitalia parallel and close together (distance  $\sim 0.2$ – $0.4$ ; Figs 23–26, 164) ..... *S. absoluti* (Kulczyński, 1914)
- Prolateral sclerite distally on procurus small, weakly sclerotized, and cylindrical (arrows in Figs 45–46, 77–78), procurus straight (Fig. 44), procurus longer (usually  $> 1.3$ , except in smallest specimens; Fig. 161), bulb measure D large ( $> 0.24$ ; Fig. 159); posterior sclerites in female internal genitalia either wider apart (Figs 55–60) or converging anteriorly (Figs 85–90) ..... 3
3. Prolateral sclerite on procurus wide (Figs 45–46); bulb measure C small ( $< 0.16$ ; Fig. 158); epigynal measure F large (usually  $> 0.39$ , smaller in specimens from near Sedlari; Figs 55–60, 164) ..... *S. skotophilus* Kratochvíl, 1940
- Prolateral sclerite on procurus narrow (Figs 77–78); bulb measure C large (usually  $> 0.23$ , smaller in eastern specimens; Fig. 158); epigynal measure F small (usually  $< 0.41$ , larger in eastern specimens; Figs 164) ..... *S. montenegrinus* Kratochvíl, 1940

*Stygopholcus absoluti* (Kulczyński, 1914)  
Figs 1, 12–42, 145–146, 153

*Holocnemus* (*Hoplopholcus*) *Absolonii* Kulczyński, 1914: 355 (part), pl. 16, figs 24, 26–27 (not fig. 25).

*Holocnemus* (*Stygopholcus*) *absoluti* – Kratochvíl 1934: 181 (part; see Remarks below).

*Hoplopholcus absoluti* – Brignoli 1971: 257, fig. 20.

*Stygopholcus absoluti* – Kratochvíl 1932: 2; 1940: 10, figs 3, 4a–b, 5a–b, 7 (left); 1978: 28. — Absolon & Kratochvíl 1932: 75. — Senglet 1971: figs 37–39; 2001: 65, fig. 21.

“S110 *Stygopholcus Bal3*” – Eberle *et al.* 2018. — Huber *et al.* 2018.

### Misidentifications

*Holocnemus* (*Stygopholcus*) *absoluti* – Kratochvíl 1934: 181 (part; see Remarks below); 1935: 11 (see Remarks below).

### Remarks

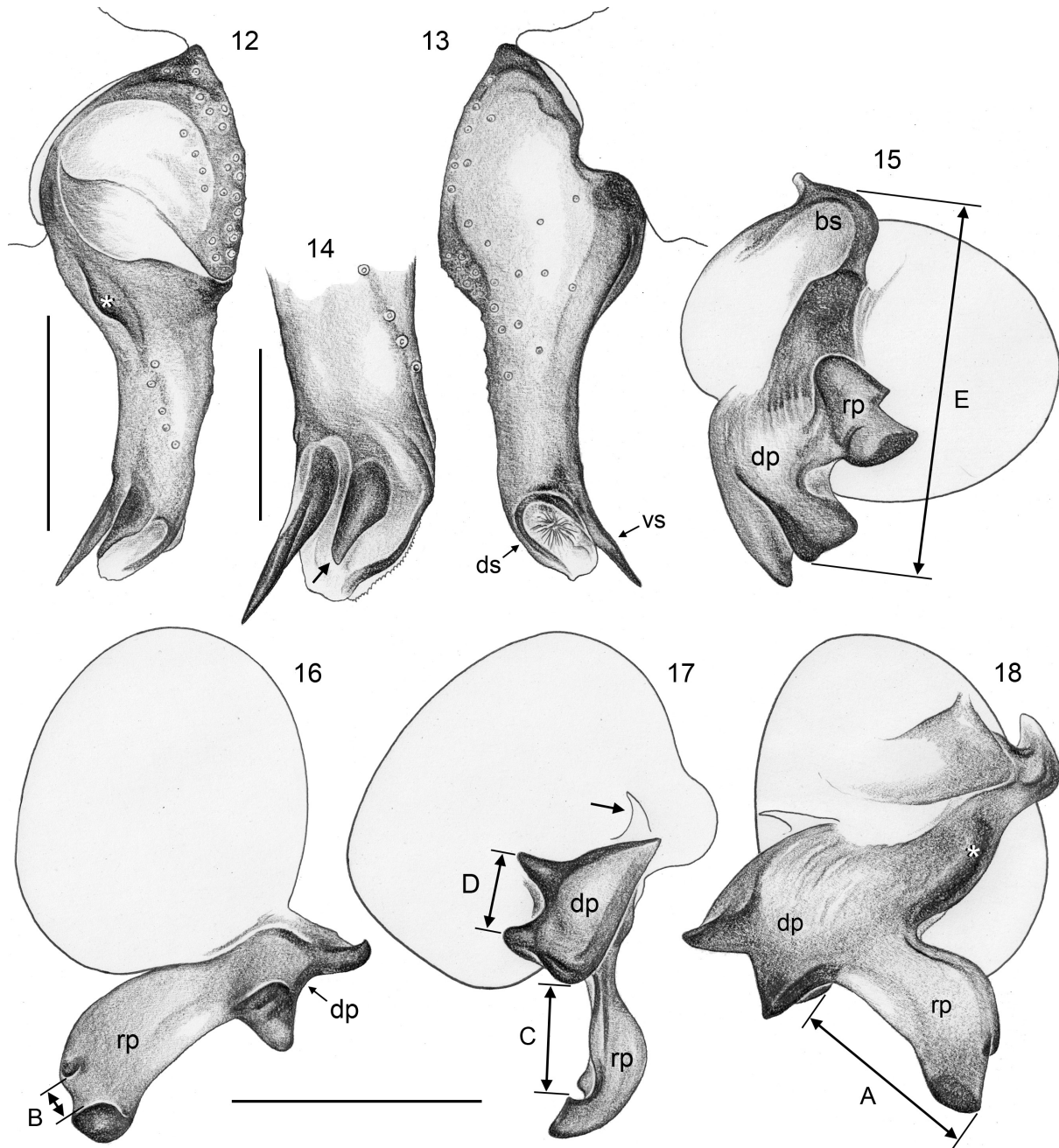
For most of the localities listed in Kratochvíl (1934), the presence of *S. absoluti* could either be confirmed or appears very probable judging from the distribution of confirmed specimens. Exceptions are the following: Ilijina pećina and “Pećina Napode” (= Vilina pećina) (see *S. skotophilus*), Medja peć na Ilijina brdu, Vodena peć kod Sedlara, Grabova peć kod Sedlara, and Trovrata peć (tentatively assigned to *S. skotophilus*), and Jamutina [pećina] (see *S. montenegrinus*). Kratochvíl’s (1934) “Pec kod Ljubova” [Ljubovo?] is not mentioned in the extensive list of localities in Kratochvíl (1940) and is thus not further considered herein.

By contrast, all caves listed in Kratochvíl (1935) probably contain *S. skotophilus*; this is either confirmed by new material or very likely judging from the distribution of confirmed specimens.

### Diagnosis

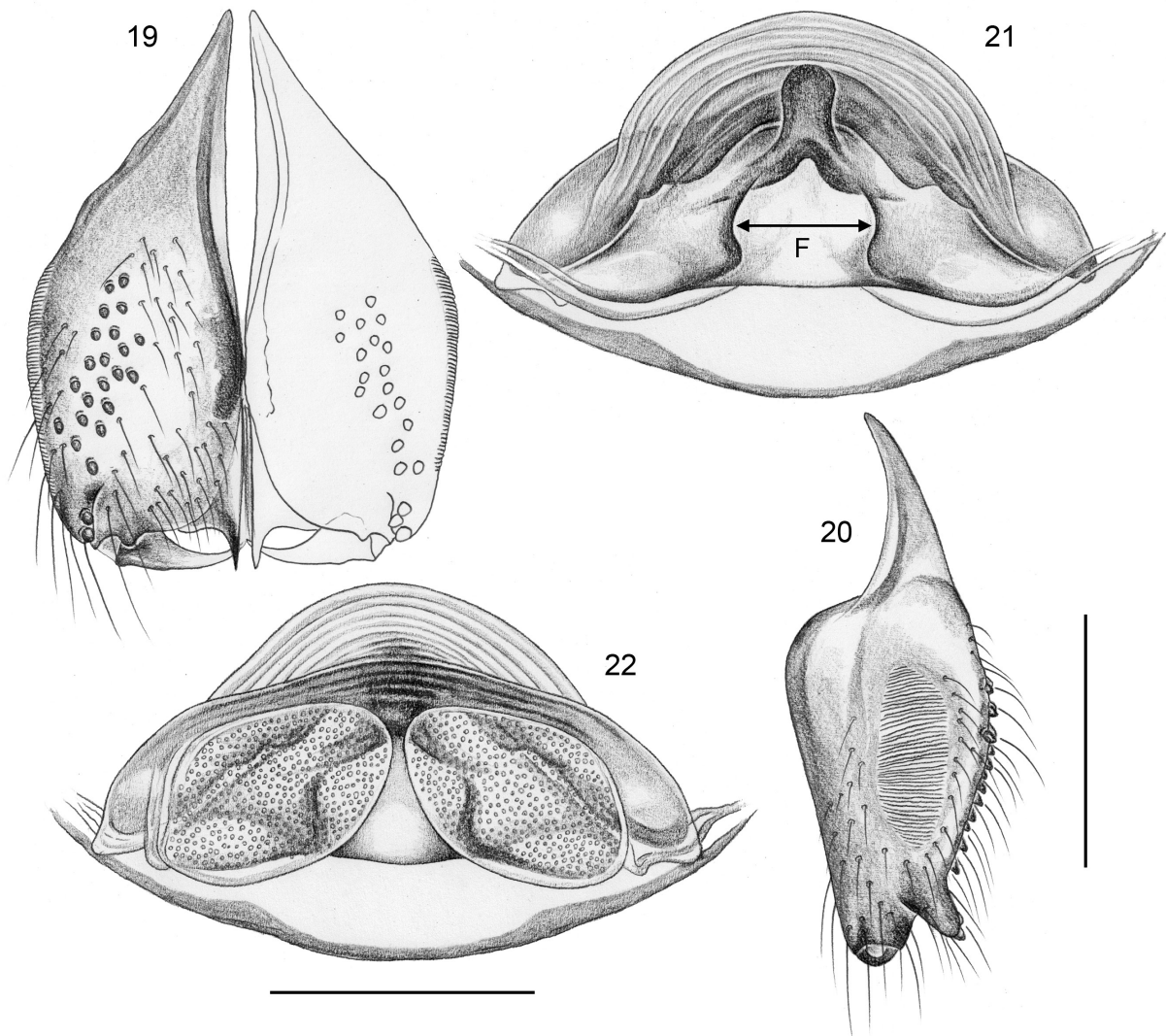
Distinguished from other species in the ‘northern clade’ (*S. skotophilus*; *S. montenegrinus*) by large prolateral sclerite on procurus (distally narrowing; arrow in Fig. 14), by procurus slightly curved





**Figs 12–18.** *Stygopholcus absoloni* (Kulczyński, 1914); male from Balićeva špilja, Croatia (ZFMK (Ar 22195)). **12–13.** Left tarsus and procurus, prolateral and retrolateral views; asterisk in Fig. 12 marks prolateral hump. **14.** Tip of left procurus, prolateral (slightly ventral) view; arrow points at distinctive prolateral sclerite. **15–18.** Left genital bulb, retrolateral, ventral, prolateral-distal, and dorso-distal views, showing bulb measures A–E; arrow in Fig. 17 points at transparent bulbal process; asterisk in Fig. 18 marks connecting sclerite that is absent in specimen from Jama na Brezdanu. Abbreviations: bs = basal sclerite; dp = dorsal process; ds = dorsal sclerite; rp = retrolateral process; vs = ventral sclerite. Scale bars: 12–13, 15–18 = 0.5 mm; 14 = 0.25 mm.

toward femur (rather than straight; Fig. 13), by shorter procurus (Fig. 161; with little overlap), by shape of retrolateral bulbal process in retrolateral view (Fig. 15; small notch on ventral side), and by bulb measures: measure B smaller (Fig. 157; with little overlap), measure D smaller (Fig. 159; no overlap), and measure E smaller (Fig. 160; no overlap). From *S. skotophilus* also by more hairs on male cheliceral base (Fig. 162; with little overlap) and by larger bulb measure C (Fig. 158; no overlap), and by smaller epigynal measure F (Fig. 164; little overlap).



**Figs 19–22.** *Stygopholcus absoloni* (Kulczyński, 1914); male from Balićeva špilja, Croatia (ZFMK (Ar 22195)), female from Zavala, Bosnia and Herzegovina (MHNG). **19–20.** Male chelicerae, frontal and lateral views. **21–22.** Cleared female genitalia, ventral and dorsal views, showing epigynal measure F. Scale bars: 0.5 mm.



**Type material**

**Lectotype**

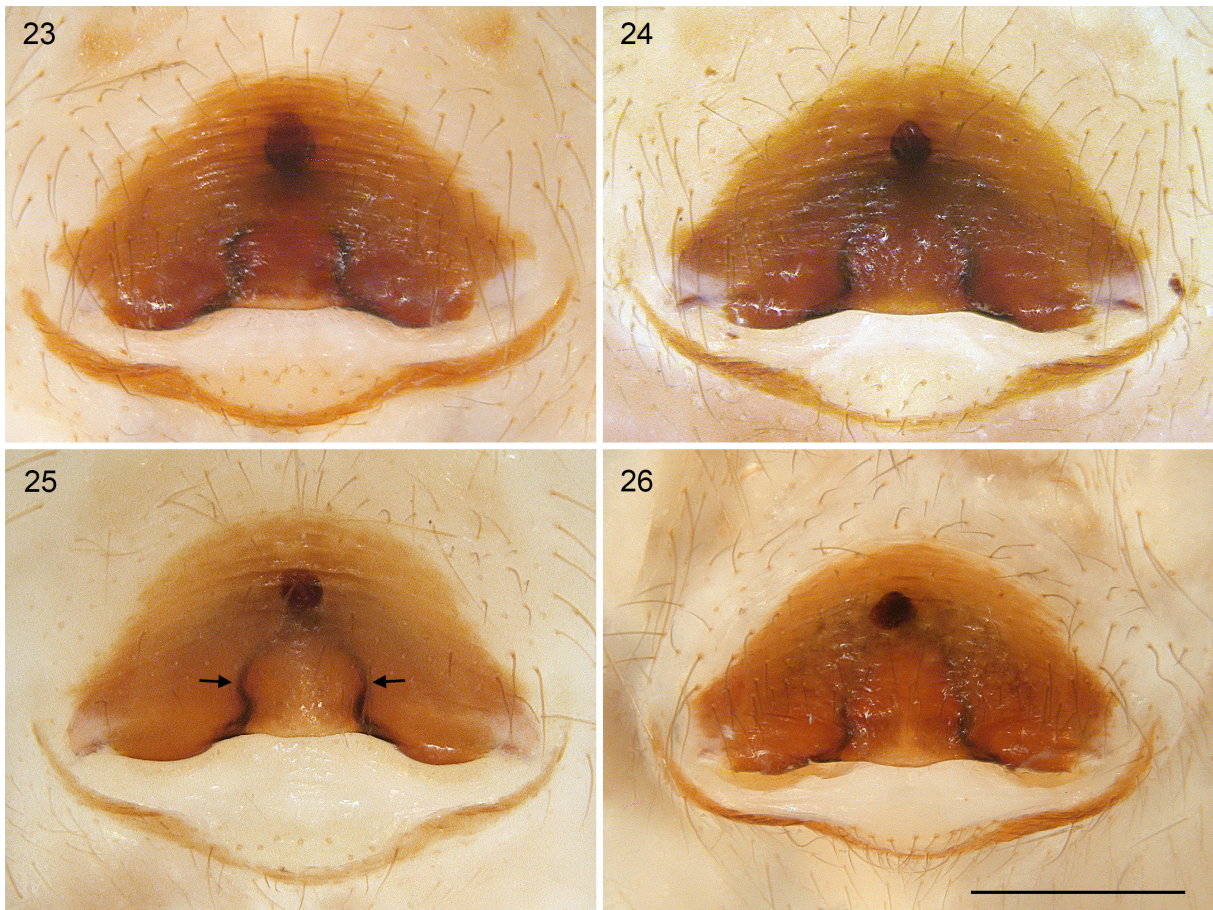
BOSNIA AND HERZEGOVINA • ♂ (designated herein, examined); “near Trebinje, Zovica jama”; ~42.7° N, 18.3° E; date unknown (1912?); K. von Arenstorff leg.; MIZW.

**Paralectotype**

BOSNIA AND HERZEGOVINA • ♀, examined; same collection data as for lectotype; MIZW,

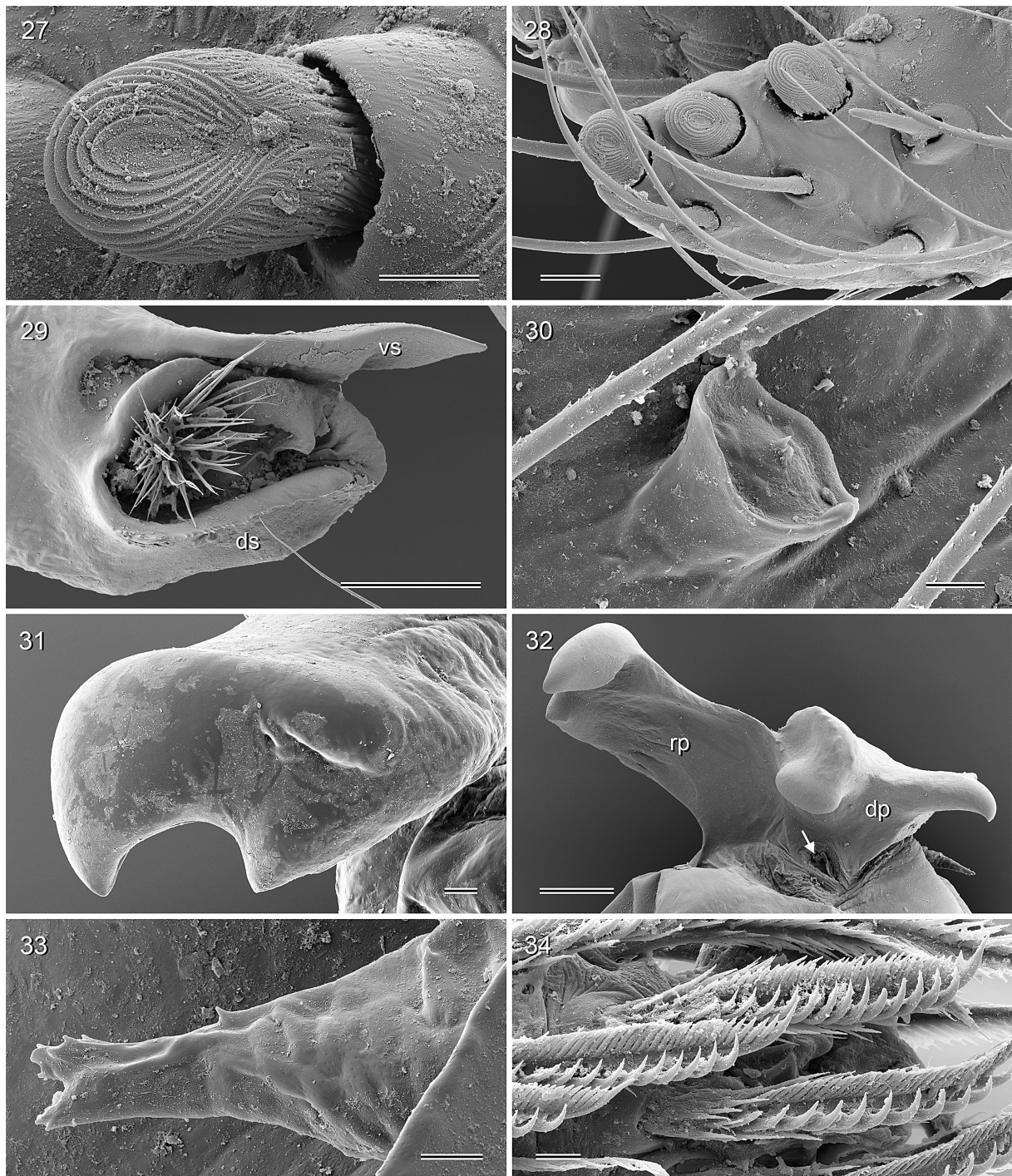
**Other material examined**

BOSNIA AND HERZEGOVINA • 1 ♂, 2 ♀♀; Vjetrenica pećina; 42.8459° N, 17.9837° E; 280 m a.s.l.; 27 May 2014; B.A. Huber and M. Komnenov leg.; in cave near entrance and outside cave, hole in ground; ZFMK (Ar 22192) • 1 ♀, 1 juv., in pure ethanol; same collection data as for preceding; ZFMK (Bal12) • 1 ♂, 1 ♀; Popovo polje, Zavala, Bjelušica, in cave; 42.8447° N, 17.9786° E; 350 m a.s.l.; 2 Dec. 2014, M. Pavlek leg.; CBSS (Ar 3480) • 1 ♂; same locality as for preceding; 26 Oct. 2015; M. Pavlek leg.; CBSS (Ar 3687) • 3 ♀♀, 5 juvs; southern limit of Zavala village, Bjelušica (“Bjelušica pećina”); 42.8447° N, 17.9786° E; 350 m a.s.l.; 15–16 Jul. 1932; J. Kratochvíl leg.(?); NMP • 15 ♂♂, 10 ♀♀; Zavala; 42.849° N, 17.978° E; 19 Sep. 1970; A. Senglet leg.; MHNG • 1 ♀; near monastery



**Figs 23–26.** *Stygopholcus absoloni* (Kulczyński, 1914); epigyna, ventral views. **23.** Balićeva špilja, Croatia (ZFMK (Ar 22195)). **24.** Biokovo, Kukor, Croatia (CBSS (Ar 3367)). **25.** Studenci (grotte), Bosnia and Herzegovina (MHNG); arrows point at distinctive internal sclerites. **26.** Vjetrenica, Bosnia and Herzegovina (ZFMK (Ar 22192)). Scale bar: 0.5 mm (all at same scale).





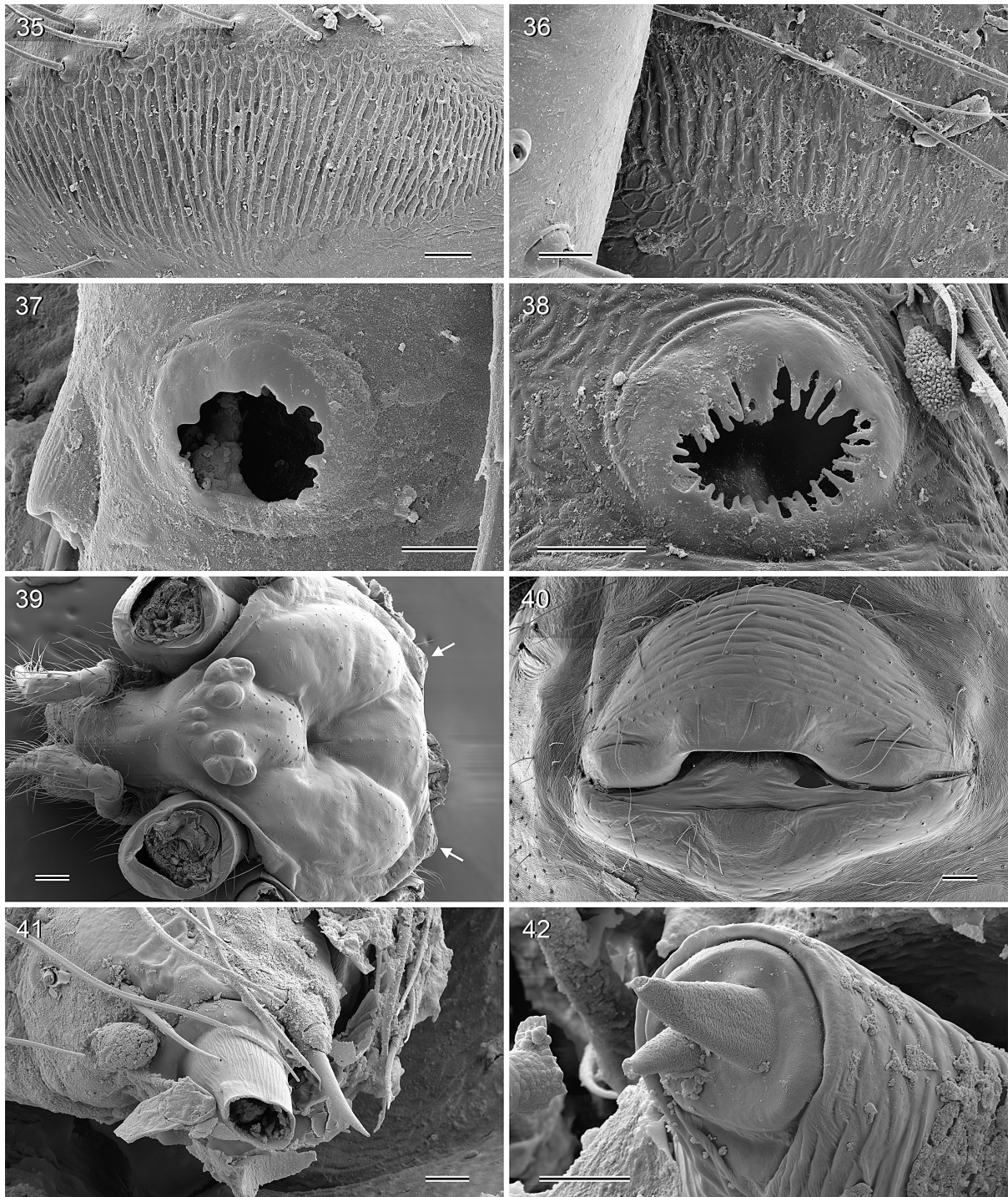
**Figs 27–34.** *Stygopholcus absoloni* (Kulczyński, 1914); male from Počitelj/Čapljina, Bosnia and Herzegovina (MHNG). **27.** Modified hair frontally on male chelicerae. **28.** Left male cheliceral apophysis with modified hairs. **29.** Tip of left procurus, retrolateral view. **30.** Male palpal tarsal organ. **31.** Retrolateral bulbal process, distal view. **32.** Bulbal processes; arrow points at opening of sperm duct. **33.** Transparent bulbal process. **34.** Comb hairs on left tarsus 4, prolateral view. Abbreviations: dp = dorsal process; ds = dorsal sclerite; rp = retrolateral process; vs = ventral sclerite. Scale bars: 27, 30, 33, 34 = 10  $\mu$ m; 28, 31 = 20  $\mu$ m; 29, 32 = 100  $\mu$ m.



of Zavala, Pećina kod Monastira; 42.850° N, 17.979° E; 16 Jul. 1932; J. Kratochvíl leg.; NMP • 1 ♂; Zavala monastery, small cave behind monastery; 42.8499° N, 17.9795° E; 300 m a.s.l.; 27 May 2014; B.A. Huber and M. Komnenov leg.; ZFMK (Ar 22193) • 1 ♂, 1 ♀; Zavala, Orlica pećina; 42.846° N, 17.973° E; 23 Oct. 1968; G. and A. Vigna leg.; MCVR • 1 ♂, 2 ♀♀; 2 km NW of Zavala, Grabova peć kod Grabova dola; 42.858° N, 17.960° E; 20 Jul. 1932; J. Kratochvíl leg.; NMP • 1 ♂, 1 ♀, with Kratochvíl's original label "*Stygopholcus Absoloni* (Kulcz.), ♀ et ♂ type! 19 b" [these are probably Kratochvíl's (1940) 'emended types' and the supposed syntypes in Růžička *et al.* (2005)]; presumably from same locality as preceding; NMP • 1 ♂, 1 ♀; "Inv. No 409"; same collection data as as for preceding ("Grabowa-Höhle, leg. Kratochvíl 1932"); NHMW • 1 ♀, 1 juv.; Čvaljina, Zavala, Baba pećina; 42.8608° N, 17.9722° E; 270 m a.s.l.; 27 Aug. 2017; M. Pavlek leg.; CBSS (Ar 5509) • 1 ♂; same locality as for preceding; 2 Dec. 2014; M. Pavlek leg.; CBSS (Ar 3479) • 1 ♂, 1 ♀, 5 juvs; between Grabova peć and Duga peć, Vukotina peć kod Čvaljinskih staja; 42.86° N, 17.96° E; date unknown; J. Kratochvíl leg.(?); NMP • 1 ♂, 1 ♀, 5 juvs; S of Zavala, near Belenići, Bezdán pod Licem; 42.813° N, 18.000° E; 25 Jul. 1932; J. Kratochvíl leg.; NMP • 1 ♂, 2 ♀♀, 1 juv.; Njavre, Donje Hrasno, Markova pećina; 42.9779° N, 17.8269° E; 400 m a.s.l.; 2 Nov. 2016; M. Pavlek leg.; CBSS (Ar 4682) • 17 ♂♂, 8 ♀♀, 1 juv. (2 vials); Počitelj/Čapljina; 43.11° N, 17.73° E; 20 Sep. 1970; A. Senglet leg.; MHNG • 4 ♂♂, 6 ♀♀, 3 juvs; Studenci ("grotte"); 43.161° N, 17.638° E; 21 Sep. 1970; A. Senglet leg.; MHNG • 1 ♂, 4 juvs; Marica pećina; 43.255° N, 17.905° E; 25 Jul. 1936; P. Rémy and A. Schweitzer leg.; MNHN (Ar 10219) • 1 ♀, 3 juvs; Kovina pećina; 43.250° N, 17.935° E; 22 Aug. 1936; P. Rémy and A. Schweitzer leg.; MNHN (Ar 10235) • 2 ♂♂; Drinovci, Majića ponor; 43.3600° N, 17.2834° E; 260 m a.s.l.; 5 Dec. 1999; M. Cukrov leg.; CBSS (Ar 3372) • 1 ♂, 1 ♀; Grude, Peć Mlini, Ravliča pećina; 43.3390° N, 17.3233° E; 250 m a.s.l.; 17 Jul. 1974; C. Deeleman leg.; NMNL (ARA 19022).

**CROATIA – Split-Dalmatia** • 1 ♂; Lećeveca, Kladnjice, Jama 7; 43.6918° N, 16.2915° E; 470 m a.s.l.; 28 Apr. 2020; T. Rožman leg.; CBSS (Ar 6962) • 1 ♂; same locality as for preceding; 17 Apr. 2020; N. Kuharić leg.; CBSS (Ar 6959) • 1 ♀; Lećeveca, Kladnjice, Trasirana jama; 43.6913° N, 16.2873° E; 460 m a.s.l.; 17 Apr. 2020; T. Rožman leg.; CBSS (Ar 6980) • 1 ♂; Muć, Neorić, Velika špilja kod Neorića; 43.686° N, 16.553° E; 705 m a.s.l.; 31 Jul. 2007; M. Pavlek leg.; CBSS (Ar 3374) • 3 ♂♂, 2 ♀♀; Dugopolje, Balići, Balićeva špilja (= Kraljeva pećina); 43.5728° N, 16.5738° E; 405 m a.s.l.; 31 Aug. 2000; F. Gasparo leg.; ZFMK (Ar 22195) • 1 ♂; same locality as for preceding; 12 May 2012; M. Pavlek leg.; CBSS (Ar 3189) • 1 ♀; same locality as for preceding; 5 Nov. 2016; M. Pavlek leg.; CBSS (Ar 4802) • 1 juv.; same locality as for preceding; date unknown; T. Delić *et al.* leg.; ZCSL (S19) • 1 ♀; Dugopolje, Balešina jama; 43.579° N, 16.581° E; 310 m a.s.l.; 28 Apr. 2012; M. Pavlek leg.; CBSS (Ar 2759) • 1 ♂; Dugopolje, Kotlenice, Maklutača, in cave; 43.5693° N, 16.6205° E; 400 m a.s.l.; 5 Nov. 2016; M. Pavlek leg.; CBSS (Ar 4978) • 1 ♂, 2 ♀♀; Dugopolje, Kotlenice, Golubinka pećina; 43.56° N, 16.65° E; 2 May 1978; C. Deeleman leg.; AMNH • 1 ♀; same collection data as for preceding; NMNL (ARA 19016) • 1 ♂, 2 ♀♀, 3 juvs; Dugopolje, near Kotlenice, Vranjača špilja kod Dugopolja ("Vranjača pećina"); 43.5622° N, 16.6482° E; 30 Jul. 1967; C. Deeleman leg.; NMNL (ARA 19020) • 1 juv., assigned tentatively; Dugopolje, Bradarići, Drinovčuća, in cave; 43.5485° N, 16.6386° E; 795 m a.s.l.; 2 Nov. 2017; T. Delić leg.; CBSS (Ar 5698) • 2 ♀♀ (2 vials); Trilj, Ugljane, pećina Turkuša; 43.5789° N, 16.7363° E; 430 m a.s.l.; 16 Apr. 1974; C. Deeleman leg.; NMNL (ARA 19017–18) • 1 ♂, 2 ♀♀; Ugljane, Jama u Krčevini; 43.57° N, 16.76° E; 15 Apr. 1974; C. Deeleman leg.; NMNL (ARA 19019) • 2 ♂♂, 1 ♀; Omiš, Kučice, Nikolina špilja; 43.4253° N, 16.8271° E; 250 m a.s.l.; 23 Mar. 2003; M. Cukrov leg.; CBSS (Ar 2003) • 2 ♂♂, 1 ♀, 1 juv.; Omiš, Cetina ("Cajetina")-Canyon, small valley with stream, dense *Fagus* forest with *Hedera* sp., with big rocks, in crevices, under stones; 95 m a.s.l.; 43.433° N, 16.762° E; 13 May 2006; A. Schönhofner leg.; SMF • 2 ♂♂, 2 ♀♀; Šestanovac, Gornji Balići, Zlatna peć ("Balica zlatna pećina, Balići"); 43.490° N, 16.905° E; 17 Jun. 1974; C. Deeleman leg.; NMNL (ARA 19021) • 5 ♂♂, 7 ♀♀, 1 juv.; Imotski, "N of Imotski near Čočić, Pećina u Solunu" (possibly Špilja u Solunu; 43.4589° N, 17.2217° E); date unknown; J. Kratochvíl leg.(?); NMP • 1 ♀; Brela, Dupci, Svetica, in cave; 43.4011° N, 16.8945° E; 300 m a.s.l.; 16 Nov. 2005; M. Pavlek leg.;





**Figs 35–42.** *Stygopholcus absoloni* (Kulczyński, 1914); male and female from Počitelj/Čapljina, Bosnia and Herzegovina (MHNG). **35–36.** Stridulatory files on male and female chelicerae. **37.** Female palpal tarsal organ. **38.** Tarsal organ on female tarsus 2. **39.** Female prosoma, oblique dorsal view; arrows point at posterior humps acting against modified areas on abdomen. **40.** Epigynum, ventral view. **41.** Female ALS. **42.** Female PMS. Scale bars: 35 = 30  $\mu\text{m}$ ; 36 = 20  $\mu\text{m}$ ; 37–38 = 10  $\mu\text{m}$ , 39 = 200  $\mu\text{m}$ ; 40 = 100  $\mu\text{m}$ ; 41–42 = 10  $\mu\text{m}$ .



CBSS (Ar 2012) • 1 ♂; Brela, Nevistine stine, Jama iznad Prozorčiča; 43.3838° N, 16.9320° E; 615 m a.s.l.; 24 Mar. 2004; H. Bilandžija leg.; CBSS (Ar 1995) • 1 ♂, 1 juv.; Šestanovac, Svaguše, Mužina špilja; 43.4170° N, 17.0076° E; 505 m a.s.l.; 18 Oct. 2002; M. Lukić leg.; CBSS (Ar 1928) • 5 ♂♂, 2 ♀♀; same locality as for preceding; 18 Apr. 1974; C. Deeleman leg.; NMNL (ARA 19011) • 2 ♂♂, 1 ♀; Zagvozd, Sridnja gora, Dedići, Mala špilja na Bukovcima; 43.4037° N, 17.0217° E; 465 m a.s.l.; 21 Nov. 2005; M. Pavlek leg.; CBSS (Ar 2007) • 1 ♀; Zagvozd, Rastovac, Dedići, Špilja u Radinovicima; 43.3873° N, 17.0103° E; 400 m a.s.l.; 25 Oct. 2006; M. Pavlek leg.; CBSS (Ar 2009) • 1 ♂; Zagvozd, Rastovac, Dedići, Raputinova špilja; 43.3865° N, 17.0199° E; 360 m a.s.l.; 24 Nov. 2005; M. Pavlek leg.; CBSS (Ar 2005) • 1 ♂; Zagvozd, Čikeši, Jama u Čikešima; 43.4161° N, 16.9670° E; 200 m a.s.l.; 23 Nov. 2005; M. Pavlek leg.; CBSS (Ar 1996) • 1 ♀; Zagvozd, cave near Zagvozd; 43.40° N, 17.05° E; 13 Oct. 2002; C. Deeleman leg.; CBSS (Ar 1930) • 1 ♂, 5 ♀♀; Zagvozd, Brnasi, Špilja u Gaju; 43.383° N, 17.041° E; 18 Oct. 2002; C. Deeleman leg.; CBSS (Ar 1993) • 2 ♂♂; Zagvozd, Prodani, Pružina špilja; 43.394° N, 17.059° E; 520 m a.s.l.; 15 Oct. 2002; C. Deeleman leg.; CBSS (Ar 1926) • 1 ♀; Zagvozd, Špilja near Katušići; 43.384° N, 17.055° E; 18 Apr. 1974; C. Deeleman leg.; NMNL (ARA 19012) • 1 ♀, 1 juv.; Zagvozd, Župa, Brikinjava špilja; 43.3452° N, 17.0969° E; 740 m a.s.l.; 17 Nov. 2005; M. Pavlek leg.; CBSS (Ar 2000) • 1 ♂; Zagvozd, Župa, Matijaševa peć; 43.3206° N, 17.1223° E; 585 m a.s.l.; 23 Jan. 2016; M. Lukić leg.; CBSS (Ar 3954) • 1 ♀; same locality as for preceding; 23 Jan. 2016; M. Pavlek leg.; CBSS (Ar 3960) • 1 ♂; Zagvozd, Župa, Gradska spila; 43.3180° N, 17.1176° E; 755 m a.s.l.; 23 Jan. 2016; M. Pavlek leg.; CBSS (Ar 3980) • 1 ♂; Zagvozd, Župa, Samogorska špilja; 43.3182° N, 17.1211° E; 715 m a.s.l.; 23 Jan. 2016; M. Pavlek leg.; CBSS (Ar 3935) • 1 ♂; same locality as for preceding; 23 Jan. 2016; M. Lukić leg.; CBSS (Ar 3962) • 1 juv.; same locality as for preceding; 23 Jun. 2017; R. Ozimec leg.; CBSS (5477) • 1 ♂, 1 ♀; Zagvozd, Župa, Stonjska peć donja; 43.3152° N, 17.1307° E; 610 m a.s.l.; 22 Jan. 2016; M. Pavlek leg.; CBSS (Ar 3975) • 1 ♂, 1 ♀, 1 juv.; Baška Voda, Bast, Kukor, in cave; 43.3556° N, 16.9917° E; 425 m a.s.l.; 2 Jan. 1999; R. Ozimec leg.; CBSS (Ar 3367) • 2 ♂♂; same locality as for preceding; 21 Jan. 2016; M. Lukić leg.; CBSS (Ar 3952) • 1 ♂; same locality as for preceding; 21 Jan. 2016; M. Pavlek leg.; CBSS (Ar 3968) • 3 ♀♀, 1 juv.; same locality as for preceding; 21 Jan. 2016; T. Rožman leg.; CBSS (Ar 3971) • 4 juvs, assigned tentatively; Makarska, Stipkovac, Jama pod Stipkovcem; 43.3090° N, 17.0651° E; 1360 m a.s.l.; 21 Jun. 2017; A. Kirin leg.; CBSS (Ar 5467) • 1 ♀, 1 juv.; Tučepi, Ravna Vlaška, Tučepska Vilenjača ("Pećina Vilenjača"); 43.2854° N, 17.0842° E; 1180 m a.s.l.; 28 Aug. 2000; F. Gasparo leg.; ZFMK (Ar 22194) • 1 ♀; same locality as for preceding; 30 Apr. 2012; A. Čukušić leg.; CBSS (Ar 3370) • 1 ♀; same locality as for preceding; 24 Jun. 2017; M. Pavlek leg.; CBSS (5035) • 1 ♂, 2 ♀♀, 1 juv.; Tučepi, Ravna Vlaška, Jama kod Tučepske Vilenjače; 43.2847° N, 17.0850° E; 1195 m a.s.l.; 17 Jun. 2002; R. Ozimec leg.; CBSS (Ar 2001) • 1 ♂, 1 juv.; Vrgorac, Kozica, Jujnovići, Jujnovića špilja; 43.2666° N, 17.1980° E; 405 m a.s.l.; 27 Apr. 2002; R. Ozimec leg.; CBSS (Ar 1999) • 3 ♀♀; same locality as for preceding; 14 Oct. 2002; C. Deeleman leg.; CBSS (Ar 1927) • 1 ♀; same locality as for preceding; 14 Oct. 2002; R. Ozimec leg.; CBSS (Ar 2006) • 1 ♀; same locality as for preceding; 1 May 2012; M. Pavlek leg.; CBSS (Ar 2773) • 1 ♀; Vrgorac, Saranač, Šošići, Jama iznad Saranača; 43.2490° N, 17.1747° E; 770 m a.s.l.; 25 Mar. 2003; R. Ozimec leg.; CBSS (Ar 1998) • 1 ♂, 1 ♀, 7 juvs; probably same locality as for preceding; ["grotje bij Saranač op berg Skok", Gornje Igrane]; 7 Jul. 1974; C. Deeleman leg.; NMNL (ARA 19010) • 1 ♂, 1 ♀; Vrgorac, Zavojane, Signalka, in cave; 43.2691° N, 17.2380° E; 1030 m a.s.l.; 29 Aug. 2018; T. Rožman leg.; CBSS (Ar 6573) • 1 ♂, 3 juvs; Vrgorac, Zavojane, Rodendanska jama; 43.2686° N, 17.2389° E; 1045 m a.s.l.; 29 Apr. 2018; F. Belak leg.; CBSS (Ar 6420) • 1 ♂, 2 juvs; Vrgorac, Zavojane, Škrapica, in cave; 43.2558° N, 17.2679° E; 720 m a.s.l.; 30 Apr. 2018; F. Belak leg.; CBSS (Ar 6578) • 2 ♀♀; Vrgorac, Baletići, Ančića velika Golubinka, in cave; 43.2584° N, 17.2842° E; 875 m a.s.l.; 8 Oct. 2018; N. Kuharić leg.; CBSS (Ar 6553) • 1 ♂, 1 ♀; Vrgorac, Zavojane, Drž gače 2, in cave; 43.2590° N, 17.2828° E; 870 m a.s.l.; 8 Oct. 2018; N. Sudar and N. Kuharić leg.; CBSS (Ar 6395) • 1 ♂, 2 ♀♀; Vrgorac, Stilja, Jama pod Gažnovcem; 43.2297° N, 17.3142° E; 510 m a.s.l.; 4 Nov. 2016; M. Pavlek leg.; CBSS (Ar 4283) • 3 ♀♀, 1 juv.; same locality as for preceding; 31 Mar. 2018; F. Belak leg.; CBSS (Ar 6587) • 1 ♂, 1 ♀, 1 juv. (2 vials); Vrgorac, Orah

[hill], Ružovača pećina; 43.229° N, 17.417° E; 390 m a.s.l.; 23 Oct. 1980 and 26 Apr. 1981; C. Deeleman leg.; NMNL (ARA 19008–9) • 1 ♀, 1 juv.; Hvar Island, Jelsa, Viskoka, Franetova jama; 43.14° N, 16.93° E; 28 Feb. 1999; R. Ozimec leg.; CBSS (Ar 3363) • 1 ♀; Hvar Island, Jelsa, Zastrazišće, Vela Stiniva cove, Špilja u Grliću; 43.1580° N, 16.8136° E; 3 m a.s.l.; 3 May 2011; D. Hmura leg.; CBSS (Ar 2513) • 2 ♂♂; same locality as for preceding; 19 Aug. 2016; M. Pavlek leg.; CBSS (Ar 3996) • 1 ♀; Hvar Island, Jelsa, Humac, Grapčeva špilja; 43.1341° N, 16.7537° E; 200 m a.s.l.; 3 May 2011; A. Čukušić leg.; CBSS (Ar 2512) • 1 ♂, 1 ♀ (epigynum missing); same locality as for preceding, “Grabčina šplija”; 20 Aug. 1968; P. Brignoli leg.; MCVR • 2 ♂♂, 1 juv. (2 vials); same locality as for preceding; 26 Oct. 1980 (one vial without date); C. Deeleman leg.; NMNL (ARA 19013–14). – **Dubrovnik-Neretva** • 1 ♀, 1 juv.; Ploče, Gradac, Ričevica, in cave; 43.0999° N, 17.3909° E; 525 m a.s.l.; 5 Nov. 2019; T. Rožman leg.; CBSS (Ar 6430) • 1 ♀, 1 juv.; Kula Norinska, Krvavac, Kokanova jama; 43.0273° N, 17.5849° E; 90 m a.s.l.; 12 Dec. 2018; B. Jalžić leg.; CBSS (Ar 6481) • 1 ♀; Zažablje, Goračić, Vidonje, Šolkina jama; 42.9665° N, 17.6625° E; 230 m a.s.l.; 27 Feb. 2016; B. Jalžić leg.; CBSS (Ar 3989) • 2 ♀♀; Zažablje, Dobranje, Kornjatuša, in cave; 42.9790° N; 17.6740° E; 610 m a.s.l.; 2 Nov. 2013; T. Čuković leg.; CBSS (Ar 3384) • 1 ♀; Dubrovačko Primorje, Slano, Točionik, Vranja peć; 42.8683° N, 17.8124° E; 230 m a.s.l.; 2 Nov. 2016; T. Rožman leg.; CBSS (Ar 5148) • 1 ♀; same locality as for preceding; 2 Nov. 2006; M. Pavlek leg.; CBSS (Ar 4877) • 1 ♂, 1 ♀; Pelješac, Ston, Ponikve, Špilja Crno jezero; 42.8473° N, 17.6365° E; 415 m a.s.l.; 15 Nov. 2018; N. Kuharić leg.; CBSS (Ar 6276) • 1 ♂; same collection data as for preceding; CBSS (Ar 6284) • 1 ♀; Pelješac, Ston, Putniković, Kameni kolačić, in cave; 42.8731° N, 17.4664° E; 420 m a.s.l.; 28 Mar. 2019; N. Kuharić leg.; CBSS (Ar 6161) • 1 ♀; Pelješac, Janjina, Vardišta, Špilja u Žarmi; 42.9354° N, 17.4382° E; 35 m a.s.l.; 28 Apr. 2019; T. Rožman leg.; CBSS (Ar 6258) • 1 ♂, 1 juv.; same collection data as for preceding; M. Pavlek leg.; CBSS (Ar 6261) • 1 ♂; Pelješac, Orebić, Oskorušno, Špilja kod Zagrada u vinogradu; 42.9666° N, 17.3227° E; 295 m a.s.l.; 13 Dec. 2019; M. Pavlek leg.; CBSS (Ar 6464) • 1 ♀; Pelješac, Orebić, below monastery, Čagjina jama; 42.9771° N, 17.1552° E; 115 m a.s.l.; 14 Nov. 2018; F. Šarc leg.; CBSS (Ar 6247) • 1 ♀; Pelješac, Orebić, Kućište, Šimunkovića špilja; 42.9786° N, 17.1291° E; 50 m a.s.l.; 3 Nov. 2016; M. Pavlek leg.; CBSS (Ar 4692) • 1 ♀, 2 juvs; same locality as for preceding; 26 Apr. 2019; T. Rožman leg.; CBSS (Ar 6781) • 1 ♂; Pelješac, Trpanj, Duba Pelješka, Špilja Rupine; 43.0053° N, 17.1580° E; 460 m a.s.l.; 6 Apr. 2019; T. Dražina leg.; CBSS (Ar 5980) • 1 ♀; same locality as for preceding; 24 Apr. 2019; M. Pavlek leg.; CBSS (Ar 5986) • 1 ♂; same locality as for preceding; 24 Apr. 2019; T. Rožman leg.; CBSS (Ar 6197) • 1 ♂; Pelješac, Trpanj, Donja Vručica, Špilja u Privoru; 43.0092° N, 17.2133° E; 180 m a.s.l.; 26 Mar. 2019; N. Kuharić leg.; CBSS (Ar 6038) • 1 ♀, 1 juv.; Pelješac, unnamed cave near Trpanj; 43.01° N, 17.27° E; 18 Jun. 1975; C. Deeleman leg.; NMNL (ARA 19015) • 1 ♂; Korčula, Žrnovo, Deukalion špilja; 42.9557° N, 17.0976° E; 110 m a.s.l.; 21 Mar. 2010; R. Ozimec leg.; ROC (R97).

**Assigned tentatively** (see Variation)

CROATIA – **Split-Dalmatia** • 1 ♂; Baška Voda, Bast, Topići, Jama na Brezdanu; 43.3670° N, 16.9732° E; 915 m a.s.l.; 20 Mar. 2004; collector unknown; CBSS (Ar 1994).

**Credible published records** (not examined or juveniles only)

BOSNIA AND HERZEGOVINA • 3 juvs; near Čvaljina, Duboka peć; 42.87° N, 17.97° E; date unknown; J. Kratochvíl leg.(?); NMP • ♂♀(?), material apparently lost; between Timor brdo and Čvaljina village, Duga peć; 42.87° N, 17.95° E; date unknown; J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; Baba pećina; 42.8608° N, 17.9722° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; 500 m W of “Bjelušica pećina”, env. Zavala, Orlica pećina; 42.846° N, 17.973° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • 1 juv.; S of Zavala, near Belenići, Jama za Jamskim vrhom; 42.81° N, 18.00° E; 28 Jul. 1932; J. Kratochvíl leg.(?); NMP.

CROATIA – **Split-Dalmatia** • ♂♀(?), material apparently lost; Muć, near Sinj, Pećina kod Sinja; 43.70° N, 16.64° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; Dugopolje, near Kotlenice, Vranjača špilja kod Dugopolja (“Vranjača pećina”); 43.5622° N, 16.6482° E; 445 m a.s.l.; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; Dugopolje, near Dugopolje, Kraljeva pećina [Kratochvíl 1940 used this present-day synonym of Balićeva špilja for a cave “near” Balićeva špilja]; 43.573° N, 16.570° E, 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; Dugopolje, near Dugopolje, Balićeva špilja; 43.573° N, 16.570° E; 405 m a.s.l.; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; Hvar Island, Jelsa, Grapčeva špilja (“Grabčina šplija”); 43.1341° N, 16.7537° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940].

## Redescription

### Male (Zavala, MHNG)

MEASUREMENTS. Total body length 5.8, carapace width 2.2. Distance PME–PME 150 µm; diameter PME 140 × 180 µm; distance PME–ALE 30 µm; diameter AME 65 µm; distance AME–AME 25 µm. Leg 1: 55.2 (14.8 + 1.1 + 14.0 + 22.1 + 3.2), tibia 2: 10.8, tibia 3: 8.7, tibia 4: 9.5; tibia 1 L/d: 62.

COLOR (in ethanol). Carapace pale whitish to ochre-yellow, ocular area and clypeus slightly darker (light brown); sternum light brown, with darker brown radial marks; legs ochre yellow, without dark rings, without dark lines; abdomen monochromous pale gray, only above spinnerets with darker mark.

BODY. Habitus as in Fig. 1. Ocular area slightly raised. Carapace with deep median pit and pair of very shallow indistinct furrows diverging from pit to posterior margin of carapace. Clypeus unmodified. Sternum wider than long (1.50/1.00), unmodified. Abdomen oval, pointed at spinnerets.

CHELICERAE. As in Figs 19–20, with pair of large frontal apophyses set with 2 and 3 modified hairs, respectively, with 17 and 18 modified hairs each on frontal face; with distinct stridulatory ridges (Fig. 35).

PALPS. In general as in *S. skotophilus* (cf. Figs 6–8); coxa with retrolateral hump; trochanter barely modified; femur with distinct retrolateral process proximally, with stridulatory pick (modified hair) proximally on prolateral side; femur-patella joints shifted towards prolateral; tibia very large, with two trichobothria; tibia-tarsus joints shifted towards retrolateral; procurus (Figs 12–13) slightly curved towards ventral, dorsally with curved hairs (distal third curved ‘upwards’), with strong hump on prolateral side (asterisk in Fig. 12). Procurus tip with evenly curved dorsal sclerite and strong hinged ventral sclerite (ds and vs in Figs 13, 29); with strong conical process on prolateral side bordering hinged sclerite (arrow in Fig. 14); membranous central part on retrolateral side with brush of hair-like processes (Fig. 29). Genital bulb (Figs 15–18) with basal sclerite connecting to tarsus (bs in Fig. 15), small transparent dorsal process (arrow in Fig. 17; Fig. 33), and main sclerite consisting of long retrolateral process and short dorsal process (rp and dp in Figs 15–18, 32); retrolateral process with bifid tip, distal part on ventral side thickened and heavily sclerotized; dorsal process with finger-shaped ventral tip slightly hooked, retrolateral tip wider, with additional strong protrusion on ventral side.

LEGS. With short spines ventrally on femur 1 in two rows, prolateral row ~19 spines, retrolateral row ~24 spines; without curved hairs; few vertical hairs; retrolateral trichobothrium of tibia 1 at 3%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 with irregular platelets rather than with distinct pseudosegments.

### Male (variation)

Most males with monochromous abdomen with one or few dark marks above spinnerets; few males with additional dark marks laterally in posterior third. Tibia 1 (N = 60): 10.4–15.1 (mean 12.8); tibia 2

(N = 64): 7.6–11.5 (mean 9.6); spines on femur 1 (N = 27): 0–48 (mean 38); modified hairs on cheliceral basis (N = 122): 11–23 (mean 17.4); modified hairs on cheliceral apophysis (N = 122): 1–4 (mean 2.6); chelicerae maximum width (N = 61): 0.66–0.85 (mean 0.78); procurus length (N = 58): 1.10–1.28 (mean 1.21); bulbal measures A–E: A (N = 28): 0.31–0.37 (mean 0.35); B (N = 28): 0.06–0.08 (mean 0.07); C (N = 20): 0.22–0.28 (mean 0.26); D (N = 20): 0.18–0.23 (mean 0.21); E (N = 22): 0.68–0.77 (mean 0.73); epiandrous spigots (N = 20): 5–7 (mean 6.1).

In the single male from Jama na Brezdanu (Croatia), the bulb differs in several respects from all other material examined, but it is unclear if this is teratological or not (even though it is symmetric). Most conspicuously, the heavy sclerite connecting the basal and distal bulbal sclerites (asterisk in Fig. 18) is much smaller and it is not connected to the basal bulbal sclerite; bulb measure E also deviates strongly (asterisk in Fig. 160).

### Female

In general similar to male, but femur 1 without spines, with pair of indistinct processes posteriorly on carapace (arrows in Fig. 39) and pair of opposing poorly visible plates on abdomen; distance between processes/plates: 1.1. Tibia 1 (N = 55): 8.2–15.1 (mean 12.0); tibia 2 (N = 59): 4.4–11.1 (mean 8.6); epigynum width (N = 57): 0.72–1.22 (mean 1.05); epigynum length (N = 57): 0.42–0.68 (mean 0.54); epigynal measure F (N = 57): 0.21–0.37 (mean 0.30). Epigynum (Figs 23–26) anterior plate semicircular, weakly protruding, with weak transversal furrows, with internal structures visible in uncleared specimens: round anterior structure and parallel sclerites posteriorly; posterior plate short but wide. Internal genitalia (Figs 21–22, 145–146) with distinctive ventral arc (va in Fig. 153; relatively shorter and wider than in other species), with large pore plates (Fig. 22).

### Distribution

Known from southern Croatia and southern Bosnia and Herzegovina (Fig. 168).

### *Stygopholcus skotophilus* Kratochvíl, 1940

Figs 2, 6–8, 43–76, 147–148, 154

*Stygopholcus skotophilus* Kratochvíl, 1940: 16, figs 1a, c, 2, 4c–d, 5c–d, 6, 7 (right).

*Holocnemus* (*Hoplopholcus*) *Absolonii* Kulczyński, 1914: 355 (part), pl. 16, fig. 25 only.

*Holocnemus* (*Stygopholcus*) *absoloni* (misidentification) – Kratochvíl 1935: 11.

*Stygopholcus skotophilus* – Senglet 1971: figs 40–41; 2001: 65, fig. 22.

*Hoplopholcus scotophilus* – Brignoli 1971: 261, fig. 19. — Tomić *et al.* 2000: 35P (specimen from Vidrovan cave).

*Stygopholcus skotophilus montenegrinus* (misidentification) – Naumova *et al.* 2016: 434 (all specimens except those from Cetinje, Golubova pećina, and Babatuša pećina).

“S112 *Stygopholcus absoloni*? Bal15” & “S108 *Stygopholcus absoloni*? Bal8” – Eberle *et al.* 2018. — Huber *et al.* 2018.

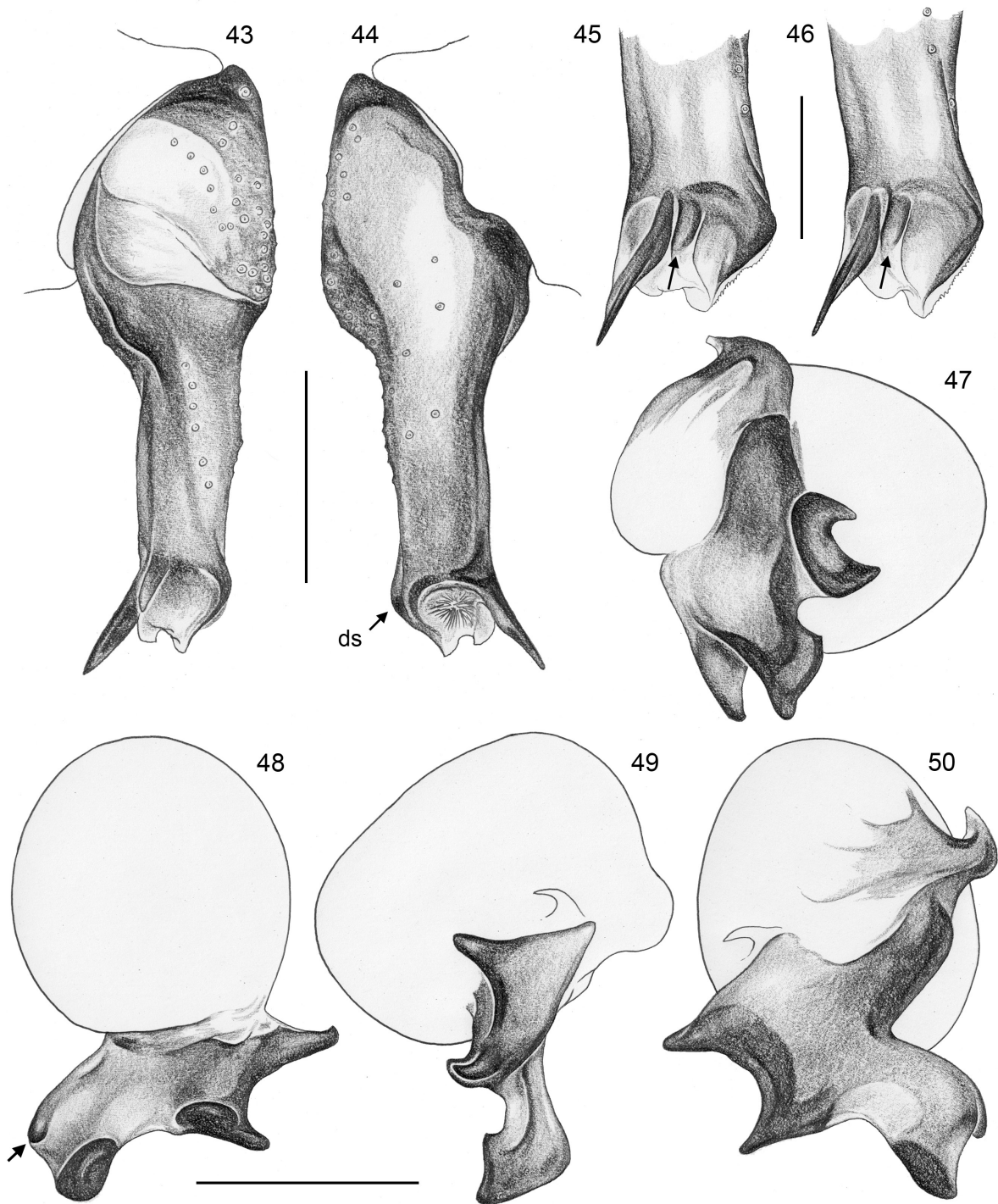
### Misidentification

*Hoplopholcus scotophilus* – Tomić *et al.* 2000: 35P (specimens from near Velja cave; see *S. montenegrinus*).

### Diagnosis

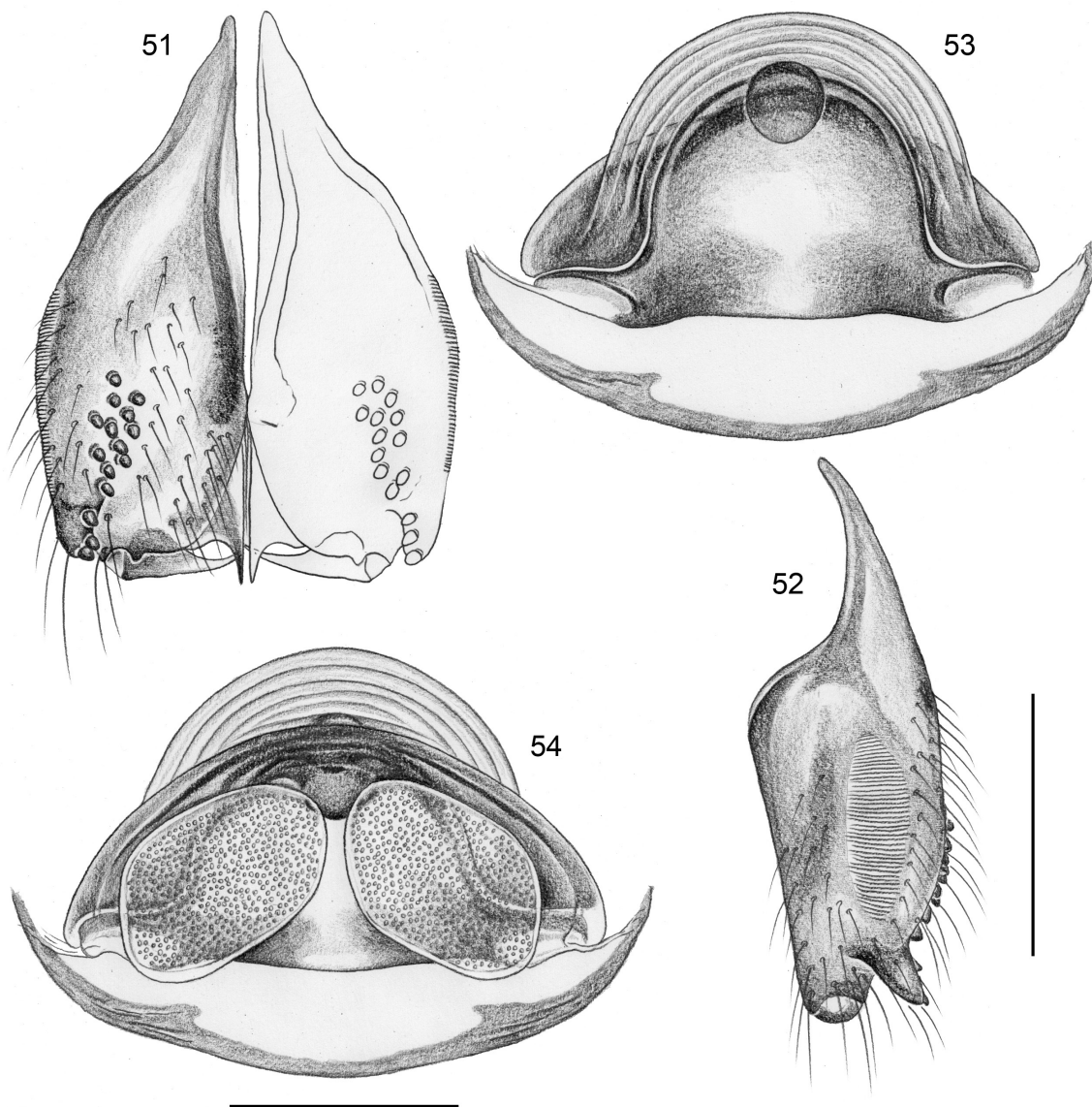
Distinguished from other species in the ‘northern clade’ (*S. absoloni*; *S. montenegrinus*) by bulb measures A and C (Fig. 158; smaller than other species, no overlap), by bulb measure D (Fig. 159; larger





**Figs 43–50.** *Stygopholcus skotophilus* Kratochvíl, 1940. **43–44.** Male from Ilijina pećina, Bosnia and Herzegovina (ZFMK (Ar 22198)), left tarsus and procurcus, prolateral and retrolateral views. **45–46.** Males from Pećina u Ivici, Montenegro (ZFMK (Ar 22196)) and from Grabova pećina, Sedlari, Bosnia and Herzegovina (MHNG), tip of left procurcus, prolateral (slightly ventral) views; arrows point at distinctive prolateral sclerites. **47–50.** Male from Ilijina pećina (ZFMK (Ar 22198)), left genital bulb, retrolateral, ventral, prolateral-distal, and dorso-distal views; arrow points at wart that is more strongly developed in specimens from near Sedlari. ds = dorsal sclerite. Scale bars: 43–44, 47–50 = 0.5 mm; 45–46 = 0.25 mm.

than other species, with little overlap), and by epigynal measure F (Fig. 164; larger than other species, with little overlap); from *S. absoloni* also by fewer hairs on male cheliceral base (Figs 51, 162; with little overlap), by smaller, weakly sclerotized prolateral sclerite on procurus (arrows in Figs 45–46), by straight procurus (rather than curved toward ventral; Fig. 44), by longer procurus (Fig. 161; with little overlap), by shape of retrolateral bulbal process in retrolateral view (Fig. 47; large notch on ventral side), and by bulb measures B and E (Figs 157, 160; larger than in *S. absoloni*, with little overlap); from *S. montenegrinus* also by wider prolateral sclerite on procurus (arrows in Figs 45–46);



**Figs 51–54.** *Stygopholcus skotophilus* Kratochvíl, 1940; male from Ilijina pećina, Bosnia and Herzegovina (ZFMK (Ar 22198)), female from Pećina u Ivici, Montenegro (ZFMK (Ar 22196)). **51–52.** Male chelicerae, frontal and lateral views. **53–54.** Cleared female genitalia, ventral and dorsal views. Scale bars: 0.5 mm.



**Type material**

MONTENEGRO – **Kotor** • 1 ♂, 1 ♀ (without epigynum), 5 juvs, 1 prosoma (juv.?), 1 damaged abdomen (juvenile?), one complete juvenile abdomen, putative syntypes (see Remark below), examined; Pećina u Ivici; 42.5384° N, 18.6207° E [Naumova *et al.* 2019: 42.569° N, 18.662° E]; date and collector unknown; NMP.

**Remark**

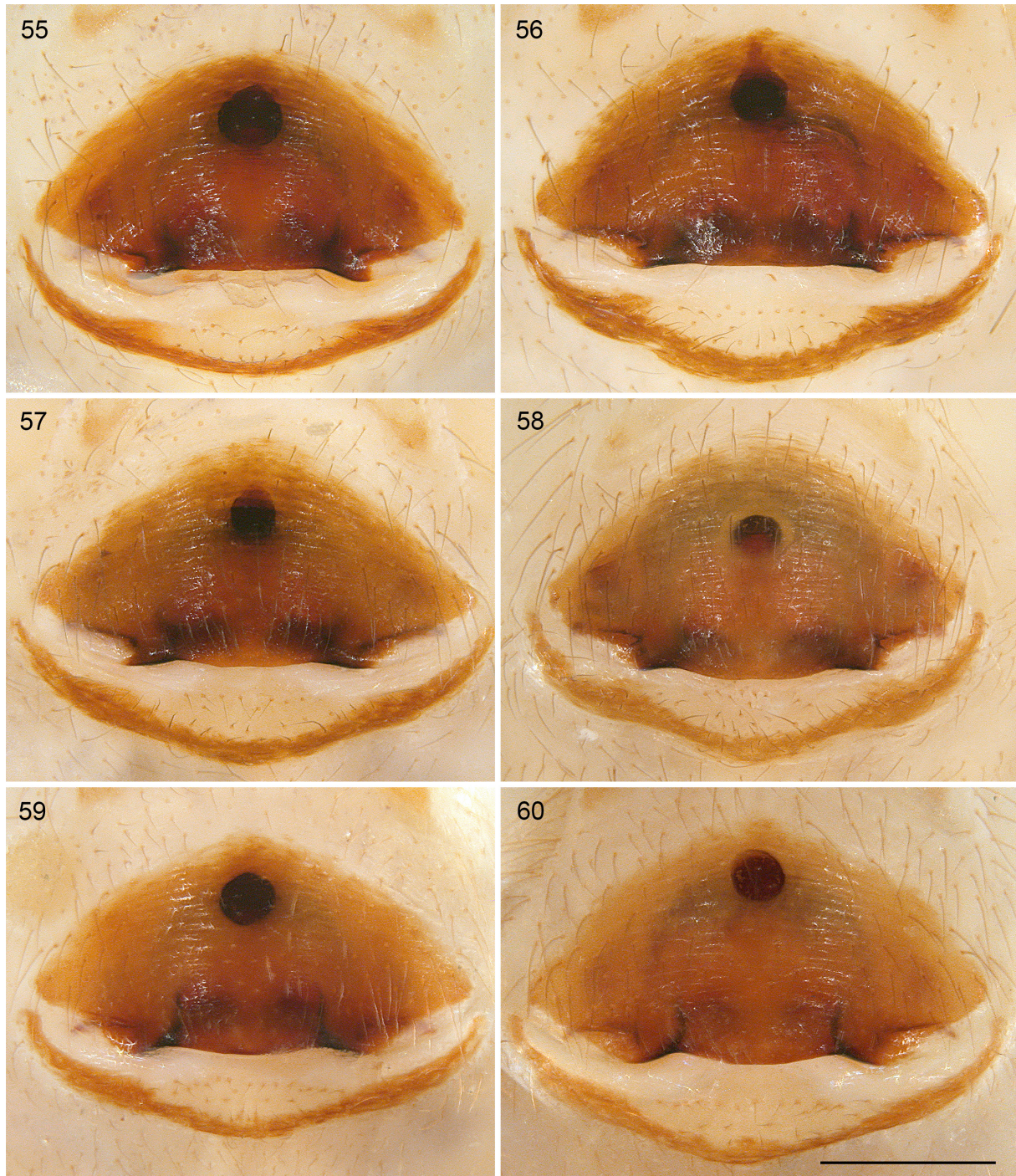
According to Růžička *et al.* (2005), the type vial originally contained two labels saying “*Stygopholcus skotophilus* sp. n.” and “Pećina u Ivici, č. III”. This agrees with other labels in Kratochvíl’s handwriting in the NMP *Stygopholcus* material. Both labels are lost. Růžička *et al.* (2005) further state that the vial contained “1♂ 3♀ (one of them without epigyne) 4 juv.”, suggesting that there were two epigyna. However, the vial does not contain any epigynum.

**Other material examined**

MONTENEGRO – **Kotor** • 7 ♂♂, 6 ♀♀, 1 juv.; near Zvečava, Pećina u Ivici, in cave; 42.5384° N, 18.6207° E; 960 m a.s.l.; 28 May 2014; B.A. Huber and M. Komnenov leg.; ZFMK (Ar 22196) • 1 ♂, 1 ♀, 3 juvs, in pure ethanol; same collection data as for preceding; ZFMK (Bal15) • 9 ♂♂, 7 ♀♀; near Zvečava, near Pećina u Ivici, under stones in forest; 42.5349° N, 18.6237° E; 1000 m a.s.l.; 28 May 2014; B.A. Huber and M. Komnenov leg.; ZFMK (Ar 22197) • 2 ♀♀, 1 juv., in pure ethanol; same collection data as for preceding; ZFMK (Bal16) • 1 ♀; Crkvice, Vilina pećina; 42.5546° N, 18.6624° E [Naumova *et al.* 2019: 42.560° N, 18.629° E]; 855 m a.s.l.; 30 Oct. 2015; M. Pavlek leg.; CBSS (Ar 3674) • 1 juv.; same locality as for preceding; 17 Jul. 1973; C. Deeleman leg.; NMNL (ARA 19032) • 1 ♂, 1 ♀; Crna Gora, Dragalj, Pećina kod Dvoriškog ždrijela; 42.5881° N, 18.6737° E; 715 m a.s.l.; 3 Dec. 2014; M. Pavlek leg.; CBSS (Ar 3482) • 1 ♂, 3 ♀♀; Crni Nugli, unnamed cave; 42.586° N, 18.697° E; 590 m a.s.l.; 26 Mar. 2006; B. Petrov and S. Lazarov leg.; NMNHS • 5 ♂♂, 1 juv., Crni Nugli, Čora pećina; 42.594° N, 18.712° E; 750 m a.s.l.; 26 Mar. 2006; B. Petrov and S. Lazarov leg.; NMNHS • 1 ♂, 1 juv.; Crni Nugli, Dragalj, Pećina s mostom; 42.5929° N, 18.7100° E; 725 m a.s.l.; 25 Aug. 2017; M. Pavlek leg.; CBSS (Ar 5387) • 1 ♀; same locality as for preceding; 25 Aug. 2017; A. Kirin leg.; CBSS (Ar 5391) • 1 ♀; Crni Nugli, Dragalj, Trokutasta pećina; 42.5931° N, 18.7107° E; 710 m a.s.l.; 25 Aug. 2017; A. Kirin leg.; CBSS (Ar 5395) • 1 ♂; 4 km SW Crni Nugli, Miljukovica pećina [Kratochvíl 1935: “Mijukovica”]; 42.57° N, 18.67° E; 1932(?); J. Kratochvíl leg.(?); NMP • 1 ♀; Risan, Teveričke Polje, Teverička pećina; 780 m a.s.l.; 42.570° N, 18.676° E; 28 Jul. 2010; M. Komnenov leg.; CMK • 1 ♀; Risan, Kameno More, Knezlaz, Bukovica pećina; 42.545° N, 18.683° E; 1 Aug. 2010; M. Komnenov leg.; CMK • 2 ♀♀; Risan, Kameno More, Gornja Pokljuka pećina; 42.542° N, 18.693° E; 580 m a.s.l.; 31 Jul. 2010; M. Komnenov leg.; CMK • 7 ♂♂, 5 ♀♀, 2 juvs; same locality as for preceding; 27 Mar. 2006; B. Petrov and S. Lazarov leg.; NMNHS • 2 ♂♂; Risan distr., Crkvice vill., potholes near Shuto Blagojević monastery; 42.568° N, 18.623° E; 1045 m a.s.l.; 17 Aug. 2006; B. Petrov and S. Lazarov leg.; NMNHS • 1 ♂; Blagojevići, Ovnova rupa, in cave; 42.5681° N, 18.6298° E; 1040 m a.s.l.; 25 Aug. 2017; M. Pavlek leg.; CBSS (Ar 5384) • 2 ♂♂, 3 juvs; Strmena pećina, selo Han, 2 km E of Bor pećina, near Veli Vrh; 42.564° N, 18.633° E; 28 Jul. 1969; J. Kratochvíl leg.; NMNL (ARA 19030) • 1 ♀; Risan, Sopot pećina; 42.5137° N, 18.6816° E; 13 Jul. 1971; C. Deeleman leg.; NMNL (ARA 19031). – **Nikšić** • 1 ♂; Grahovo, Pećina Vojvode Dakovića; 42.6558° N, 18.6758° E; 680 m a.s.l.; 6 Nov. 2015; M. Lukić leg.; CBSS (Ar 3780) • 1 ♂; same locality as for preceding; 6 Nov. 2015; A. Kirin leg.; CBSS (Ar 3776) • 2 ♂♂, 1 ♀; same locality as for preceding; 28 Mar. 2006; B. Petrov and S. Lazarov leg.; NMNHS • 1 ♂, 4 ♀♀; Trubjela, Krstac, Pećina kod Krstaca; 42.7659° N, 18.8031° E; 925 m a.s.l.; 21 Aug. 2017; M. Pavlek leg.; CBSS (Ar 5355) • 1 ♂; same collection data as for preceding; CBSS (Ar 5356) • 2 ♂♂ (2 vials); Trubjela, Kita, pećina Ledenica na Kiti; 42.7729° N, 18.7843° E; 6 Aug. 1969 and 24 Jul. 1970; C. Deeleman leg.; NMNL (ARA 19033–34) • 1 ♂, 2 ♀♀, 3 juvs; Podkita, Širbaba pećina; 42.786° N, 18.825° E; 940 m a.s.l.; 28 Mar. 2006; B. Petrov and S. Lazarov leg.; NMNHS • 1 ♂, 1 ♀,

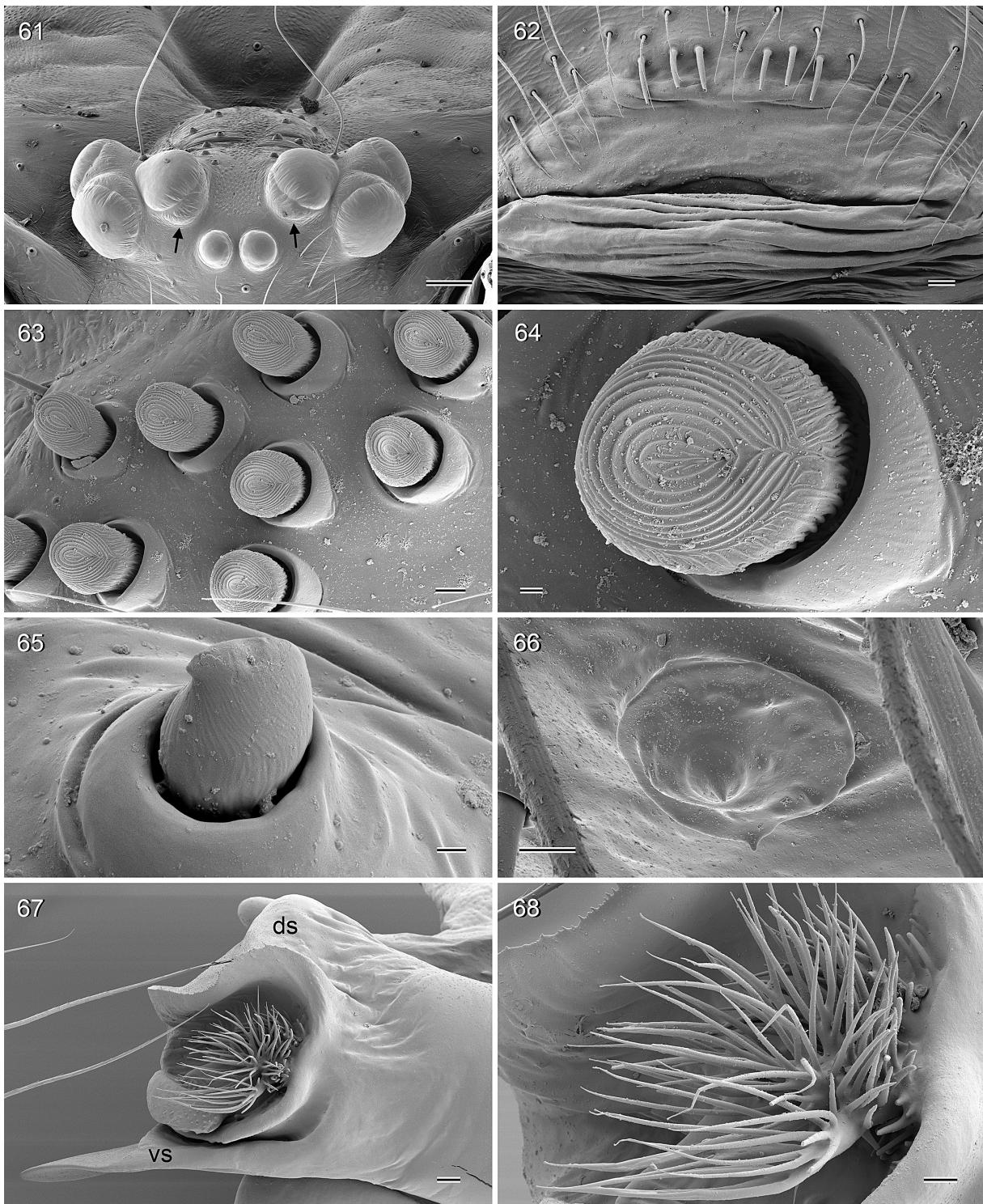


1 juv.; Vidrovan, Vidrovanska pećina; 42.858° N, 18.937° E; 660 m a.s.l.; 29 Apr. 2016; T. Delić, D. Škufca and Zamolo leg.; ZCSL (S227) • 2 ♂♂, 2 ♀♀; same locality as for preceding; 17 Aug. 2011; M. Komnenov leg.; CMK • 1 ♂; same locality as for preceding; 5 Sep. 2000; B. Čurčić leg.; IZUB • 1 ♂, 1 ♀; Golija Mt., Donje Čarađe, Drljača pećina; 43.023° N, 18.674° E; 1035 m a.s.l.; 13 Aug. 2010; M.



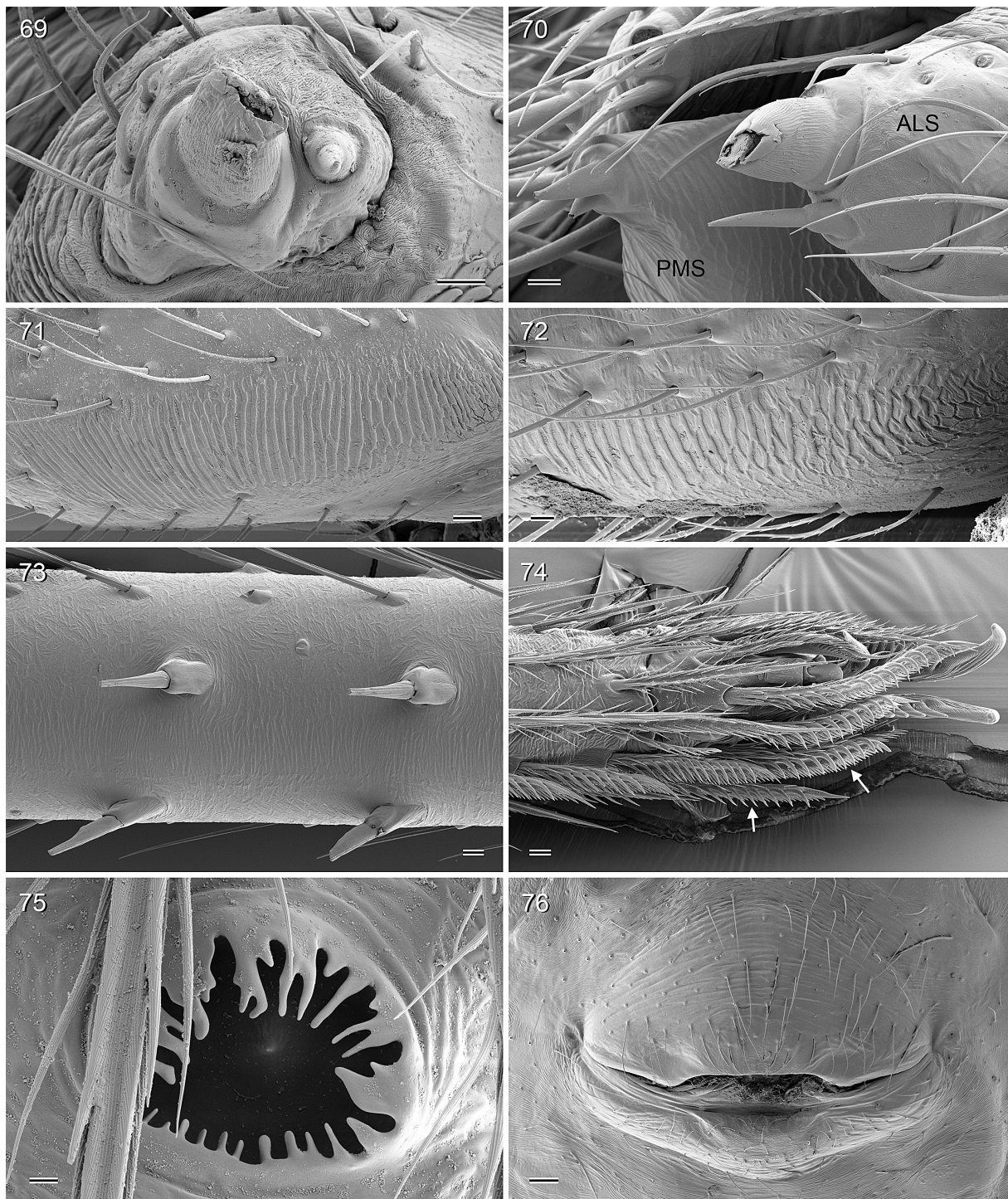
**Figs 55–60.** *Stygopholcus skotophilus* Kratochvíl, 1940; epigyna, ventral views. **55–56.** Pećina u Ivici, Montenegro (ZFMK (Ar 22196)). **57.** Ilijina pećina, Bosnia and Herzegovina (ZFMK (Ar 22198)). **58.** Studena pećina, Bosnia and Herzegovina (CMK). **59–60.** Specimens assigned tentatively from Grabova pećina, Sedlari, Bosnia and Herzegovina (MHNG). Scale bar: 0.5 mm (all at same scale).





**Figs 61–68.** *Stygopholcus skotophilus* Kratochvíl, 1940; male and female from Ilijina pećina, Bosnia and Herzegovina (ZFMK (Ar 22198)). **61.** Male ocular area, frontal view; arrows point at ‘pseudo-eyes’. **62.** Male gonopore and epiandrous spigots. **63–64.** Modified hairs frontally on male chelicerae. **65.** Stridulatory pick on male palpal femur. **66.** Male palpal tarsal organ. **67.** Tip of left procurus, retrolateral view. **68.** Hair-like structures on tip of procurus (detail of previous image). Abbreviations: ds = dorsal sclerite; vs = ventral sclerite. Scale bars: 61 = 100  $\mu\text{m}$ ; 62, 67 = 20  $\mu\text{m}$ ; 63, 66, 68 = 10  $\mu\text{m}$ ; 64–65 = 2  $\mu\text{m}$ .





**Figs 69–76.** *Stygopholcus skotophilus* Kratochvíl, 1940; male and female from Ilijina pećina, Bosnia and Herzegovina (ZFMK (Ar 22198)). 69. Male ALS. 70. Female ALS and PMS. 71–72. Stridulatory files on male and female chelicerae. 73. Spines on male femur 1. 74. Tip of male right tarsus 4, ventral view; arrows point at comb-hairs. 75. Tarsal organ on male tarsus 4. 76. Epigynum, ventral view. Abbreviations: ALS = anterior lateral spinneret; PMS = posterior median spinneret. Scale bars: 69–70, 72, 74 = 10  $\mu$ m; 71, 73 = 20  $\mu$ m; 75 = 2  $\mu$ m; 76 = 100  $\mu$ m.



Komnenov leg.; CMK • 1 ♀; [near Javljem], Kerovačka pećina; 42.9981° N, 18.7273° E; 4 Aug. 1969; C. Deeleman leg.; NMNL (ARA 19036) • 1 ♂, 1 ♀; Golija Mt., Stozi, Stoška pećina; 42.952° N, 18.781° E; 1230 m a.s.l.; 10 Aug. 2010; M. Komnenov leg.; CMK • 1 ♂; Golija Mt., Jasikovice, Lazareva pećina; 43.038° N, 18.699° E; 8 Aug. 2010; M. Komnenov leg.; CMK. – **Plužine** • 1 ♂; Zaborije, (Golija) Donja Brezna, Đokova Ledenica pećina; 43.0333° N, 18.8528° E; 1 Aug. 1972; C. Deeleman leg.; NMNL (ARA 19037).

BOSNIA AND HERZEGOVINA • 8 ♂♂, 6 ♀♀; near Trebinje, Kličanj brdo (hill), Ilijina pećina, in cave near eastern entrance; 42.7188° N, 18.3303° E; 550 m a.s.l.; 26 May 2014; B.A. Huber and M. Komnenov leg.; ZFMK (Ar 22198) • 2 ♀♀, 2 juvs, in pure ethanol; same collection data as for preceding; ZFMK (Bal8) • 2 ♂♂, 1 ♀; same locality as for preceding; 3 Apr. 2012; M. Lukić leg.; CBSS (Ar 3376, 3379) • 1 ♀, 1 juv.; Trebinje, Kličanj brdo, Vučja pećina; 42.716° N, 18.326° E; 425 m a.s.l.; 27 Jan. 2007; J. Bedek leg.; CBSS (Ar 3383) • 2 ♂♂, 4 ♀♀; same locality as for preceding; 6 Dec. 2014; M. Pavlek leg.; CBSS (Ar 3481) • 2 juvs; same locality as for preceding; 27 Jan. 2007; H. Bilandžija leg.; CBSS (Ar 3375) • 3 ♂♂, 2 ♀♀; Trebinje, Arenstorfova pećina; 42.695° N, 18.364° E; 6 Sep. 2006; M. Komnenov leg.; CMK • 1 ♂, 1 ♀; Trebinje, Petrina, Matulićeva pećina; 42.694° N, 18.362° E; 6 Sep. 2006; M. Komnenov leg.; CMK • 2 ♂♂, 1 ♀; Trebinje, Zupci, Vilina pećina; 42.663° N, 18.364° E; 5 Sep. 2006; M. Komnenov leg.; CMK • 1 ♂, 2 ♀♀, 21 juvs (2 vials); same locality as for preceding; 22 Jul. 1969; J. Kratochvíl leg.; NMNL (ARA 19025–6) • 3 ♂♂, 3 ♀♀; Trebinje, Ilijin vrh, Narančivi, Mitrušica pećina; 42.732° N, 18.268° E; 20 Sep. 2008; M. Komnenov leg.; CMK • 3 ♂♂, 2 ♀♀, 7 juvs; Trebinje, Dražin Do, Pećina kod Rupe [“pećina kod rupa, selo Dražin”]; 42.71° N, 18.30° E; 24 Jul. 1969; J. Kratochvíl leg.; NMNL (ARA 19029) • 1 ♀, 3 juvs; Trebinje, Dražin do, Tučevac, in cave; 42.7142° N, 18.3033° E; 21 Aug. 2017; A. Kirin leg.; CBSS (Ar 5372) • 1 ♀, Trebinje, Taleža, Taleža pećina; 42.714° N, 18.231° E; 270 m a.s.l.; 7 Sep. 2006; M. Komnenov leg.; CMK • 1 ♂, 4 ♀♀; near Trebinje, Bihovo, Pavlova pećina [= Ilijina pećina near Bihovo; cf. Lukić *et al.* 2020], in cave near entrance; 42.6665° N, 18.3078° E; 420 m a.s.l.; 26 May 2014; B.A. Huber and M. Komnenov leg.; ZFMK (Ar 22199–22200) • 1 ♀, 2 juvs, in pure ethanol; same collection data as for preceding; ZFMK (Bal9) • 1 ♀, misidentified paralectotype of *S. absoloni*; same locality as for preceding; 20 Jul. 1912; K. Absolon leg.; MIZW • 1 ♀, 3 juvs; same locality as for preceding (“Eliashöhle”); date unknown; Verhoeff leg.; ZMB (9067) • 1 ♀ [and 1 male palp, possibly from different locality, according to label by P. Brignoli]; same collection data as for preceding; MCVR • 1 ♂, 1 ♀; Zupci, Lemov do, Lemova pećina; 42.609° N, 18.399° E; 14 Sep. 2006; M. Komnenov leg.; CMK • 1 ♂; Orjen, Ubla, Čavčina jama; 42.598° N, 18.520° E; 18 Aug. 2007; M. Komnenov leg.; CMK • 1 ♀; Grebci, Debelin pećina [“Debeljin pećina, Osojnik”]; 42.7202° N, 18.0955° E; 420 m a.s.l.; 16 Jul. 1972; J. Kratochvíl leg.; NMNL (ARA 19023) • 1 ♂, 1 juv.; Grebci, Kali pećina; 42.7406° N, 18.0626° E; 525 m a.s.l.; 17 Jul. 1972; C. Deeleman leg.; NMNL (ARA 19024) • 1 ♀; Njemanica, unnamed cave below Jametina jama; 43.081° N, 18.482° E; 1025 m a.s.l.; 14 Aug. 2007; M. Komnenov leg.; CMK • 3 ♂♂, 5 ♀♀, 10 juvs (2 vials); Gacko, Korita, Pećina u Pejevim Torinama; 43.055° N, 18.493° E; 11 Aug. 1968; C. Deeleman leg.; NMNL (ARA 19027–8) • 1 ♂, 1 ♀; Gacko, Dramešina, Studena pećina; 43.213° N, 18.609° E; 15 Aug. 2007; M. Komnenov leg.; CMK • 2 ♂♂; Gacko, Lukovice, Pećina u Lukovicama; 43.1838° N, 18.4458° E; 975 m a.s.l.; 12 Nov. 2015; M. Lukić leg.; CBSS (Ar 3766) • 1 ♂; same locality as for preceding; 12 Nov. 2015; A. Kirin leg.; CBSS (Ar 3764) • 1 ♂, 1 ♀; same collection data as for preceding; CBSS (Ar 3799).

CROATIA – **Dubrovnik-Neretva** • 1 ♂; Konavle, Sniježnica, “Jama V= 13”; 42.574° N, 18.352° E; 20 Nov. 2011; M. Kajinić leg.; CBSS (Ar 2776) • 2 ♂♂, 1 ♀, 3 juvs; Konavle, Sniježnica, Jezero, in cave; 42.5804° N, 18.3561° E; 905 m a.s.l.; 16 Mar. 2002; R. Ozimec leg.; CBSS (Ar 3356) • 1 ♂; same locality as for preceding; 1 Nov. 2016; A. Kirin leg.; CBSS (Ar 5255) • 1 ♀, 5 juvs; same locality as for preceding; 1 Nov. 2016; T. Rožman leg.; CBSS (Ar 4776) • 2 juvs; same locality as for preceding; 28 May 2004; M. Pavlek leg.; CBSS (Ar 3360) • 1 ♂; Konavle, Sniježnica, Škrabuljica, in cave; 42.5670° N,

18.3851° E; 685 m a.s.l.; 1 Nov. 2016; M. Pavlek leg.; CBSS (Ar 4772) • 1 ♂, Dubrovnik, Gromača, Špilja za Gromačkom vlakom; 42.7435° N, 18.0274° E; 605 m a.s.l.; 22 Feb. 2019; A. Kirin leg.; CBSS (Ar 6819) • 1 ♀; same locality as for preceding; 11 Dec. 2019; M. Pavlek leg.; CBSS (Ar 6833) • 1 ♂; Konavle, Gruda, Vilina špilja; 42.5066° N, 18.3913° E; 205 m a.s.l.; 6 Apr. 2010; R. Ozimec and A. Schönhofer leg.; ROC (R260).

#### Localities unknown or unspecified

• 1 ♂, 1 ♀; “Herzegowina, Tartarushöhle”; Verhoeff leg.; ZMB (9073) • 1 ♂, 1 juv.; “c 86, 1935” [no further data]; NMP • 1 juv.; “Wolfshöhle, Südherzegowina”, “Vukovo jama bei Vrbanja”; Verhoeff leg.; ZMB (9069).

#### Credible published records (not examined or juveniles only)

MONTENEGRO – **Kotor** • ♂♀(?), material apparently lost; near Zvečava, Lopata pećina; 42.537° N, 18.622° E [Naumova *et al.* 2019: 42.569° N, 18.662° E]; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • 1 juv.; 2 km W Čora pećina, Matjaševica pećina; 42.595° N, 18.700° E [Naumova *et al.* 2019: 42.569° N, 18.662° E]; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940]; NMP • ♂♀(?), material apparently lost; Dragaljsko polje, near Dvoriško ždrijelo (“Dvorečko zdrielo”), Tomova pećina; 42.603° N, 18.675° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; Dragaljsko polje, above Crni Nugli, Lakičević pećina; 42.597° N, 18.700° E [Naumova *et al.* 2019: 42.263° N, 19.033° E]; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; 1 km above Lakičević pećina, Čora pećina; 42.594° N, 18.712° E [Naumova *et al.* 2019: 42.586° N, 18.697° E]; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near Jankovo selo, Pećina na Jankovom vrhu; 42.590° N, 18.658° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; 4 km N of Pećina na Jankovom vrhu, Pećina za Jankovim vrhom; 42.620° N, 18.656° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near road Crkvice-Veli vrh, cave near Crkvice; 42.560° N, 18.630° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near Crkvice, 1 km W of Blagojević, Pećina kod Blagojevića; 42.573° N, 18.620° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near Poljana, Pećina kod Šunjevca; 42.577° N, 18.648° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near Knezlac, Izeta pećina; 42.544° N, 18.689° E [Naumova *et al.* 2019: 42.524° N, 18.646° E]; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near Knezlac, near Izeta pećina, Studena pećina; 42.544° N, 18.689° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; Pokljuka donja [Kratochvíl 1935: “dolnja”]; 4 km SE Knezlac; 42.542° N, 18.693° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near Napode, near Risan-Crkvice road, Vilina (“Vilna”) pećina; 42.5546° N, 18.6624° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near Vilina pećina, Pecinis kod Napode; 42.555° N, 18.662° E [Naumova *et al.* 2019: 42.519° N, 18.716° E]; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; 1 km SW Risan, Golodražnica pećina; 42.503° N, 18.699° E [Naumova *et al.* 2019: 42.535° N, 18.689° E]; 185 m a.s.l.; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940]. – **Nikšić** • ♂♀(?), material apparently lost; near Jabukovac, Leskova pećina; 42.83° N, 18.47° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near Leskova pećina, Golubnjačka pećina; 42.83° N, 18.47° E [Naumova *et al.* 2019: 42.397° N, 18.841° E]; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; near Grahovac, on Brdo Omutič mountain, Vodena pećina; 42.687° N, 18.617° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; above Osječenica, Bobjerska pećina; 42.699° N, 18.634° E [Naumova *et al.* 2019: 42.674° N, 18.662° E]; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost, Elazov dô, near Zagora, Elazova pećina; 42.704° N, 18.655° E [Naumova *et al.* 2019: 42.706° N, 18.673° E]; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940] • ♂♀(?), material apparently lost; Troškarica planina mountains; Vranova jama; 42.838° N, 18.551° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940].



**Possible record** (not examined)

The following record in Kratochvíl (1940) is dubious because he assigned his specimen(s) to *S. absoloni*, but specimens from the closest caves we examined (Debelin pećina, Kali pećina, Špilja za Gromačkom vlakom) were all unambiguous *S. skotophilus*. We thus assume that Kratochvíl misidentified his specimen(s) from this cave.

BOSNIA AND HERZEGOVINA • ♂♀(?), material apparently lost; near Grebci, Grabovica pećina; 42.733° N, 18.081° E; 1932(?); J. Kratochvíl leg.(?) [Kratochvíl 1940].

**Material assigned tentatively**

The material listed here originates from caves around Sedlari in Bosnia and Herzegovina. This material has been studied before by Kratochvíl (1940) and Senglet (2001), and both authors assigned most of the specimens to *S. skotophilus* (only the female from Medja pećina was assigned to *S. absoloni* by Kratochvíl 1940). However, both males and females from these caves show some small but consistent differences to *S. skotophilus* (see section on variation below) so the material is here listed apart to draw attention to this potential separate species (of which no fresh material is available).

BOSNIA AND HERZEGOVINA • 2 ♂♂, 13 ♀♀, 3 juvs (2 vials); “Sedlari/Popovo-Polje” [according to Senglet 2001 the specimens were collected in Grabova pećina]; ~42.825° N, 18.055° E; 18 Sep. 1970; A. Senglet leg.; MHNG • 2 juvs; same locality as for preceding (“Grabova peć kod Sedlari”); 17 Jul. 1932; J. Kratochvíl leg.(?); NMP • 3 ♂♂, 6 juvs; “Trovrata peć kod Sedlari” (according to Kratochvíl 1940, this cave is near Grabova pećina); 17 Jul. 1932; J. Kratochvíl leg.(?); NMP • 6 juvs; “Vodena peć kod Sedlari” [according to Kratochvíl 1940, this cave is near Trovrata pećina and Grabova pećina]; 17 Jul. 1932; J. Kratochvíl leg.(?); NMP • 1 ♀, 2 juvs; “Medja peć na Ilijina brdu, Grmljani” [according to Kratochvíl 1940 this cave is located 2 km W of Grmljani]; ~42.84° N, 18.01° W; 1932(?); J. Kratochvíl leg.(?); NMP.

**Redescription**

**Male** (type locality; ZFMK (Ar 22196))

MEASUREMENTS. Total body length 5.5, carapace width 2.2. Distance PME–PME 160 µm; diameter PME 150 × 180 µm; distance PME–ALE 20 µm; diameter AME 65 µm; distance AME–AME 30 µm. Leg 1: 51.2 (13.7 + 0.9 + 13.6 + 20.3 + 3.2), tibia 2: 10.0, tibia 3: 8.2, tibia 4: 8.9; tibia 1 L/d: 62.

COLOR (in ethanol). Carapace pale whitish to ochre-yellow, posterior half, ocular area, and clypeus slightly darker (light brown); sternum light brown, with dark brown margins and three pairs of dark triangular radial marks; legs pale ochre-yellow to light brown, without dark rings, without dark lines; abdomen pale gray, with distinct dark dorsal marks in posterior third and lateral marks in posterior half; ventrally with light brown genital area, indistinct diffuse purplish marks in front and behind genital area and in front of spinnerets.

BODY. Habitus as in Fig. 2. Ocular area slightly raised. Carapace with deep median pit (Fig. 61) and pair of very shallow indistinct furrows diverging from pit to posterior margin of carapace. Clypeus unmodified. Sternum wider than long (1.50/1.05), unmodified. Abdomen oval, pointed at spinnerets; gonopore with six epiandrous spigots (Fig. 62); ALS with two spigots each (Fig. 69).

CHELICERAE. As in Figs 51–52, with pair of large frontal apophyses set with 2 modified hairs each, with 12 and 13 modified hairs each on frontal face (Figs 63–64); with stridulatory ridges (Fig. 71).

PALPS. As in Figs 6–8; coxa with low retrolateral hump; trochanter barely modified; femur with distinct retrolateral process proximally, with stridulatory pick (modified hair) proximally on prolateral side (Fig. 65); femur-patella joints shifted towards prolateral (arrows in Fig. 6); tibia very large, with two

trichobothria; tibia-tarsus joints shifted towards retrolateral (arrows in Fig. 8); tarsus with exposed tarsal organ (Fig. 66); procurus dorsally with curved hairs (distal third curved ‘upwards’), with strong hump on prolateral side; procurus tip with projecting dorsal sclerite, strong hinged ventral sclerite, and membranous central part with brush of hair-like processes on retrolateral side (Figs 67–68), with weakly sclerotized cylindrical process on prolateral side bordering ventral sclerite (arrow in Fig. 45). Genital bulb (Figs 47–50) with basal sclerite connecting to tarsus, small transparent dorsal process, and main sclerite consisting of retrolateral process and dorsal process; retrolateral process with bifid tip, distal part on ventral side thickened and heavily sclerotized; dorsal process with two finger-shaped tips, ventral tip simple, retrolateral tip with additional strong protrusion on ventral side.

**LEGS.** With short spines ventrally on femur 1 in two rows (Fig. 73), prolateral row ~23 spines, retrolateral row ~28 spines; without curved hairs; few vertical hairs; retrolateral trichobothrium of tibia 1 at 4%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 with irregular platelets rather than with distinct pseudosegments.

#### **Male** (variation)

Males from most other localities paler, without lateral dark marks on abdomen, with fewer median dark marks (restricted to area above spinnerets), rarely without abdominal marks. Tibia 1 (N = 35): 11.1–14.7 (mean 12.8); tibia 2 (N = 37): 8.1–10.8 (mean 9.6); spines on femur 1: 32–58 (mean 52); modified hairs on each cheliceral basis (N = 74): 9–16 (mean 12.3); modified hairs on each cheliceral apophysis (N = 74): 1–5 (mean 2.7); chelicerae maximum width (N = 36): 0.74–0.86 (mean 0.80); procurus length (N = 37): 1.28–1.48 (mean 1.39); bulbal measures A–E: A (N = 20): 0.28–0.31 (mean 0.30); B (N = 20): 0.08–0.10 (mean 0.09); C (N = 20): 0.13–0.15 (mean 0.14); D (N = 20): 0.28–0.33 (mean 0.31); E (N = 15): 0.82–0.90 (mean 0.87); epiandrous spigots (N = 26): 5–8 (mean 6.1).

Males from near Sedlari differ slightly in bulbal measure A smaller (0.25–0.28) and bulbal measure B smaller (0.07–0.08); in addition, the smaller wart on the retrolateral bulbal process (arrow in Fig. 48) is more strongly developed.

#### **Female**

In general similar to male, but femur 1 without spines, with pair of indistinct processes posteriorly on carapace and pair of opposing poorly visible plates on abdomen; distance between processes/plates: 1.1. Tibia 1 (N = 36): 10.4–14.3 (mean 12.4); tibia 2 (N = 36): 7.2–10.3 (mean 9.0); epigynum width (N = 36): 1.02–1.46 (mean 1.21); epigynum length (N = 36): 0.54–0.68 (mean 0.61); epigynal measure F (N = 36): 0.42–0.58 (mean 0.47). Epigynum anterior plate semicircular, weakly protruding, with weak transversal furrows (Figs 55–58, 76), with internal structures visible in uncleaned specimens: round anterior structure, short and indistinct parallel sclerites posteriorly wide apart; posterior plate short but wide. Internal genitalia (Figs 53–54, 147–148) with distinctive ventral arc (Fig. 154; approximately as long as wide), with large pore plates (Fig. 54).

Females from near Sedlari differ in having the parallel sclerites posteriorly in the female internal genitalia closer together (epigynal measure F: 0.32–0.36; Figs 59–60) and slightly more distinct.

#### **Distribution**

Known from the southern border area separating Bosnia and Herzegovina from Montenegro, and from the southernmost tip of Croatia (Fig. 168).



*Stygopholcus montenegrinus* Kratochvíl, 1940 orig. stat.  
Figs 3, 77–112, 149–150, 155

*Stygopholcus montenegrinus* Kratochvíl, 1940: 20, fig. 8.

*Stygopholcus skotophilus montenegrinus* – Senglet 1971: 354, figs 42–43; 2001: 65. — Naumova *et al.* 2016: 434 (part; see *S. skotophilus*).

*Stygopholcus photophilus* (misidentification) – Deltšev *et al.* 2011: 130 (specimen from near Kozhnja only).

*Hoplopholcus scotophilus* (misidentification) – Tomić *et al.* 2000: 35P (specimens from near Velja cave). “S109 *Stygopholcus absoloni*? Bal11” – Eberle *et al.* 2018. — Huber *et al.* 2018.

### Diagnosis

Distinguished from other species in the ‘northern clade’ (*S. absoloni*; *S. skotophilus*) by narrow, weakly sclerotized prolateral sclerite on procurus (arrows in Figs 77–78, 100); from *S. skotophilus* also by bulb measures A and C (Fig. 158; larger than in *S. skotophilus*, no overlap), by epigynal measure F (Fig. 164; smaller than in *S. skotophilus*, with little overlap); from *S. absoloni* also by straight procurus (rather than curved toward ventral; cf. Fig. 44), by longer procurus (Fig. 161; with little overlap), by shape of retrolateral bulbal process in retrolateral view (Fig. 79; large notch on ventral side), by bulb measures B and D (Figs 157, 159; larger than in *S. absoloni*, no overlap) and bulb measure E (Fig. 160; larger than *S. absoloni*, with little overlap).

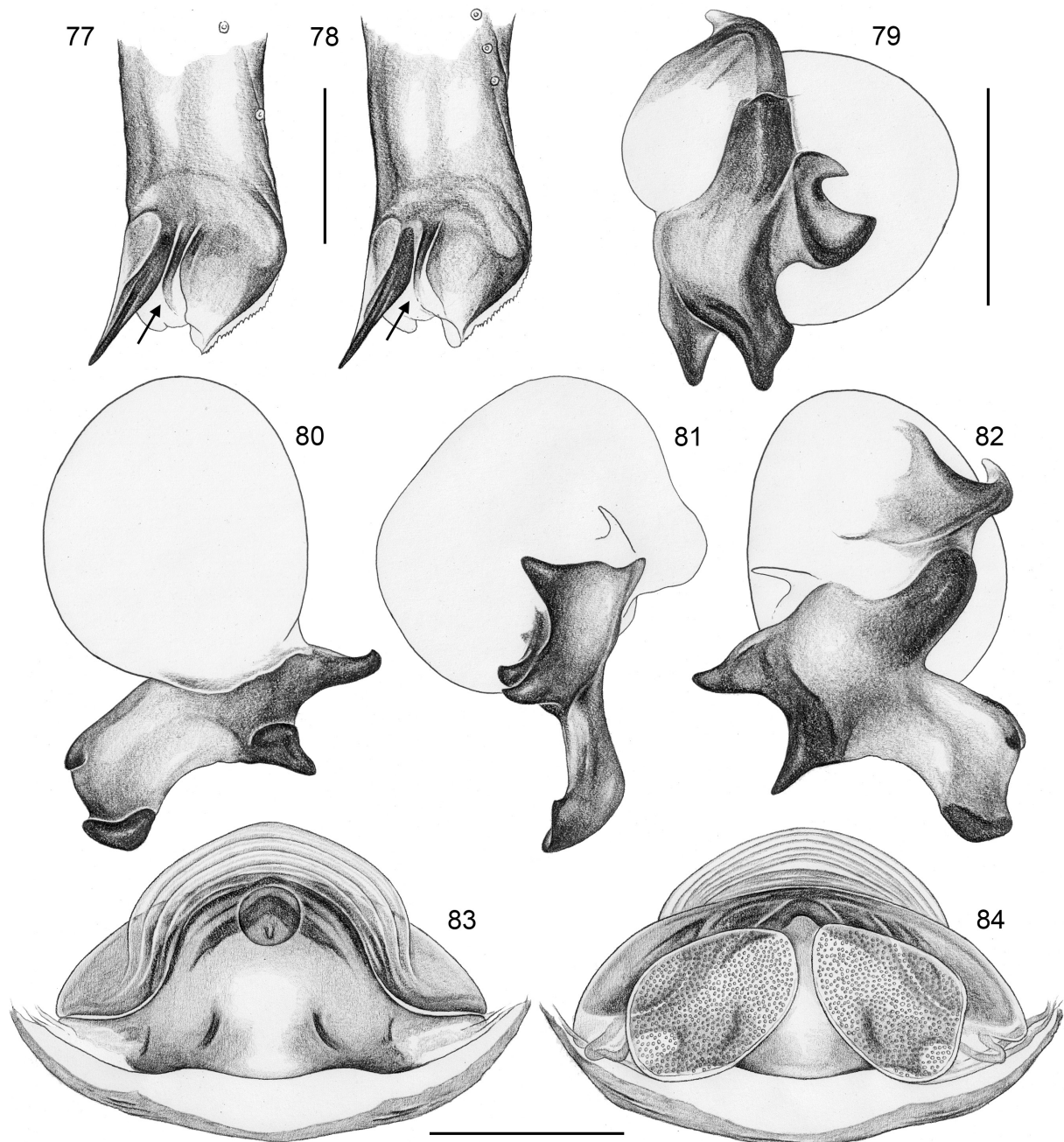
### Type material

#### Holotype

MONTENEGRO – Nikšič • ♀ (without epigynum), near Nikšič, Studenačka pećina; 42.7680° N, 18.9312° E [Naumova *et al.* 2019: 42.826° N, 18.786° E]; 6 Sep. 1936; J. Kratochvíl leg.(?); NMP.

#### Other material examined

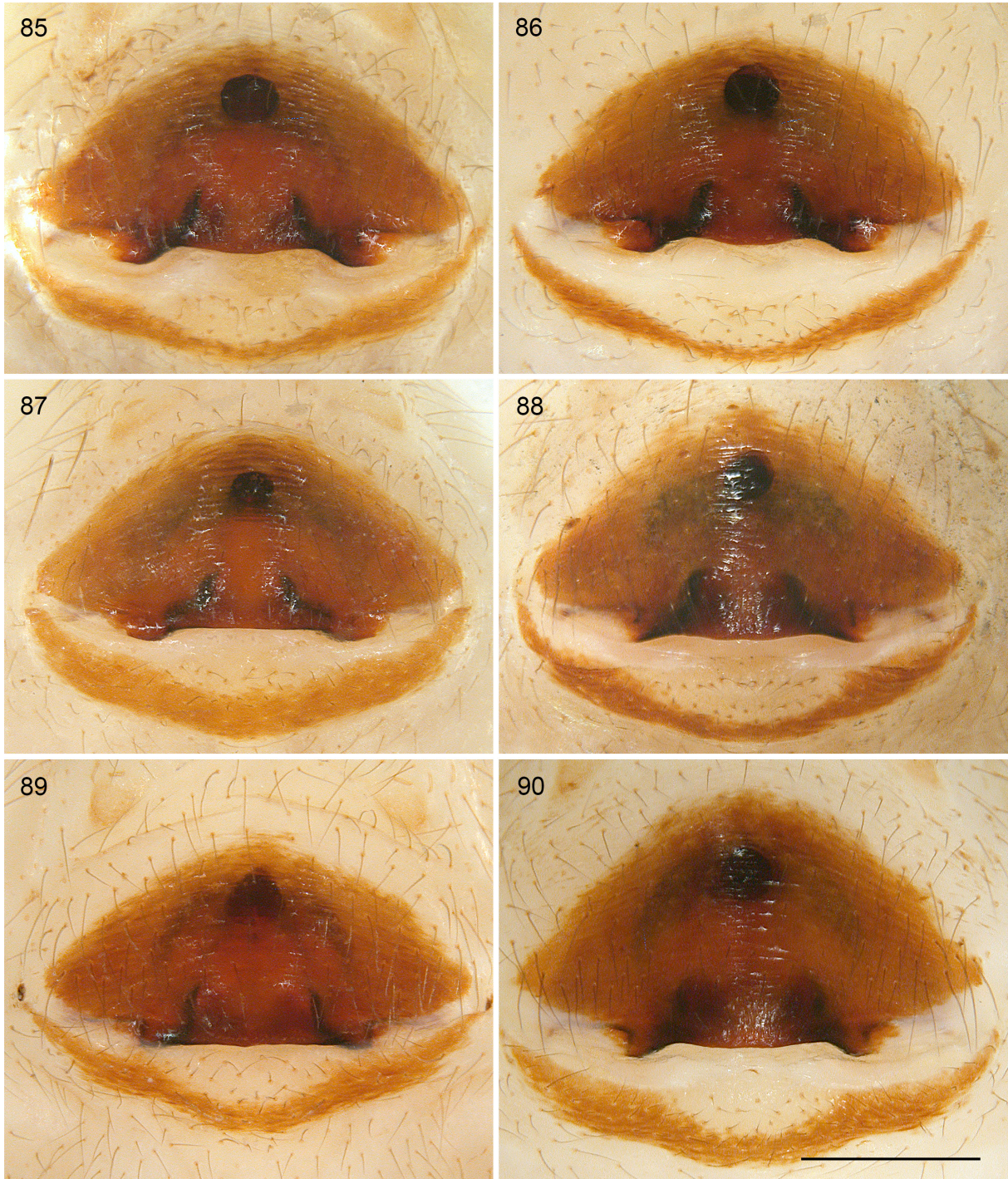
MONTENEGRO – Nikšič • 1 juv.; same collection data as for holotype; NMP • 9 ♂♂, 8 ♀♀; near Nikšič, Studenačka pećina, in cave near entrance and among rocks near cave; 42.7680° N, 18.9312° E; 640 m a.s.l.; 27 May 2014; B.A. Huber and M. Komnenov leg.; ZFMK (Ar 22201) • 1 ♂, 1 ♀, 1 juv. in pure ethanol; same collection data as for preceding; ZFMK (Bal11) • 4 ♂♂, 8 ♀♀; same locality as for preceding; 16 Sep. 1970; A. Senglet leg.; MHNG • 1 ♂, 1 ♀; Trebjesa, Vojna pećina; 42.765° N, 18.959° E; 19 Aug. 2011; M. Komnenov leg.; CMK • 1 ♂, 1 ♀; Velja pećina; 42.728° N, 18.943° E; 16 Aug. 2011; M. Komnenov leg.; CMK • 1 ♂, 3 ♀♀, totally fragmented; unnamed cave above Velja pećina; 42.73° N, 18.94° E; 6 Sep. 2000; B. Čurčić leg.; IZUB • 2 ♀♀; Carev Most, Budoška pećina; 42.7303° N, 18.9498° E; 26 Jul. 1969; C. Deeleman leg.; NMNL (ARA 19035) • 2 ♂♂, 2 ♀♀; Slivlje, Golubešnica pećina, 42.724° N, 19.013° E; 18 Aug. 2011; M. Komnenov leg.; CMK. – **Podgorica** • 2 ♀♀; Velje Brdo, Megara pećina; 42.463° N, 19.199° E; 17 Feb. 2010; M. Komnenov leg.; CMK • 2 ♂♂, 3 ♀♀; Ljubovići, artificial tunnel; 42.433° N, 19.255° E; 21 Apr. 2011; M. Komnenov leg.; CMK • 2 ♂♂, 2 ♀♀; Vranjina, Golubinja pećina (= Pećina na Vranjini); 42.2703° N, 19.1308° E; 21 Apr. 2011; M. Komnenov leg.; CMK • 1 ♂, 4 juvs; same locality as for preceding; 23 Aug. 2017; A. Kirin leg.; CBSS (Ar 5342) • 1 ♂, 1 juv.; same locality as for preceding; 23 Aug. 2017; M. Pavlek leg.; CBSS (Ar 5329) • 1 juv.; same locality as for preceding; 23 Aug. 2017; A. Kirin leg.; CBSS (Ar 5334) • 10 juvs; same locality as for preceding; 31 Jul. 1969; J. Kratochvíl leg.; NMNL (ARA 19041). – **Cetinje** • 2 ♂♂, 1 ♀; Cetinjska pećina; 42.389° N, 18.921° E [Naumova *et al.* 2019: 42.401° N, 18.935° E]; 10 Aug. 2011; M. Komnenov leg.; CMK • 1 ♂; Lipska pećina; 42.375° N, 18.955° E [Naumova *et al.* 2019: 42.375° N, 19.952° E]; 21 Apr. 2011; M. Komnenov leg.; CMK • 2 ♂♂, 2 ♀♀; presumably same locality as for preceding (“Lipa Dobersko”); 16 Sep. 1970; A. Senglet leg.; MHNG • 1 ♂; Začir,



**Figs 77–84.** *Stygopholcus montenegrinus* Kratochvíl, 1940. **77–78.** Males from Studenačka pećina, Montenegro (ZFMK (Ar 22201)) and from Zeze Cave, Albania (CMK), tips of left procursi, prolateral (slightly ventral) views; arrows point at distinctive prolateral sclerites. **79–82.** Male from Studenačka pećina (ZFMK (Ar 22201)), left genital bulb, retrolateral, ventral, prolateral-distal, and dorso-distal views. **83–84.** Female from Studenačka pećina (ZFMK (Ar 22201)), cleared female genitalia, ventral and dorsal views. Scale bars: 0.5 mm.

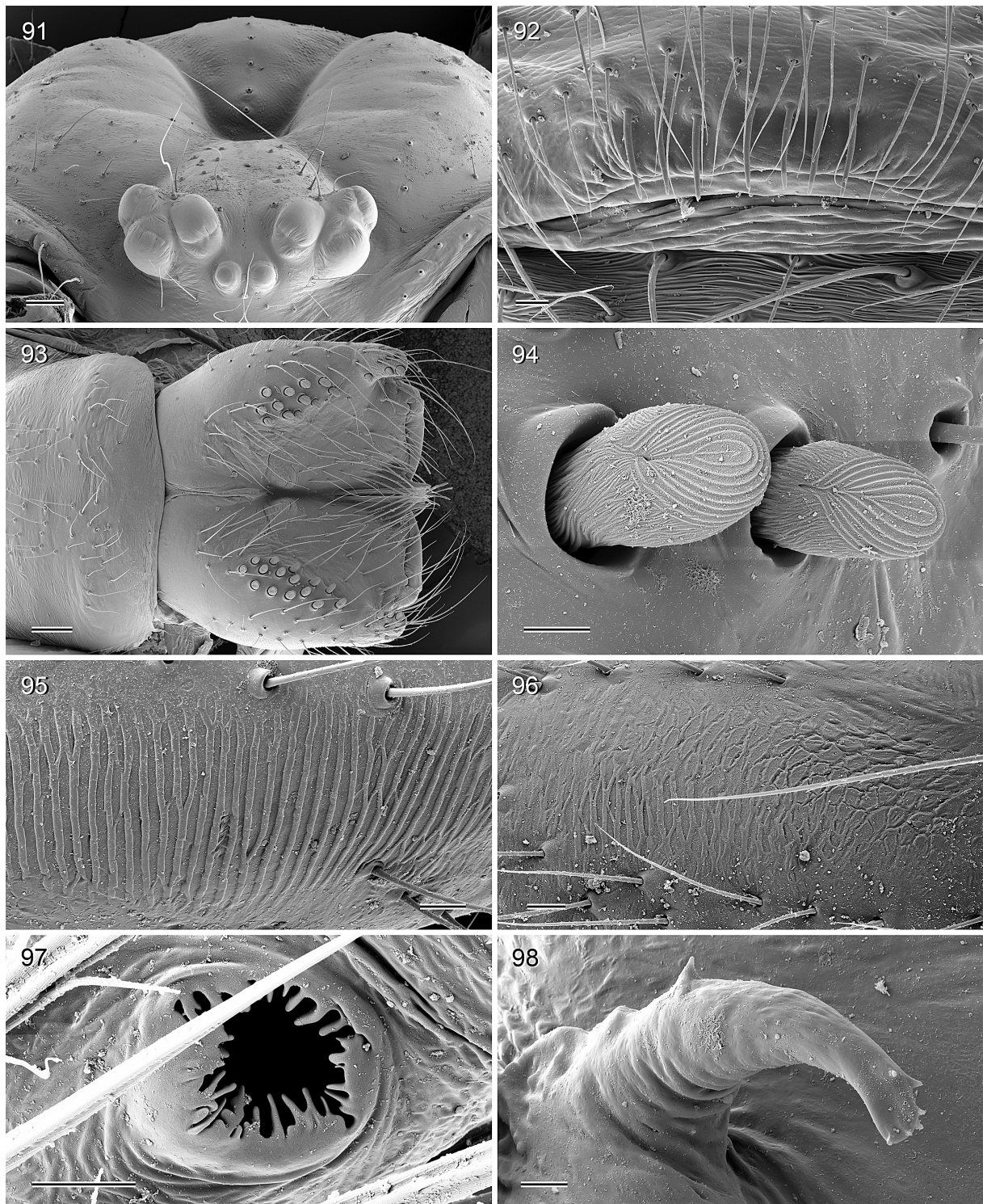


Začirska pećina; 42.343° N, 18.992° E; 5 Oct. 2010; M. Pavičević leg.; CMK • 1 ♂; same locality as for preceding; 21 Aug. 2017; T. Rožman leg.; CBSS (Ar 5405) • 3 ♂♂, 1 ♀; Rijeka Crnojevića, Obodska pećina; 42.352° N, 19.005° E; 19 Apr. 2011; M. Komnenov leg.; CMK • 1 ♀; same locality



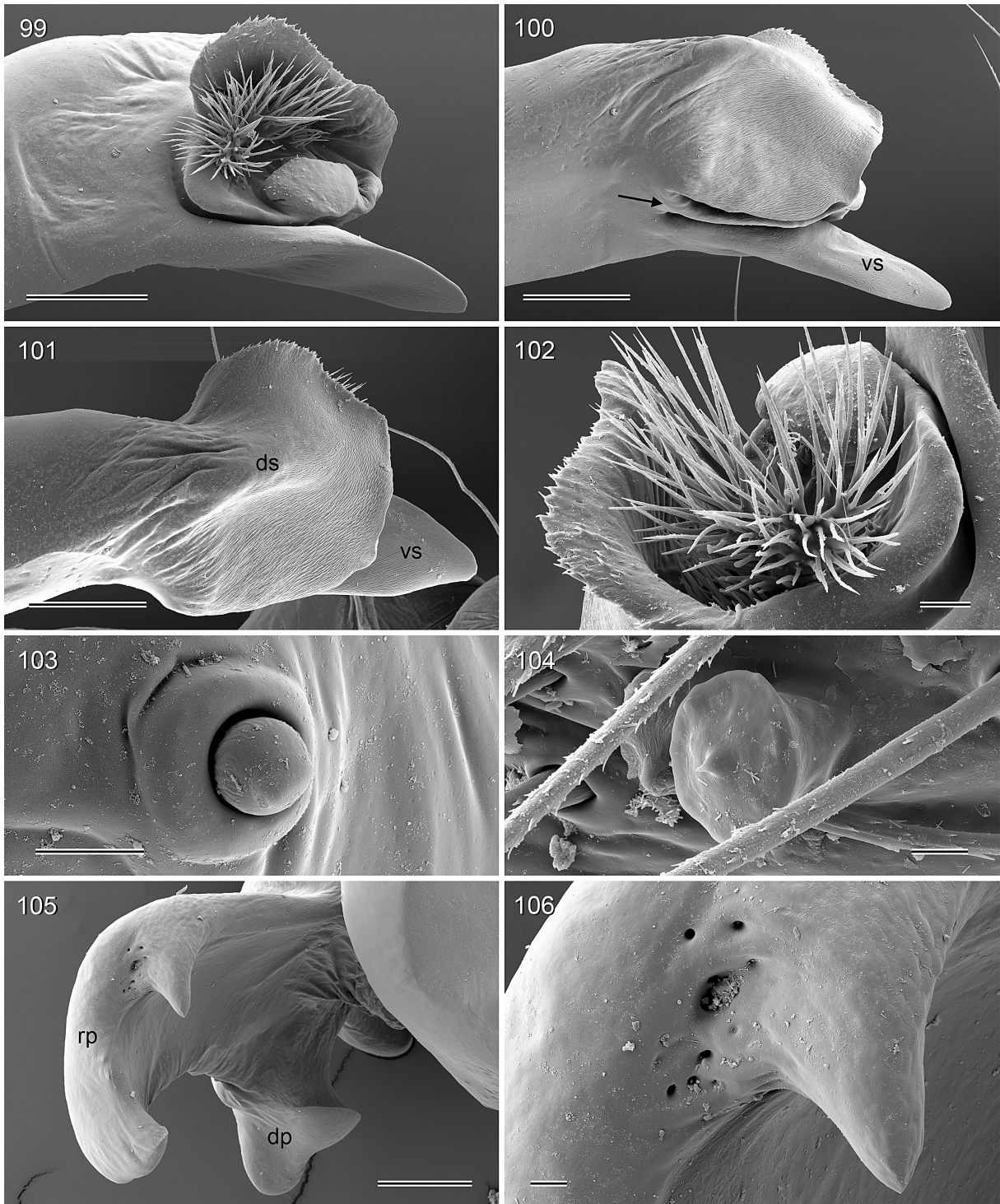
**Figs 85–90.** *Stygopholcus montenegrinus* Kratochvíl, 1940; epigyna, ventral views. **85–86.** Studenačka pećina, Montenegro (ZFMK (Ar 22201)). **87.** Golubinja pećina, Montenegro (CMK). **88.** Ljubovići, Montenegro (CMK). **89.** Nēngurit Cave, Albania (CMK). **90.** Petnjik Cave, Montenegro (CMK). Scale bar: 0.5 mm (all at same scale).





**Figs 91–98.** *Stygopholcus montenegrinus* Kratochvíl, 1940; male and female from Studenačka pećina, Montenegro (ZFMK (Ar 22201)). **91.** Male carapace and ocular area, frontal-dorsal view. **92.** Male gonopore and epiandrous spigots. **93.** Male clypeus and chelicerae, frontal view. **94.** Modified hairs frontally on male chelicerae. **95–96.** Stridulatory files on male and female chelicerae. **97.** Tarsal organ on male tarsus 1. **98.** Transparent process on genital bulb. Scale bars: 91, 93 = 100  $\mu\text{m}$ ; 92, 95–96 = 20  $\mu\text{m}$ ; 94, 97–98 = 10  $\mu\text{m}$ .

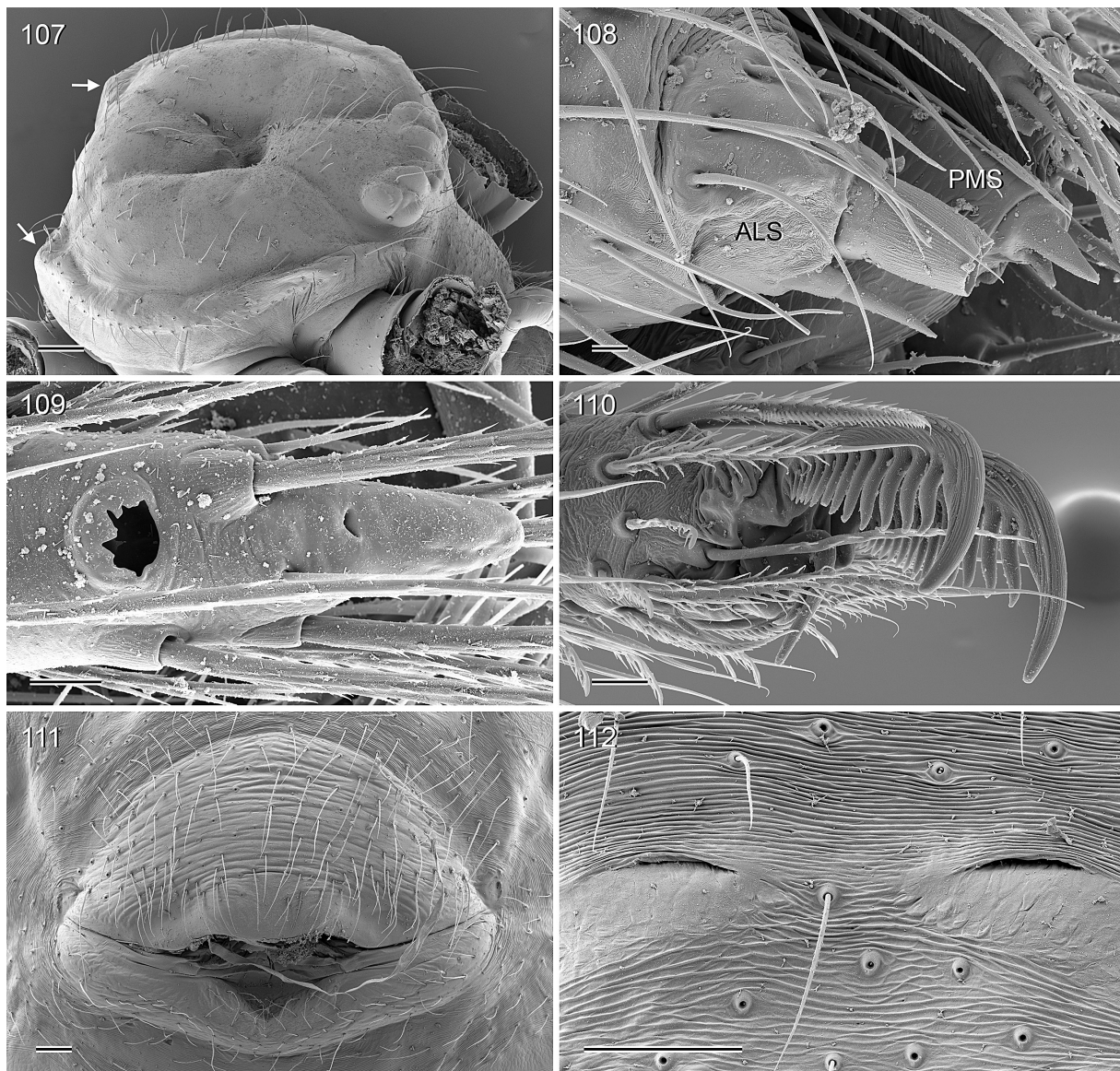




**Figs 99–106.** *Stygopholcus montenegrinus* Kratochvíl, 1940; male and female from Studenačka pećina, Montenegro (ZFMK (Ar 22201)). **99.** Tip of right procurcus, retrolateral view. **100–101.** Tip of left procurcus, prolateral and dorsal views; arrow points at distinctive prolateral sclerite. **102.** Hair-like structures on tip of procurcus. **103.** Stridulatory pick on male palp femur. **104.** Male palp tarsal organ. **105.** Retrolateral bulbal process, distal view. **106.** Possible glandular pores on retrolateral bulbal process (detail of previous photo). Abbreviations: dp = dorsal process; ds = dorsal sclerite; rp = retrolateral process; vs = ventral sclerite. Scale bars: 99–101, 105 = 100  $\mu$ m; 102 = 20  $\mu$ m; 103–104, 106 = 10  $\mu$ m.



as for preceding; 23 Aug. 2017; M. Pavlek leg.; CBSS (Ar 5484) • 1 ♂, 4 juvs; same collection data as for preceding; A. Kirin leg.; CBSS (Ar 5485) • 3 ♂♂, 1 ♀; Jankovići Krš, Duruk pećina; 42.364° N, 19.023° E; 16 Apr. 2011; M. Komnenov leg.; CMK • 1 ♀; near river Rijeka Crnojevića, Žmrljeva pećina; 42.361° N, 19.050° E; 16 Apr. 2011; M. Komnenov leg.; CMK • 1 ♂; Vrela, Pećina u Vrelima; 42.3247° N, 18.9233° E; 730 m a.s.l.; 27 Oct. 2015; M. Pavlek leg.; CBSS (Ar 4169) • 2 ♂♂; same collection data as for preceding; CBSS (Ar 3669) • 2 ♂♂, 1 ♀; Trnovo, Babatuša pećina; 42.291° N, 19.034° E [Naumova *et al.* 2019: 42.229° N, 19.096° E]; 15 Feb. 2010; M. Komnenov leg.; CMK • 1 ♂ (palps and chelicerae missing); same locality as for preceding, (“Bobotuša pećina”); 1932(?); J. Kratochvíl leg.(?); NMP • 1 ♂, 2 ♀♀; Trnovo, Grbočica pećina; 42.288° N, 19.036° E; 15 Apr. 2011;



**Figs 107–112.** *Stygopholcus montenegrinus* Kratochvíl, 1940; male and female from Studenačka pećina, Montenegro (ZFMK (Ar 22201)). **107.** Female prosoma; arrows point at humps opposing modified areas on abdomen. **108.** Female anterior lateral spinneret (ALS) and posterior median spinneret (PMS). **109.** Tip of female palp, dorsal view. **110.** Tip of female tarsus 1. **111.** Epigynum, ventral view. **112.** Indentations (muscle attachment sites) between epigynum and spinnerets. Scale bars: 107 = 200  $\mu$ m; 108 = 10  $\mu$ m; 109–110 = 20  $\mu$ m; 111–112 = 100  $\mu$ m.



M. Komnenov leg.; CMK • 1 ♂, 1 juv.; same locality as for preceding; 9 Nov. 2015; A. Kirin leg.; CBSS (Ar 3727). – **Bar** • 2 ♂♂, 2 ♀♀; Virpazar, Donja Seoca, Ivanina pećina; 42.228° N, 19.136° E; 100 m a.s.l.; 3 Apr. 2007; M. Komnenov leg.; CMK • 1 ♀; Seoca, Golubova pećina, hillside forest, under stones and sieving; 42.208° N, 19.131° E; 440 m a.s.l.; 12 Aug. 2006; B. Petrov and S. Lazarov leg.; NMNHS. – **Kolašin** • 1 ♂, 1 ♀; Monastery Morača; 42.7648° N, 19.3931° E; 300 m a.s.l.; 8 May 2006; A. Schönhofer leg.; SMF.

MONTENEGRO – **unknown municipality** • 3 ♀♀ prosomata and 2 ♀♀ abdomens; “Južna Crna Gora, neka pećina” (= southern Montenegro, some cave); date unknown; P. Dabović leg.; NMP.

ALBANIA – **Shkodra** • 2 ♂♂, 1 ♀; Galeria Iliriana, Tuneli i Gencit; 42.032° N, 19.474° E; 24 Nov. 2000; A. Zhalov leg.; NMNHS.

#### Credible published records (not examined)

MONTENEGRO – **Cetinje** • 5 ♂♂, 5 ♀♀, 1 juv.; Trnovo vill., Babatuša pećina, “109a”; 42.291° N, 19.034° E; 24 Mar. 2006; S. Lazarov and B. Petrov leg. [Naumova *et al.* 2016] • 1 ♂, 1 ♀, 1 juv., Cetinje town, unnamed cave above monastery, “102”; 42.39° N, 18.92° E; 25 Mar. 2006; B. Petrov and S. Lazarov leg. [Naumova *et al.* 2016].

#### Material assigned tentatively

The material listed here originates from SE Montenegro (Podgorica) and NW Albania. It strongly resembles *S. montenegrinus* but shows some small though consistent differences (see section on variation below). The material is listed apart to draw attention to this potential separate species.

MONTENEGRO – **Podgorica** • 1 ♂, 1 ♀; cave in Morača canyon [“grotje langs de Morača, ~14 km from Titograd”]; 42.53° N, 19.34° E; 22 Jul. 1972; C. Deeleman leg.; NMNL (ARA 19038) • 3 ♂♂, 2 ♀♀, 4 juvs; Peuta, Dučica pećina; 42.4621° N, 19.3307° E; 19 Jul. 1972; C. Deeleman leg.; NMNL (ARA 19039) • 1 juv.; Peuta, Pećina od Zavora; 42.46° N, 19.33° E; 19 Jul. 1972; C. Deeleman leg.; NMNL (ARA 19040) • 2 ♂♂, 2 ♀♀; Kuči, Ubalac, Petnjik pećina; 42.520° N, 19.382° E; 565 m a.s.l.; 23 Mar. 2013; M. Komnenov leg.; CMK • 3 ♂♂, 1 ♀; Kuči, Liješta Karantin pećina; 42.483° N, 19.395° E; 575 m a.s.l.; 23 Mar. 2013; M. Komnenov leg.; CMK • 2 ♀♀; Kučke Mt., Kučka korita, Radeča, beech forest; 42.500° N, 19.534° E; 22 Jul. 2010; M. Komnenov leg.; CMK • 1 juv. assigned tentatively; Kučka korita, Jama J008; 42.4747° N, 19.5247° E; 1350 m a.s.l.; 10 Nov. 2015; A. Kirin leg.; CBSS (Ar 4178).

ALBANIA – **Shkodra** • 1 ♂; K2 Cave nr. Kozhnje [Kozhnja]; 42.457° N, 19.607° E; 30 Aug. 1996; “P.B.” leg.; NMNHS. – **Kukës** • 1 ♂; Hekurave Mt., Qereç-Mulaj, Zeze Cave; 42.362° N, 19.930° E; 18 Aug. 2010; M. Komnenov leg.; CMK • 2 ♂♂; below Hekurave Mt., Qereç-Mulaj, small cave near River Kuqit; 42.364° N, 19.933° E; 17 Aug. 2010; M. Komnenov leg.; CMK • 1 ♀; Prokletije, Curaj i Epërm, Nëngurit Cave; 42.339° N, 19.927° E; 19 Aug. 2010; M. Komnenov leg.; CMK.

#### Redescription

##### Male (type locality; ZFMK (Ar 22201))

MEASUREMENTS. Total body length 5.5, carapace width 2.15. Distance PME–PME 150 µm; diameter PME 130 × 160 µm; distance PME–ALE 30 µm; diameter AME 60 µm; distance AME–AME 20 µm. Leg 1: 50.6 (13.7 + 0.8 + 13.3 + 19.6 + 3.2), tibia 2: 9.7, tibia 3: 8.0, tibia 4: 8.5; tibia 1 L/d: 65.

COLOR (in ethanol). Carapace pale whitish to ochre-yellow; ocular area, clypeus, and posteriorly between furrows slightly darker (light brown); sternum light brown, with dark brown margins and irregular dark triangular radial marks; legs ochre yellow to light brown, without dark rings, without dark lines; abdomen mostly monochromous pale gray, only above spinnerets and ventrally in gonopore area some dark marks.

**BODY.** Habitus as in Fig. 3. Ocular area slightly raised. Carapace with deep median pit and pair of shallow furrows diverging from pit to posterior margin of carapace (Fig. 91). Clypeus unmodified. Sternum wider than long (1.40/1.05), unmodified. Abdomen oval, pointed at spinnerets.

**CHELICERAE.** Very similar to *S. skotophilus* (cf. Figs 51–52; see also Fig. 93), with pair of frontal apophyses set with 3 and 4 modified hairs, respectively, with 16 and 18 modified hairs each on frontal face (Fig. 94); with stridulatory ridges (Fig. 95).

**PALPS.** In general as in *S. skotophilus* (cf. Figs 6–8); coxa with retrolateral hump; trochanter barely modified; femur with distinct retrolateral process proximally, with stridulatory pick (modified hair) proximally on prolateral side (Fig. 103); femur-patella joints shifted towards prolateral; tibia very large, with two trichobothria; tibia-tarsus joints shifted towards retrolateral; tarsal organ exposed (Fig. 104); procurus dorsally with ~8 curved hairs (distal third curved ‘upwards’), with strong hump on prolateral side. Procurus tip (Figs 77, 99–102) with slightly projecting dorsal sclerite, strong hinged ventral sclerite (flat, wider in ventral than in lateral view), and membranous central part with brush of hair-like processes on retrolateral side, with narrow and weakly sclerotized process on prolateral side bordering ventral sclerite. Genital bulb (Figs 79–82) with basal sclerite connecting to tarsus, small transparent dorsal process (Fig. 98), and main sclerite consisting of retrolateral process and dorsal process; retrolateral process with bifid tip, distal part on ventral side thickened and heavily sclerotized, possibly with glandular pores distally (Figs 105–106); dorsal process with two finger-shaped tips, ventral tip simple, retrolateral tip with additional strong protrusion on ventral side.

**LEGS.** With short spines ventrally on femur 1 in two rows in distal third, prolateral row ~19 spines, retrolateral row ~24 spines; without curved hairs; few vertical hairs; retrolateral trichobothrium of tibia 1 at 4%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 with irregular platelets rather than with distinct pseudosegments.

#### **Male (variation)**

Some specimens with more and larger dark marks dorsally on abdomen (posterior third), few specimens without abdominal marks; dark pattern on sternum slightly variable. Tibia 1 (N = 29): 11.3–14.5 (mean 12.9); tibia 2 (N = 35): 8.1–10.8 (mean 9.6); spines on femur 1 (N = 23): 24–53 (mean 40); modified hairs on cheliceral basis (N = 70): 11–22 (mean 14.7); modified hairs on cheliceral apophysis (N = 69): 2–4 (mean 3.0); chelicerae maximum width (N = 35): 0.72–0.84 (mean 0.79); procurus length (N = 35): 1.22–1.46 (mean 1.37); bulbal measures A–E: A (N = 17): 0.34–0.43 (mean 0.37); B (N = 17): 0.10–0.15 (mean 0.13); C (N = 17): 0.24–0.27 (mean 0.25); D (N = 17): 0.25–0.29 (mean 0.27); E (N = 8): 0.82–0.90 (mean 0.88); epiandrous spigots (N = 25): 5–9 (mean 6.2).

Males from SE Montenegro (Podgorica) and NW Albania differ slightly from other specimens, most conspicuously in bulbal measure C (smaller: 0.19–0.22).

#### **Female**

In general similar to male (Fig. 3), but femur 1 without spines, with pair of indistinct processes posteriorly on carapace (Fig. 107) and pair of opposing poorly visible plates on abdomen, distance between processes/plates: 1.1. Tibia 1 (N = 28): 8.3–15.3 (mean 12.9); tibia 2 (N = 30): 6.0–10.9 (mean 9.3); epigynum width (N = 31): 0.94–1.50 (mean 1.27); epigynum length (N = 31): 0.50–0.70 (mean 0.62); epigynal measure F (N = 31): 0.22–0.40 (mean 0.30). Epigynum anterior plate semicircular, weakly protruding, with weak transversal furrows (Figs 85–88, 111), with internal structures visible in uncleared specimens: round anterior structure, short sclerites originating from posterior margin and slightly converging anteriorly; posterior plate short but wide. Internal genitalia (Figs 83–84, 149–150) with distinctive ventral arc (Fig. 155; approximately as long as wide), with large pore plates (Fig. 84).



Females from SE Montenegro (Podgorica) and NW Albania tend to have a slightly larger epigynal measure F: 0.37–0.43 (N = 6) (cf. Figs 89–90).

### Distribution

Known from Montenegro and NW Albania (Fig. 168).

#### *Stygopholcus photophilus* Senglet, 1971

Figs 4–5, 9–11, 113–144, 151–152, 156

*Stygopholcus photophilus* Senglet, 1971: 356, figs 44–54.

*Hoplopholcus kratochvili* – Brignoli, 1971: 259, figs 1–6. — Deltshv 1985: 43. Synonymized by Brignoli (1976).

*Hoplopholcus photophilus* – Brignoli 1976: 561.

*Stygopholcus photophilus* – Senglet 2001: 47, 65, figs 15–20, 23–25, 28.

### Diagnosis

Easily distinguished from known congeners by many characters, including: distinct dark marks on entire abdomen (Figs 4–5), also ventrally; dark rings on femora and tibiae, dark lines on femora (Figs 127–128); male chelicerae with strongly sculptured median margins (Figs 130–131); larger number of modified hairs on male cheliceral base (Fig. 162; with little overlap); male palpal femur distally more strongly widened (Fig. 11); palpal tibia widest in distal half (Fig. 11); procurus distally with strongly projecting dorsal sclerite (Figs 113–114); dorsal bulbal process not divided into two separate tips (Figs 115, 118); spines on male femur 1 in single row; male tibia 1 much longer than tibia 2 (tibia 1/tibia 2 > 1.40; in other species < 1.40; Fig. 165); strong transversal ridges on anterior part of epigynum (Fig. 144); relatively longer epigynum (epigynum width/length: usually < 1.7, in other species usually > 1.7, with little overlap; Fig. 163); female without stridulatory ridges on chelicerae (Fig. 134), and without stridulatory apparatus between prosoma and abdomen.

#### Type material of *Stygopholcus photophilus*

##### Holotype

GREECE – Thessaly • ♂, examined; Larissa, Omolion (Tembe) [Omolio, Tempi Valley]; 39.900° N, 22.628° E; 17 Jun. 1970; A. Senglet leg.; MHNG.

##### Paratypes

GREECE – Thessaly • 27 ♂♂, 14 ♀♀ (3 vials), examined; same collection data as for holotype; MHNG.

For further paratypes from other localities, see below.

#### Type material of *Hoplopholcus kratochvili*

##### Holotype

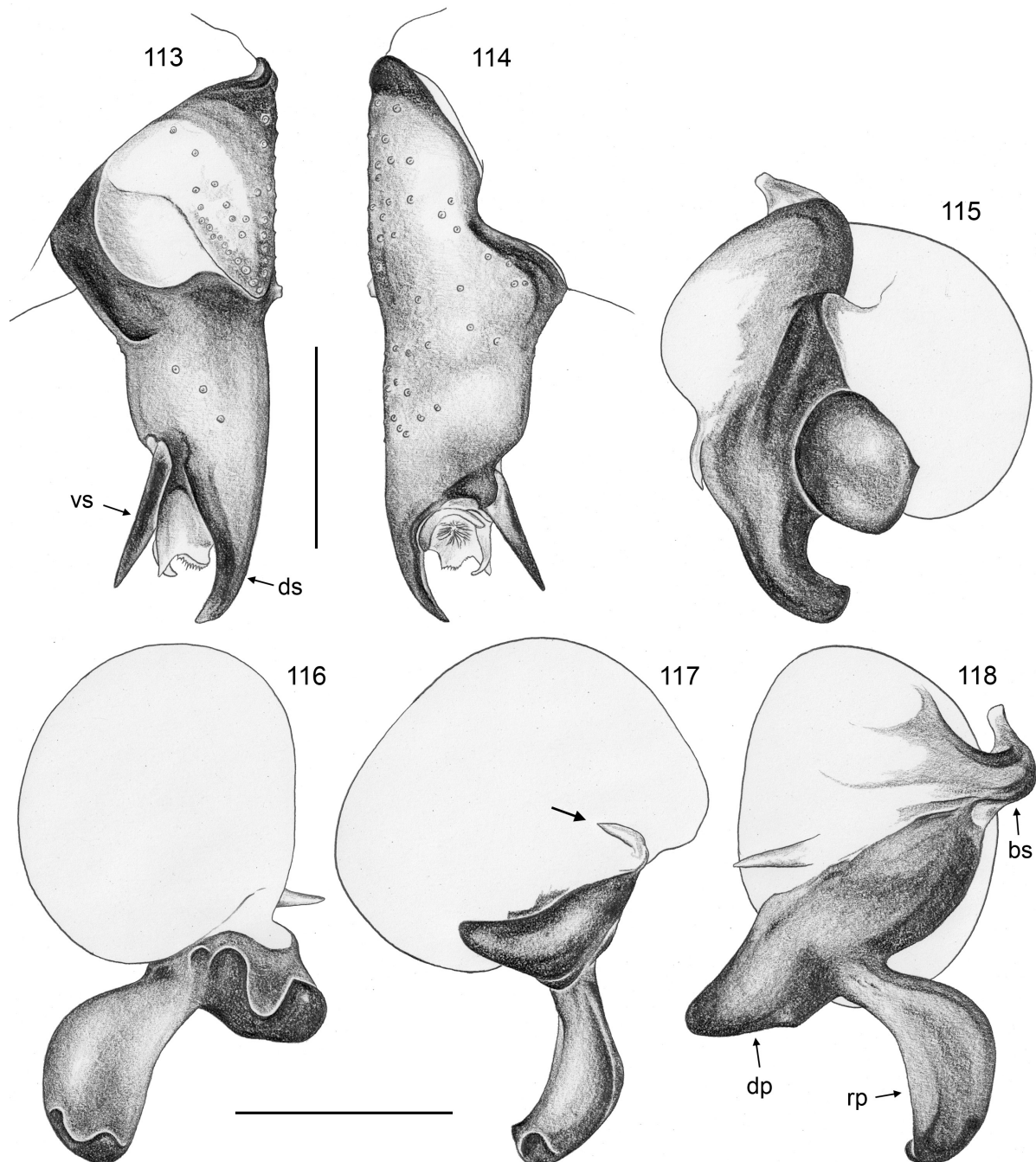
GREECE – Epirus • ♂, examined; Prosgoli [= Megálo Peristéri]; 39.723° N, 21.062° E; date and collector unknown; ZMB (9077).

##### Paratypes

GREECE – Epirus • 1 ♂, 1 juv. (2 vials), examined; same collection data as for holotype; ZMB (9077)  
• 1 ♂, examined; same collection data as for holotype; MCVR.

**Other material examined**

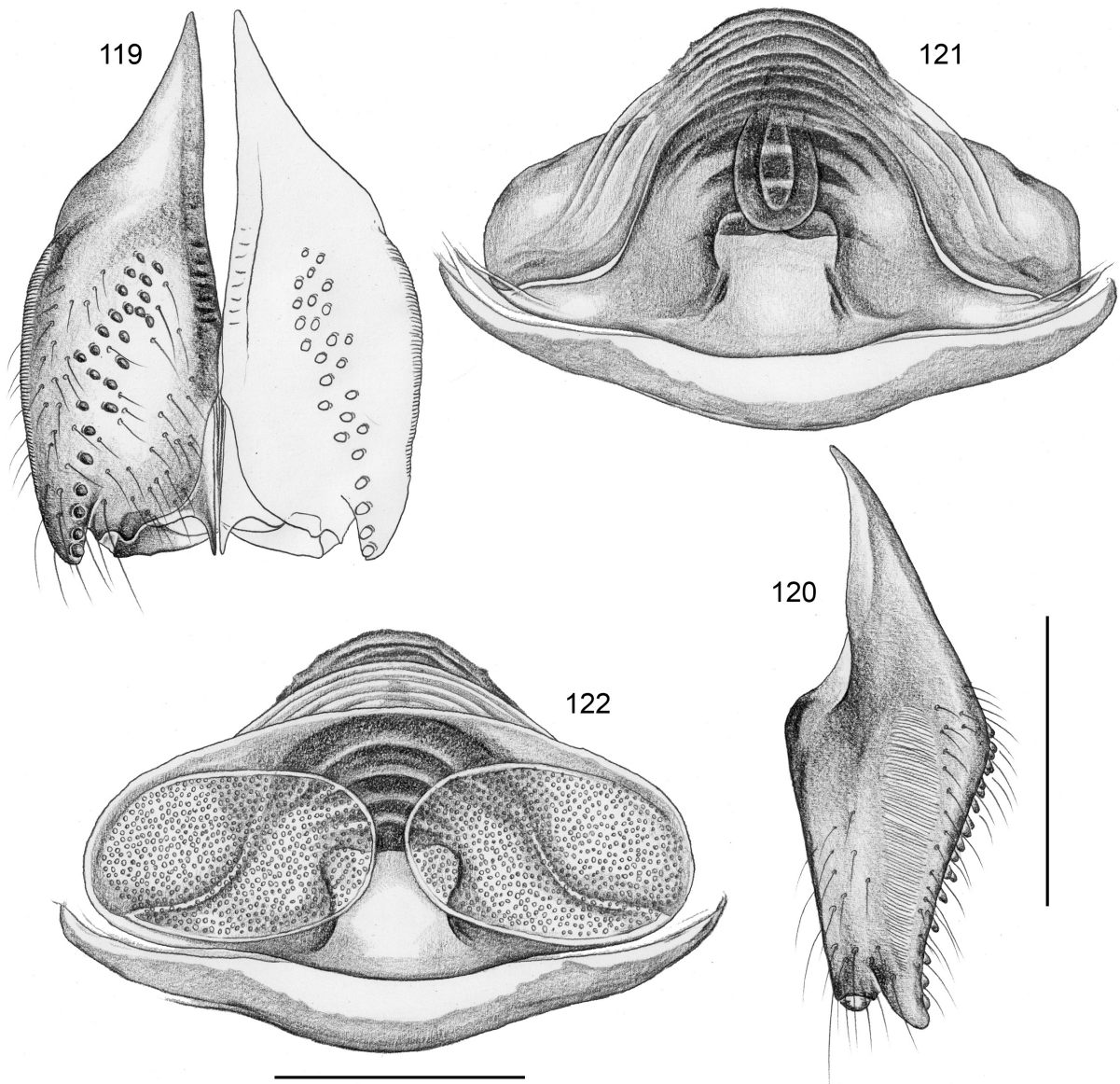
GREECE – **Thessaly** • 2 ♂♂, 3 ♀♀; Monte Ossa above Ampelakia, unnamed cave near church Profitis Elias, “The-76/13”; 39.862° N, 22.572° E; 600 m a.s.l.; 14 May 1976; B. Hauser leg.; MHNG • 3 ♂♂, 2 ♀♀; same locality as for preceding, “Kri 78/27”; 10 Apr. 1978; B. Hauser leg.; MHNG • 1 ♂; Monte



**Figs 113–118.** *Stygopholcus photophilus* Senglet, 1971; male from Episkopi, Crete (ZFMK (Ar 22205)). **113–114.** Left tarsus and procurcus, prolateral and retrolateral views. **115–118.** Left genital bulb, retrolateral, ventral, prolateral-distal, and dorso-distal views; arrow points at weakly sclerotized process. Abbreviations: bs = basal sclerite; dp = dorsal process; ds = dorsal sclerite; rp = retrolateral process; vs = ventral sclerite. Scale bars: 0.5 mm.



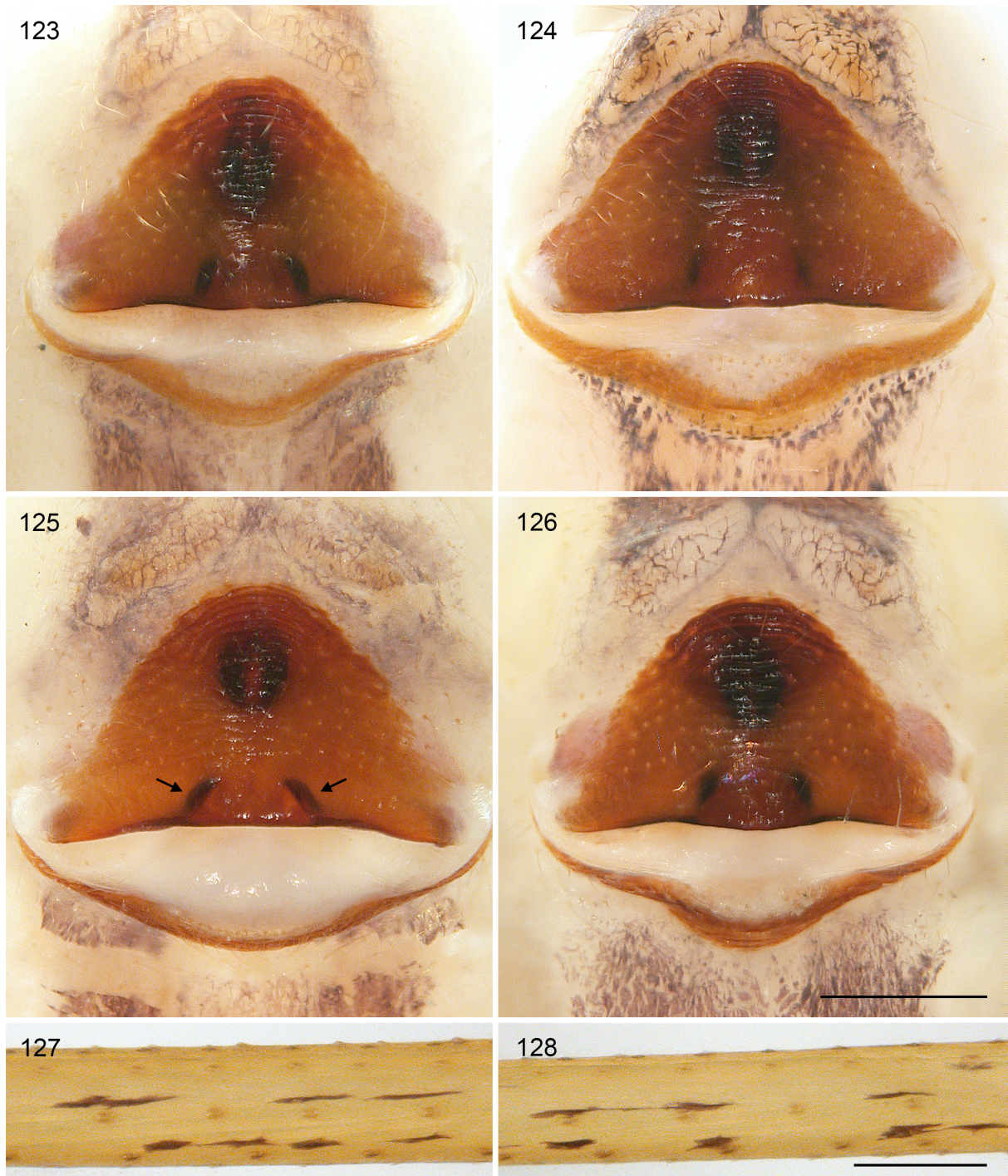
Ossa, near Spilia, Tsari Tripa cave on Mt. Psyiodendron [= Spilaio Nymfon], “Kri-78/30”; 39.821° N, 22.641° E; 11 Apr. 1978; B. Hauser leg.; MHNG • 2 ♀♀; ravine near Stomio (“Ossa-Geb., Stomio, Bachgraben”), “TH 234”; 39.86° N, 22.72° E; 22 Sep. 1995; K. Thaler and B. Knoflach leg.; ZFMK (Ar 22202). – **Athos** • 1 ♀; Dafni, “Ba 69-12”; 40.213° N, 24.223° E; 10 m a.s.l.; 4 May 1969; Ausobsky leg.; ZFMK (Ar 22203) • 1 ♂, 1 ♀, 1 juv.; Mount Athos, Agia Anna monastery, Lost Glasses Cave; 40.14° N, 24.30° E; 8 Sep. 2012; A. Zhalov leg.; NMNHS. – **Central Macedonia** • 1 ♂; Chalkidiki, Sithonia, 1 km W of Zografou, humid stream valley with *Osmunda*, under logs and stones; 40.1702° N, 23.8545° E; 20 m a.s.l.; 22 Aug. 2009; S. Huber and A. Schönhofer leg.; SMF. – **Eastern Macedonia**



**Figs 119–120.** *Stygopholcus photophilus* Senglet, 1971; male from Episkopi, Crete (ZFMK (Ar 22205)), female from Choumerion/Pérama, Crete (MHNG). **119–120.** Male chelicerae, frontal and lateral views. **121–122.** Cleared female genitalia, ventral and dorsal views. Scale bars: 0.5 mm.

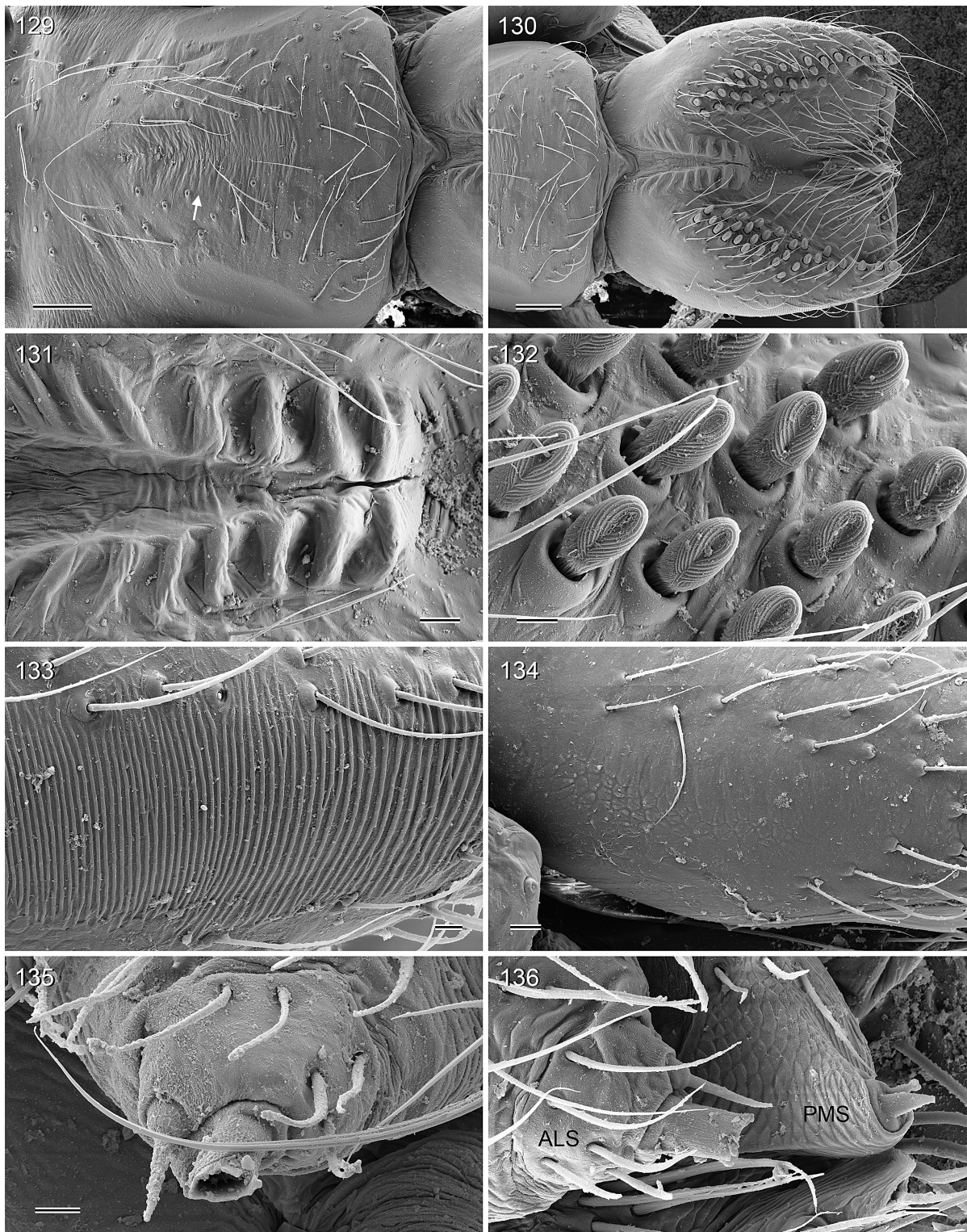


**and Thrace** • 2 ♂♂, 5 ♀♀; Thasos, Panagia, Drakotrypa cave; 40.732° N, 24.732° E; 28 Dec. 1982; P. Beron and S. Andreev leg.; NMNHS • 1 ♂; Kavala, Zygos, Aghia Helleni cave [Spilaio Agias Elenis]; 41.018° N, 24.394° E; 28 Dec. 1982; P. Beron and S. Andreev leg.; NMNHS. – **Epirus** • 4 ♂♂, 2 ♀♀;



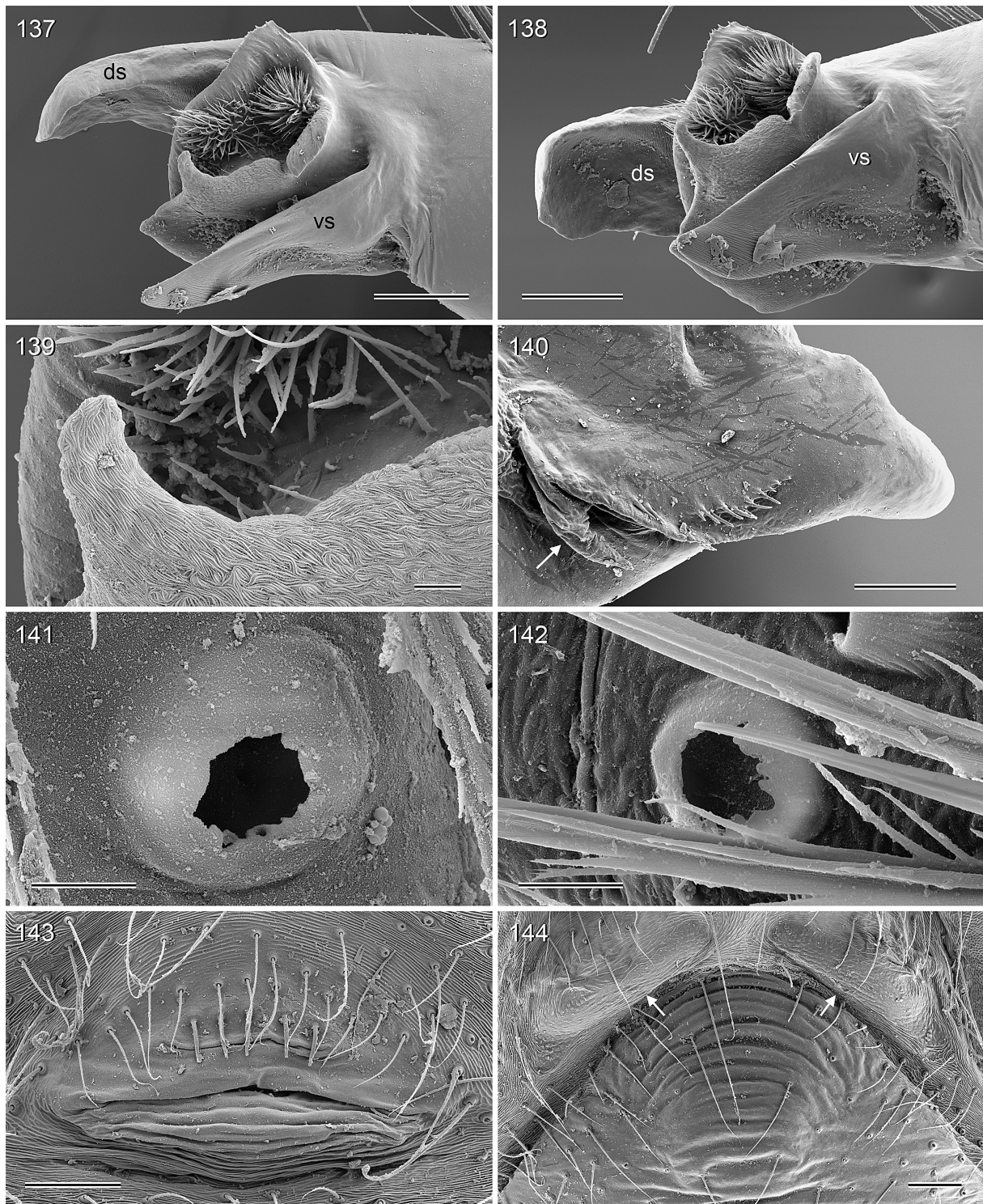
**Figs 123–128.** *Stygopholcus photophilus* Senglet, 1971; epigyna, ventral views, and details of male femora 2 and 3, dorsal views. **123.** Thessaly, Omolio, Tempi Valley (MHNG). **124.** Corfu, Loutsas (MHNG). **125.** Peloponnese, Agios Dimitrios/Lefktro (MHNG); arrows point at internal sclerites. **126–128.** Crete, Episkopi (ZFMK (Ar 22205)). Scale bars: 123–126 = 0.5 mm; 127–128 = 0.2 mm.





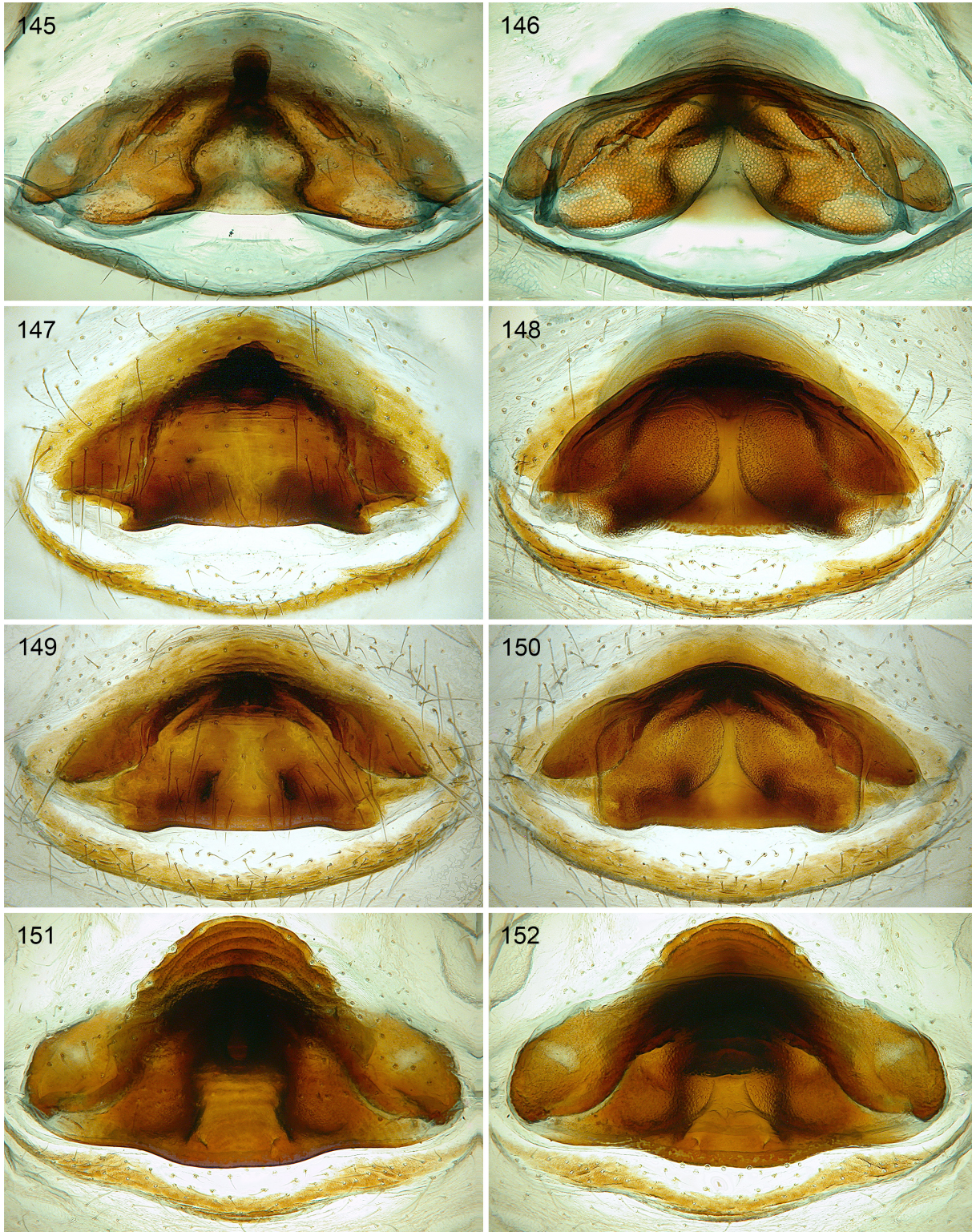
**Figs 129–136.** *Stygopholcus photophilus* Senglet, 1971; male and female from Choumerion/Pérama, Crete (MHNG). **129.** Male clypeus, frontal view; arrow points at modified median area. **130.** Male chelicerae, frontal view. **131.** Modified area medially on male chelicerae. **132.** Modified hairs frontally on male chelicerae. **133.** Stridulatory files on male chelicerae. **134.** Absence of stridulatory files on female chelicerae. **135.** Male ALS. **136.** Female anterior lateral spinneret (ALS) and posterior median spinneret (PMS). Scale bars: 129–130 = 100  $\mu$ m; 131, 134–136 = 20  $\mu$ m; 132–133 = 10  $\mu$ m.





**Figs 137–144.** *Stygopholcus photophilus* Senglet, 1971; male and female from Choumerion/Pérama, Crete (MHNG). **137–138.** Tip of left procurrus, retrolateral (slightly ventral) and ventral views. **139.** Detail of previous figure. **140.** Dorsal bulbular process and transparent bulbular process (arrow); note hair-like structures on dorsal bulbular process. **141.** Female palpal tarsal organ. **142.** Tarsal organ on female tarsus 4. **143.** Male gonopore and epiandrous spigots. **144.** Anterior part of epigynum showing strong ridges; arrows point at pair of anterior bulges. Abbreviations: ds = dorsal sclerite; vs = ventral sclerite. Scale bars: 137–138, 140, 143–144 = 100  $\mu\text{m}$ ; 139, 141–142 = 10  $\mu\text{m}$ .

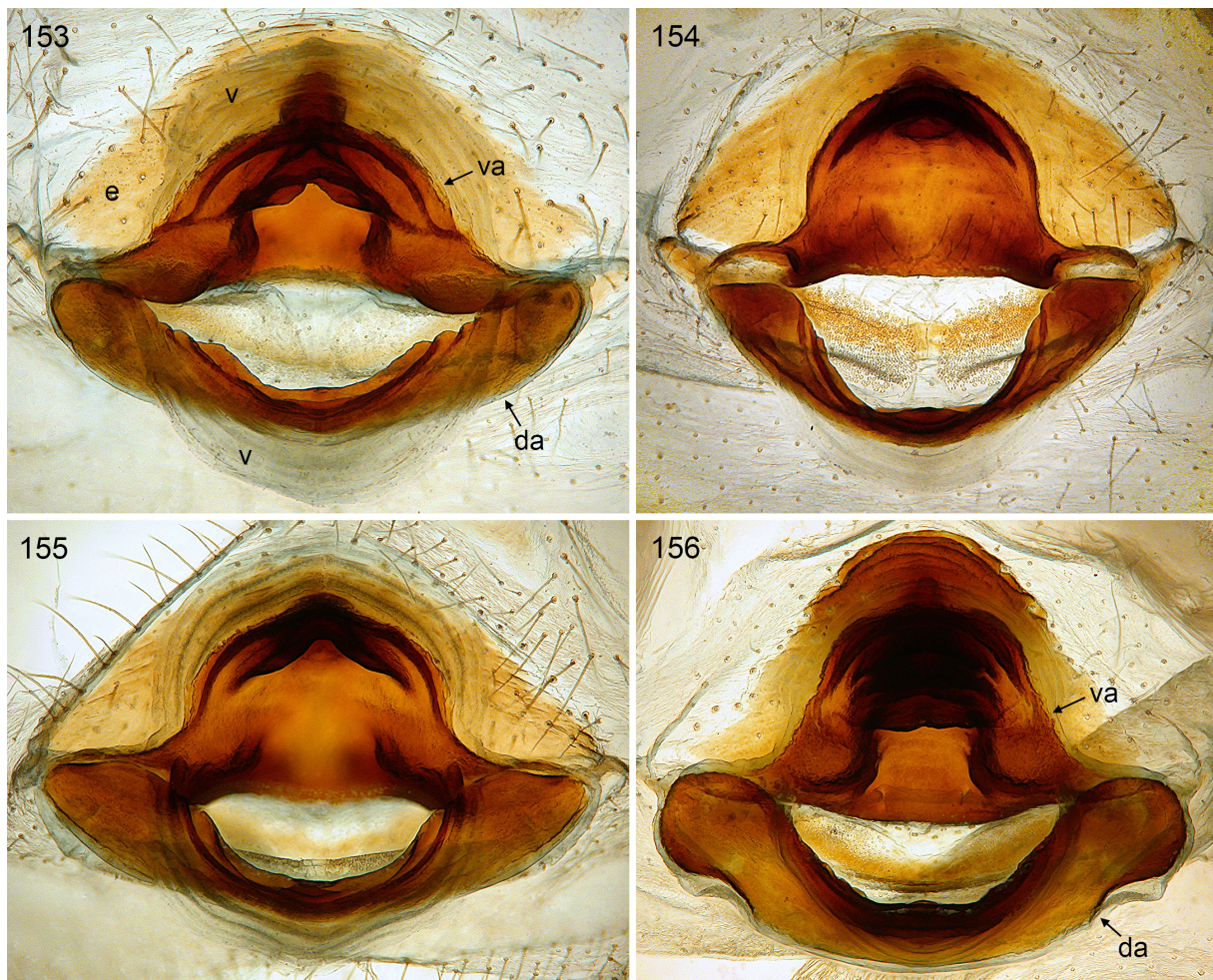




**Figs 145–152.** *Stygopholcus* Kratochvíl, 1932; cleared female genitalia, ventral and dorsal views. 145–146. *S. absoloni* (Kulczyński, 1914); from Zavala, Bosnia and Herzegovina (MHNG). 147–148. *S. skotophilus* Kratochvíl, 1940; from Pećina u Ivici, Montenegro ((ZFMK Ar 22196)). 149–150. *S. montenegrinus* Kratochvíl, 1940; from Golubinja pećina, Montenegro (CMK). 151–152. *S. photophilus* Senglet, 1971; from Choumerion/Pérama, Crete (MHNG).



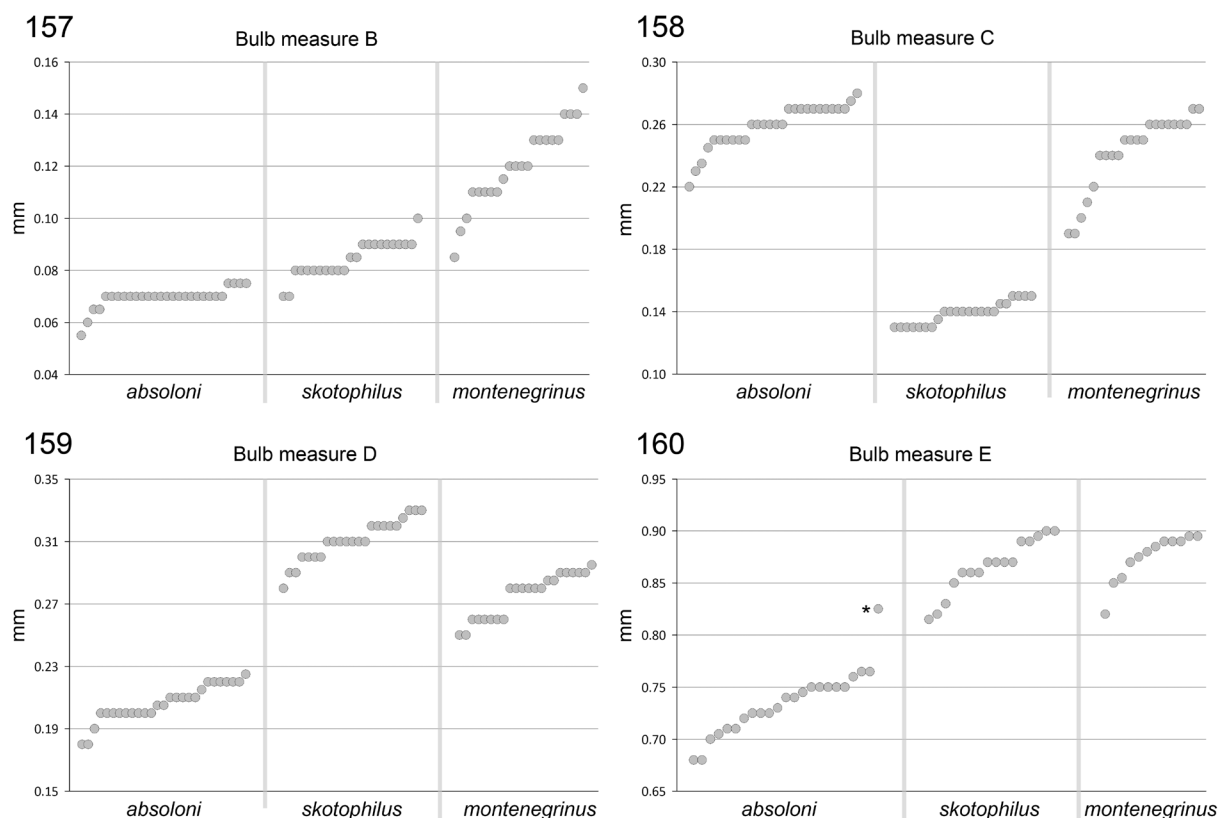
Monodendri, dry valley before monastery, oak and hard-leaved forest, under stones and wood; 39.883° N, 20.749° E; 1000 m a.s.l.; 14 Aug. 2009; S. Huber and A. Schönhofer leg.; SMF. – **Peloponnese** • 1 ♂; Ag. Taxiarchi, 12 km W of Leonidion, cellar of church ruin; 37.150° N, 22.760° E; 29 Sep. 2006; H. Pieper leg.; ZFMK (Ar 22204) • 6 ♂♂, 7 ♀♀, paratypes; Laconia, Mystras/Sparta; 37.067° N, 22.375° E; 16 Aug. 1970; A. Senglet leg.; MHNG • 3 ♂♂, 2 ♀♀; Laconia, Mystras; 37.067° N, 22.375° E; 23 May 1983; A. Senglet leg.; MHNG • 2 ♂♂; Kastoreio, Spilaio Skreti; 37.1676° N, 22.3052° E; 490 m a.s.l.; 5 Dec. 2016; C. Cenni leg.; MCVR • 5 ♂♂, 5 ♀♀, 6 juvs, paratypes; Messinia, Agios Dimitrios/Lefktro (“Leuktron”); 37.039° N, 22.102° E; 20 Aug. 1970; A. Senglet leg.; MHNG • 1 ♀, 4 juvs; Arkadia, Kapsia, Spilaio Kapsias; 37.623° N, 22.354° E; 29 Sep. 1997; K. Paragamian leg.; HISR (1845) • 1 ♀; Arkadia, Leonidio, Spilaio Dionysou; 37.1485° N, 22.8185° E; 19 Sep. 1997; K. Paragamian leg.; HISR (1836). – **Crete** • 10 ♂♂, 15 ♀♀, paratypes; Rethymno, Choumerion/Pérama; 35.355° N, 24.720° E; 1 Jul. 1970; A. Senglet leg.; MHNG • 7 ♂♂, 11 ♀♀, 1 juv., paratypes; Rethymno, Keramoto/Pérama; 35.333° N, 24.740° E; 2 Jul. 1970; A. Senglet leg.; MHNG • 1 ♂, 1 ♀; Rethymno, Archaia Eleftherna; 35.324° N, 24.676° E; 17 May 2006; H. Eikamp and U Kluge leg.; SMF (56590) • 1 ♂; Rethymno,



**Figs 153–156.** *Stygopholcus* Kratochvíl, 1932; cleared female genitalia in dorsal views; dorsal sclerotized arcs tilted towards the back. **153.** *S. absoloni* (Kulczyński, 1914); from Balićeva špilja, Croatia (ZFMK (Ar 22195)). **154.** *S. skotophilus* Kratochvíl, 1940; from Pećina u Ivici, Montenegro (ZFMK (Ar 22196)). **155.** *S. montenegrinus* Kratochvíl, 1940; from Studenačka pećina, Montenegro (ZFMK (Ar 22201)). **156.** *S. photophilus* Senglet, 1971; from Choumerion/Pérama, Crete (MHNG). Abbreviations: da = dorsal arc; e = epigynal plate; v = ‘valve’; va = ventral arc.



Myloi, Spilaio Skoteinospilios; 35.336° N, 24.505° E; 1 Mar. 1987; K. Paragamian leg.; HISR (1640) • 1 ♂, 1 ♀; Rethymno, Episkopi, along stream; 35.3417° N, 24.7656° E; 230 m a.s.l.; 7 Jul. 2015; B.A. Huber leg.; NHMC • 2 ♂♂, 1 ♀; same collection data as for preceding; ZFMK (Ar 22205) • 3 ♂♂, 2 ♀♀, in pure ethanol; same collection data as for preceding; ZFMK (Cre19) • 2 ♂♂, 2 juvs; Irakleion, Zaros; 35.13° N, 24.90° E; 7 May 2009; K. Eckl and H. Eikamp leg.; SMF • 2 ♂♂, 4 ♀♀, 1 juv.; Chania, Topolia, Spilaio Agias Sofias; 35.417° N, 23.683° E; 30 Dec. 2001; K. Paragamian leg.; HISR (2008) • 4 ♂♂, 4 ♀♀; same locality as for preceding; 10 Oct. 1999; A. Senglet leg.; MHNG. – **Central Greece** • 2 ♂♂, 5 ♀♀; Euboea, Artemisio/Istiaia; 39.00° N, 23.22° E (Senglet 2001: 39.02° N, 23.25° E); 31 Aug. 1972; A. Senglet leg.; MHNG • 1 ♂, 4 ♀♀; Euboea, Kato Steni; 38.571° N, 23.825° E (Senglet 2001: 38.583° N, 23.850° E); 2 Sep. 1972; A. Senglet leg.; MHNG. – **Ionian Islands** • 3 ♂♂, 4 ♀♀, 2 juvs; Lefkada, waterfalls 3 km W of Nidri, rocky caves and mossy stones; 38.7263° N, 20.6858° E; 200 m a.s.l.; 27 Mar. 2006; A. Schönhofer leg.; SMF • 1 ♂, 1 ♀; Kefallonia, Lake Avithos, lakeside buildings; 38.109° N, 20.528° E; 28 May 1987; J. Murphy leg.; MMUE • 7 ♂♂, 13 ♀♀; Corfu, Loutsas; 39.786° N, 19.880° E; 20 Sep. 1972; A. Senglet leg.; MHNG • 1 ♂; Corfu, S of Loutsas, Spilaio Megali Grava / Peristerograva, on ground of cave, under stones; 39.777° N, 19.890° E; 350 m a.s.l.; 22 Mar. 2006; A. Schönhofer leg.; SMF • 6 ♂♂, 2 ♀♀; same locality as for preceding, (“Halbhöhle am Nordabhang des Pantokratorgebirges”), “Ko-60/11”; 19 Apr. 1960; B. Hauser leg.; MHNG • 6 ♂♂, 13 ♀♀; Corfu, Pantocrator, Spilaio Katsampa (“Katsaba cave”) near Strinilas, “Pel74/19”; 39.744° N, 19.839° E; 12 May 1974; B. Hauser leg.; MHNG.



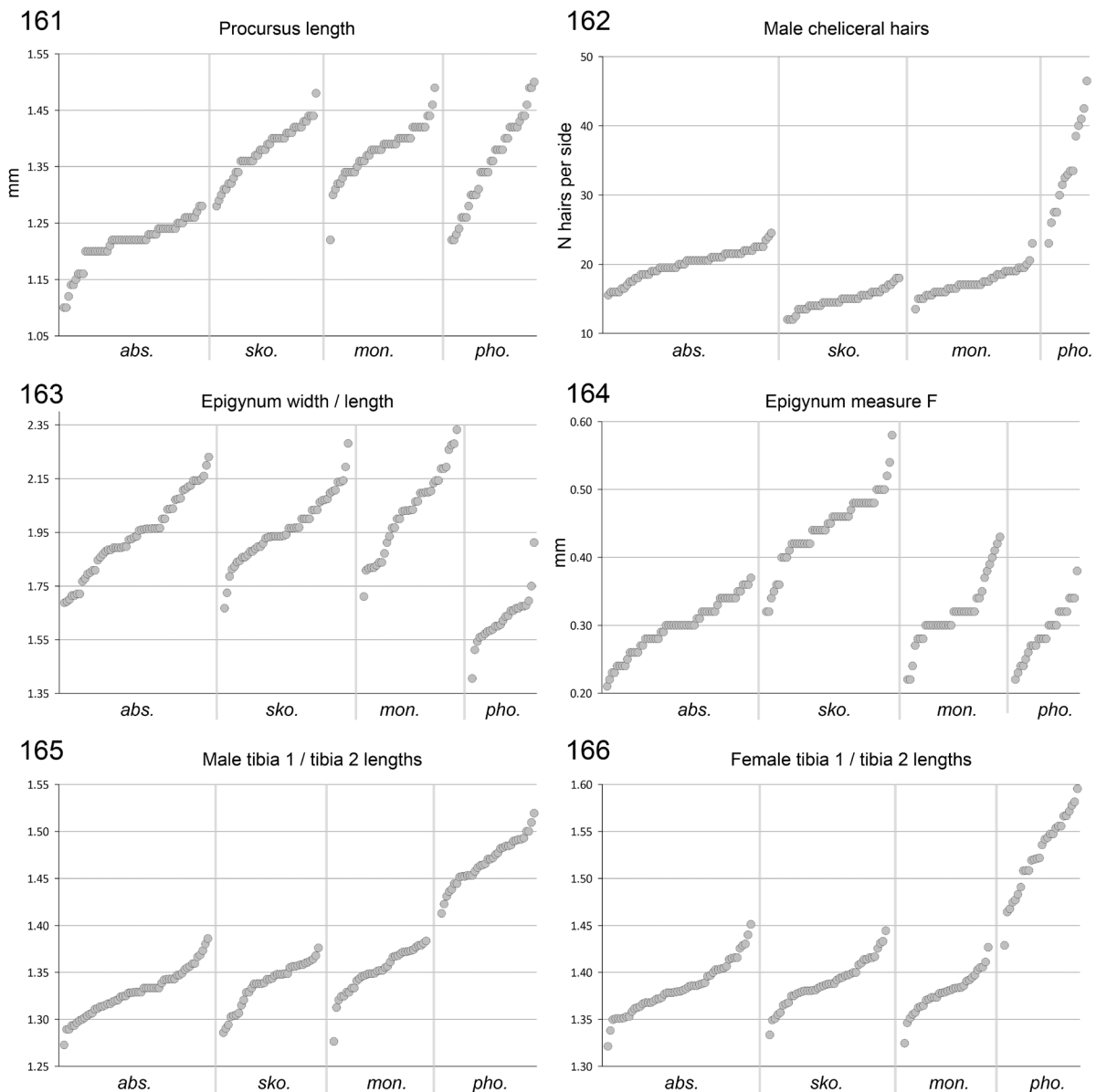
**Figs 157–160.** Bulbal measures B–E for the three species of the ‘northern clade’ of *Stygopholcus* Kratochvíl, 1932 (cf. Figs 15–18). Bulbal measure A is strongly correlated with measure C and therefore not shown. Bulbal measures sorted from smallest to biggest for each species of the ‘northern clade’. The bulb of *S. photophilus* was not measured (it differs strongly in shape, and measure D is inapplicable). Asterisk in Fig. 160 = dubious specimen from Jama na Brezdanu (see text).

ALBANIA – **Gjirokaštër** • 1 ♂, 1 ♀; Përmet, near Petran, artificial gallery; 40.208° N, 20.419° E; 12 May 1995; B. Petrov and R. Stoev leg.; NMNHS.

**Credible published records** (not examined)

GREECE – **Epirus** • 1 ♀; 11 km SE of Konitsa, in gorge of river Voithomatis [“Bogsomatis”, side river of Aaos river], “Ep-73/48”; 40.019° N, 20.785° E; 30 Apr. 1973; V. Mahnert leg.; (Brignoli 1976); MHNG(?).

ALBANIA – (the following material could not be found, C. Deltshv pers. comm., 30 Sep. 2020)  
**Durrës** • ♂♀ (not specified); Durrës; 41.3° N, 19.5° E; 26 May 1993; P. Stoev and D. Zapryanova leg.



**Figs 161–166.** Procursus length, number of modified hairs on each male chelicera, epigynum width/length, epigynum measure F (cf. Fig. 21), and relationships between tibia 1 and tibia 2 lengths in males and females. Measures/counts sorted from smallest to biggest for each species. Abbreviations: *abs.* = *S. absoloni*; *sko.* = *S. skotophilus*; *mon.* = *S. montenegrinus*; *pho.* = *S. photophilus*.



(Deltshev *et al.* 2011). – **Korçë** • ♂♀ (not specified); Cave 2 near Leskovik; 40.150° N, 20.600° E; 1 Jun. 1994; T. Ivanova leg. (Deltshev *et al.* 2011). – **Gjirokastrë** • ♂♀ (not specified), Dragot, Vijoshe River; 40.288° N, 20.069° E; 1 Jun. 1994; G. Blagoev leg. (Deltshev *et al.* 2011).

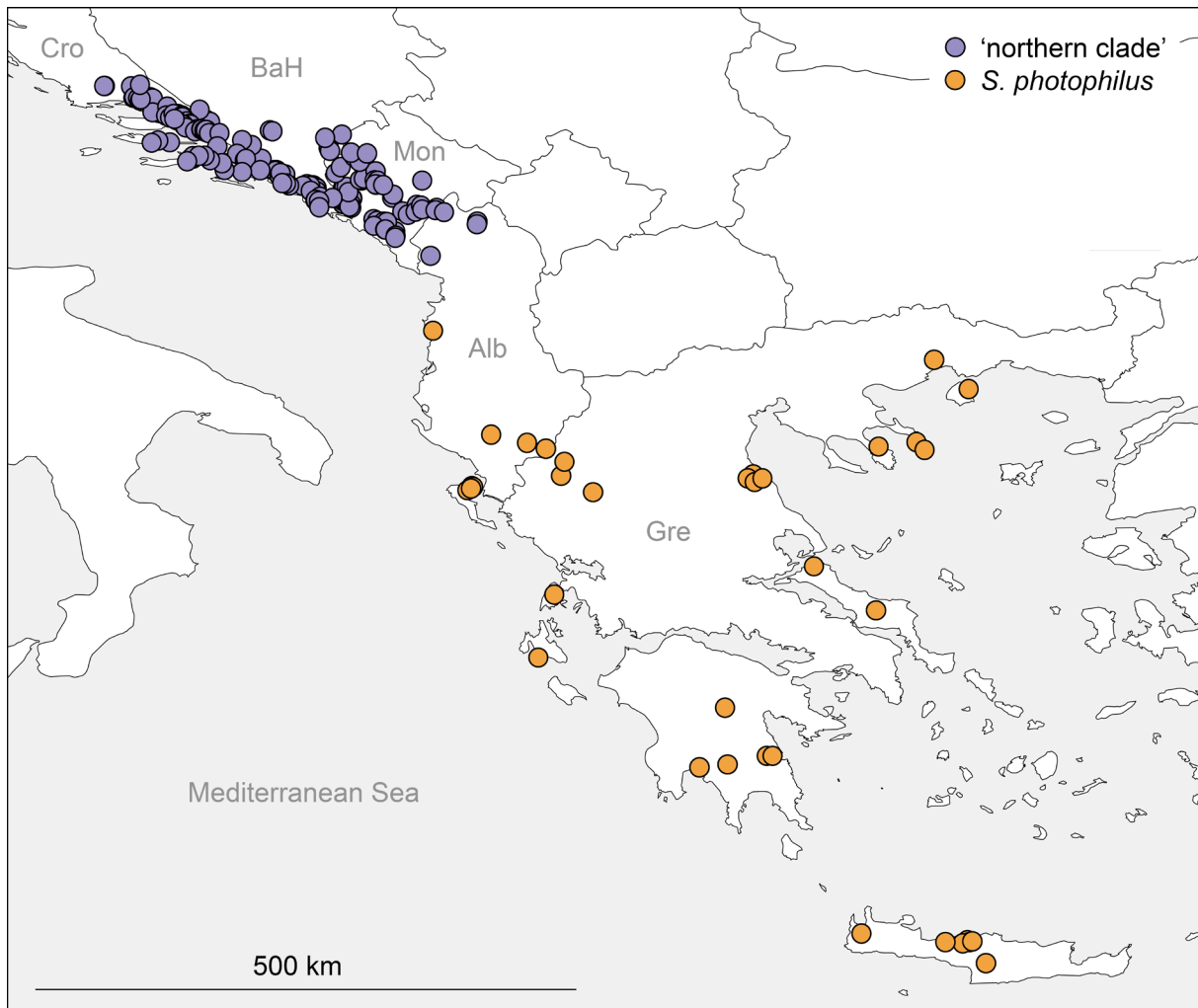
**Unidentified and unspecified localities**

GREECE • 1 ♀; Crete, “Chassia” [misspelling on copied label?], “RII/8”; May 1926; Roewer leg.; SMF • 1 ♂, 1 ♀, paratypes; “7002”; no further data; MNHN (Ar 10230) • 1 ♂; Peloponnese, “Mühlenbach”; 6 Oct. 1980; Malicky leg.; SMF.

**Redescription**

**Male** (Crete; ZFMK (Ar 22205))

MEASUREMENTS. Total body length 4.3, carapace width 1.5. Distance PME–PME 130 µm; diameter PME 120 × 140 µm; distance PME–ALE 30 µm; diameter AME 60 µm; distance AME–AME 30 µm. Leg 1: 40.4 (10.7 + 0.7 + 10.5 + 16.0 + 2.5), tibia 2: 6.9, tibia 3: 5.1, tibia 4: 5.7; tibia 1 L/d: 75.



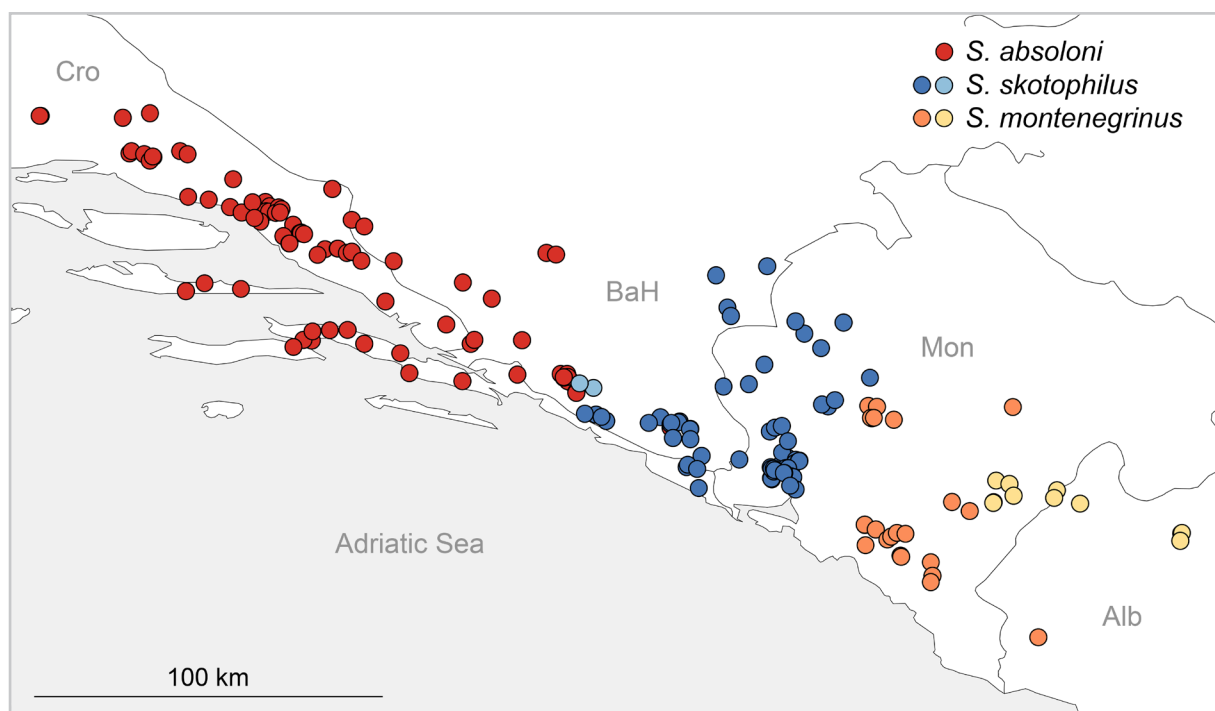
**Fig. 167.** Known distribution of *Stygopholcus* Kratochvíl, 1932. For the ‘northern clade’, see Fig. 168. Abbreviations: Alb = Albania; BaH = Bosnia and Herzegovina; Cro = Croatia; Gre = Greece; Mon = Montenegro.

**COLOR** (in ethanol). Carapace pale whitish to ochre-yellow, ocular area and clypeus slightly darker (light brown), ocular area posteriorly with darker brown V-mark; sternum very dark brown, almost black; legs ochre yellow, with darker (light brown) rings on femora (subdistally) and tibiae (proximally and subdistally), with short dark longitudinal lines dorsally on femora (Figs 127–128); abdomen ochre-gray, with distinct dorsal pattern consisting of brown band around heart and dorsal and lateral marks in posterior half; with white internal marks; ventrally with wide dark brown band, interrupted at two thirds between gonopore and spinnerets.

**BODY**. Habitus as in Fig. 4. Ocular area slightly raised. Carapace with deep median pit and pair of very shallow indistinct furrows diverging from pit to posterior margin of carapace. Clypeus with very indistinct modified area medially (arrow in Fig. 129) and sclerotized margin. Sternum wider than long (1.05/0.70), unmodified. Abdomen oval to short cylindrical.

**CHELICERAE**. As in Figs 119–120, with pair of frontal apophyses set with 2 and 3 modified hairs, respectively, with 23 modified hairs each on frontal face (Figs 130, 132); with strongly sculptured median margins (Fig. 131); with stridulatory ridges (Fig. 133).

**PALPS**. As in Figs 9–11; coxa with prominent retrolateral hump; trochanter barely modified; femur with distinct retrolateral process proximally, with stridulatory pick (modified hair) proximally on prolateral side, with transversal dark line retrolaterally, distally strongly widened and with rounded ventral protrusion; femur-patella joints shifted towards prolateral; tibia very large, thickest at two thirds, with two trichobothria; tibia-tarsus joints shifted towards retrolateral; procurus dorsally with ~5 weakly curved hairs, with strong hump on prolateral side. Procurus tip (Figs 113–114, 137–138) with scoop-shaped dorsal sclerite, strong hinged ventral sclerite (triangular in ventral view), and complex membranous central part with brush of hair-like processes on retrolateral side. Genital bulb (Figs 115–118) with basal



**Fig. 168.** Known distribution of the ‘northern clade’ of *Stygopholcus* Kratochvíl, 1932. Pale blue and pale orange marks denote specimens that are assigned tentatively to the respective species. Abbreviations: Alb = Albania; BaH = Bosnia and Herzegovina; Cro = Croatia; Mon = Montenegro.



sclerite connecting to tarsus, small dorsal process weakly sclerotized, and main sclerite consisting of retrolateral process and dorsal process; retrolateral process distally widening, distal margin with pair of heavily sclerotized bulges on ventral side; dorsal process with single slightly curved tip, proximally with two small apophyses.

LEGS. With ~12 short spines in one row ventrally on femur 1; without curved hairs; few vertical hairs; retrolateral trichobothrium of tibia 1 at 2%; prolateral trichobothrium absent on tibia 1, present on other tibiae; tarsus 1 with irregular platelets rather than with distinct pseudosegments.

#### Male (variation)

Color pattern consistent but individual elements slightly variable in size and distinctness; median section of ventral abdominal band sometimes divided into three parallel longitudinal bands; dark abdominal marks sometimes divided into many small round dots. Tibia 1 (N = 104): 9.7–15.3 (mean 12.7); tibia 2 (N = 41): 6.5–10.4 (mean 8.4); spines on femur 1 (N = 11): 0–34 (mean 19); modified hairs on cheliceral basis (N = 50): 19–44 (mean 30); modified hairs on cheliceral apophysis (N = 50): 3–4 (mean 3.3); chelicerae maximum width (N = 35): 0.60–0.81 (mean 0.70); procurus length (N = 35): 1.22–1.50 (mean 1.36).

#### Female

In general similar to male (Fig. 5), but femur 1 without spines, clypeus unmodified. Without modifications posteriorly on carapace and anteriorly on abdomen. Tibia 1 (N = 91): 8.9–13.7 (mean 11.2); tibia 2 (N = 46): 5.3–9.5 (mean 7.2); epigynum width (N = 25): 0.98–1.34 (mean 1.16); epigynum length (N = 25): 0.62–0.86 (mean 0.72); epigynal measure F (N = 25): 0.22–0.38 (mean 0.29). Epigynum anterior plate roughly triangular, weakly protruding, with very strong transversal ridges in anterior part (Fig. 144); with internal structures visible in uncleared specimens: oval to drop-shaped anterior structure, short parallel (anteriorly slightly converging) sclerites posteriorly; posterior plate short but wide. Internal genitalia (Figs 121–122, 151–152) with distinctive ventral arc (Fig. 156; with several transversal, crescent-shaped sclerites and slightly elongate ventral pocket), with large pore plates (Fig. 122).

#### Distribution

Widely distributed in Greece (including Crete and the Ionian Islands) and southern Albania; the species seems to be largely absent from the Aegean Islands (except Thasos) (Fig. 167).

## Discussion

### *Stygopholcus montenegrinus* – species or subspecies?

*Stygopholcus montenegrinus* was originally described as a full species (Kratochvíl 1940) but later reduced to a subspecies of *S. skotophilus* by Senglet (1971). Senglet's argument focused on the small morphological differences between the two former species. While this observation is certainly correct, the conclusion is less evident. Countless species differ from the most similar species by minute differences. The most consistently applied criterion among arachnologists for separating species seems to be the presence of a gap, usually morphological, irrespective of how big the difference is. Kraus (2000) suggested that such gaps (usually in genital morphology) are almost universal in spiders, explaining the low number of subspecies in araneology.

Kraus (2000) certainly played down the problem of intraspecific genital variation (“There is practically no variation ... [in] ... the taxonomically decisive genital structures”), but it is a widespread pattern that genital structures are less variable within species than other morphological traits (Eberhard *et al.* 1998). As a result, there is less or no overlap among species, usually producing distinct gaps that facilitate

taxonomic decisions. However, the majority of spider species are known from minimal samples, often from only one locality. Many of the observed gaps may thus be artifacts, resulting from insufficient knowledge. As a logical consequence, it has been argued that subspecies in general “cannot be known until the species is known” (Blackwelder 1967). Subspecies are arguably easier to justify in well-studied taxa like mammals, birds, and butterflies than in spiders.

In the case of *Stygopholcus skotophilus* and *S. montenegrinus*, our data, even though still limited, suggest that there are several small but consistent morphological (genital) differences and that there are no intermediate forms in the region where the two taxa come close to each other (they never share a locality). In addition, a multi-gene analysis of a limited sample of specimens resolved each taxon as monophyletic (L. Dietz *et al.*, unpubl. data). This makes both taxa diagnosable, supposedly reproductively isolated, independent evolutionary lines, satisfying the main criteria of several major species concepts (Wheeler & Meier 2000).

### Remarks on distribution

The natural distribution of Smeringopinae (i.e., excluding synanthropic and anthropophilic species) ranges from South Africa to the Iberian Peninsula, the Balkan Peninsula, the Caucasus, and Central Asia (Huber 2011b). *Stygopholcus* thus marks the northern limit of Smeringopinae in Europe. In the absence of a reliable dated phylogeny of *Stygopholcus* and its putative closest relatives (*Crossopriza*, *Holocnemus*) (Eberle *et al.* 2018), the biogeographic history of *Stygopholcus* remains somewhat speculative. However, patterns paralleled in other groups give some indications about plausible scenarios.

First, the large majority of present-day Smeringopinae live in tropical and subtropical environments. Part of the present-day flora and fauna of the Balkan Peninsula is thought to constitute a ‘Palaeo-Mediterranean’ contingent that evolved under pre-Pliocene tropical climatic conditions (Scarascia-Mugnozza *et al.* 2000). It is thus plausible that *Stygopholcus* is derived from ancestors that were present in the area before the Pliocene, in climatic conditions similar to those that its closest relatives still experience today.

Second, a relatively warm climate was maintained in the Balkan Peninsula during Pleistocene glaciations, particularly in the western part: glaciations in this area affected only higher elevations; orographic barriers prevented winter intrusions of cold polar air; and the Adriatic Sea had a moderating effect on temperatures along the coast (Mihevc *et al.* 2010). This made the Balkan Peninsula a refugium for many taxa that recolonized neighboring regions in the north after the last glaciation (Hewitt 2000). At the same time, however, glaciations resulted in drier climate (Sinopoli *et al.* 2019), and epigeal ancestors of some present-day troglophile and troglobite taxa may have disappeared during this time. It is thus plausible that the epigeal ancestor of the present-day northern clade of *Stygopholcus* disappeared during this period, and only descendants that had adapted to subterranean life survived. However, earlier climate-related phenomena could have had the same effect, i.e., *Stygopholcus* may have adapted to subterranean conditions earlier than the Pleistocene. For example, a dry period at the end of the Miocene (Hsü *et al.* 1973) that is thought to have affected the *salax* group of the spider genus *Troglohyphantes* (Deeleman-Reinhold 1978); or the disappearance of Lake Pannon and the bordering Dinarid Lake System, which is thought to have caused the extinction of all epigeal species of the bivalve genus *Congeria* (Bilandžija *et al.* 2013).

Third, taxa that exhibit a so-called ‘mero-Dinaric’ distribution may shed some light on the northern limit of *Stygopholcus*. The term mero-Dinaric was introduced for taxa that show either a northwest or southeast distribution in the Dinarides or a disjunct distribution, with the gap consistently in the same region in the central Dinarides (Sket 1994). Examples of mero-Dinaric taxa are species groups of the genus *Troglohyphantes* (Deeleman-Reinhold 1978), several genera of the spider family Dysderidae



(Deeleman-Reinhold 1993; Pavlek & Mammola 2021), and the diplopod subfamily Acherosomatinae (Antić *et al.* 2015). The northern limit of *Stygopholcus* matches closely to this gap, suggesting that the factors affecting mero-Dinaric taxa may also affect or have affected *Stygopholcus*. Reasons for this exclusive northwest or southeast distribution are largely unknown. One possible explanation is that in this area, much of the carbonate rocks that were exposed between ~3–6 Ma remained covered by impermeable flysch sediments for longer than in the neighboring areas, impeding access to the moisture-retaining limestone habitat (Deeleman-Reinhold 1978; Sket 1994; Mihevc *et al.* 2010). This, together with decreasing temperatures towards the north may explain the northern limit of *Stygopholcus*, in spite of the ubiquity of suitable habitats (including caves) that would seem to allow for more northern occurrences and that have been sampled extensively.

Fourth, the Dinarides can be seen as ultimately continuing into Greece and the Greek islands, but a major distinction can be made in geological terms across the transition known as the Scutari-Peć transverse zone which runs through northern Albania, south of which the geology is dominated instead by volcanic or metamorphic rocks (Kissel *et al.* 1995, Reed *et al.* 2004). This geological line coincides closely with the current southern limit of the northern clade of *Stygopholcus*, suggesting that the presence of karst may have been a crucial factor in the evolution and survival of *Stygopholcus* in the western Balkan. However, Albania is relatively poorly sampled, so we cannot exclude the possibility that the southern limit of the northern clade is just a sampling artifact.

In summary, the northern clade of *Stygopholcus* may have been derived from an epigeal ancestor that lived in the area before the Pliocene when the climate was more tropical or subtropical; during historical climatic perturbations the spiders survived because they could access exposed karst habitats in the southwest Dinarides; access to such habitats was presumably not possible further north and further south, for different reasons. The only surviving epigeal congener, *S. photophilus* in Greece, may have largely retained the ancestral mode of life.

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