

# The enigmatic Alpine opilionid *Saccarella schilleri* gen. n., sp. n. (Arachnida: Nemastomatidae)—isolated systematic placement inferred from comparative genital morphology

Axel L. Schönhofer · Jochen Martens

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**Abstract** In Opiliones, male genital morphology plays a key role in systematics and understanding the evolution of the group because functional modifications often outline higher taxonomic levels. In Nemastomatidae, different lateral stabilizing structures on the penial truncus cane developed independently. These wing-like protuberances serve as anchor points for two muscular tendons and are interpreted traditionally as generic characters. A newly discovered species from Monte Saccarello in the Ligurian Alps of North-western Italy is unique in providing anchor points as stabilizing parts of the distal truncus cane below the glans by short and narrow lateral folds. To place this unusual species within the Nemastomatidae one must re-evaluate the usefulness of male genital morphological and other characters used in the systematics of the family. The resulting phylogenetic framework is supplemented with available molecular genetic data. Based on both datasets, the creation of a new genus seems justified. *Saccarella schilleri* gen. n. sp. n. is subsequently described and further defined. The endemism and biogeography of the harvestmen fauna in the South-western Alps are discussed with respect to this enigmatic genus.

**Keywords** Morphology-based systematics · South-western Alps · Endemism · Biogeography

A. L. Schönhofer (✉)  
Department of Biology, Life Sciences North,  
San Diego State University,  
San Diego, CA 92182-4614, USA  
e-mail: Axel.Schoenhofer@uni-mainz.de

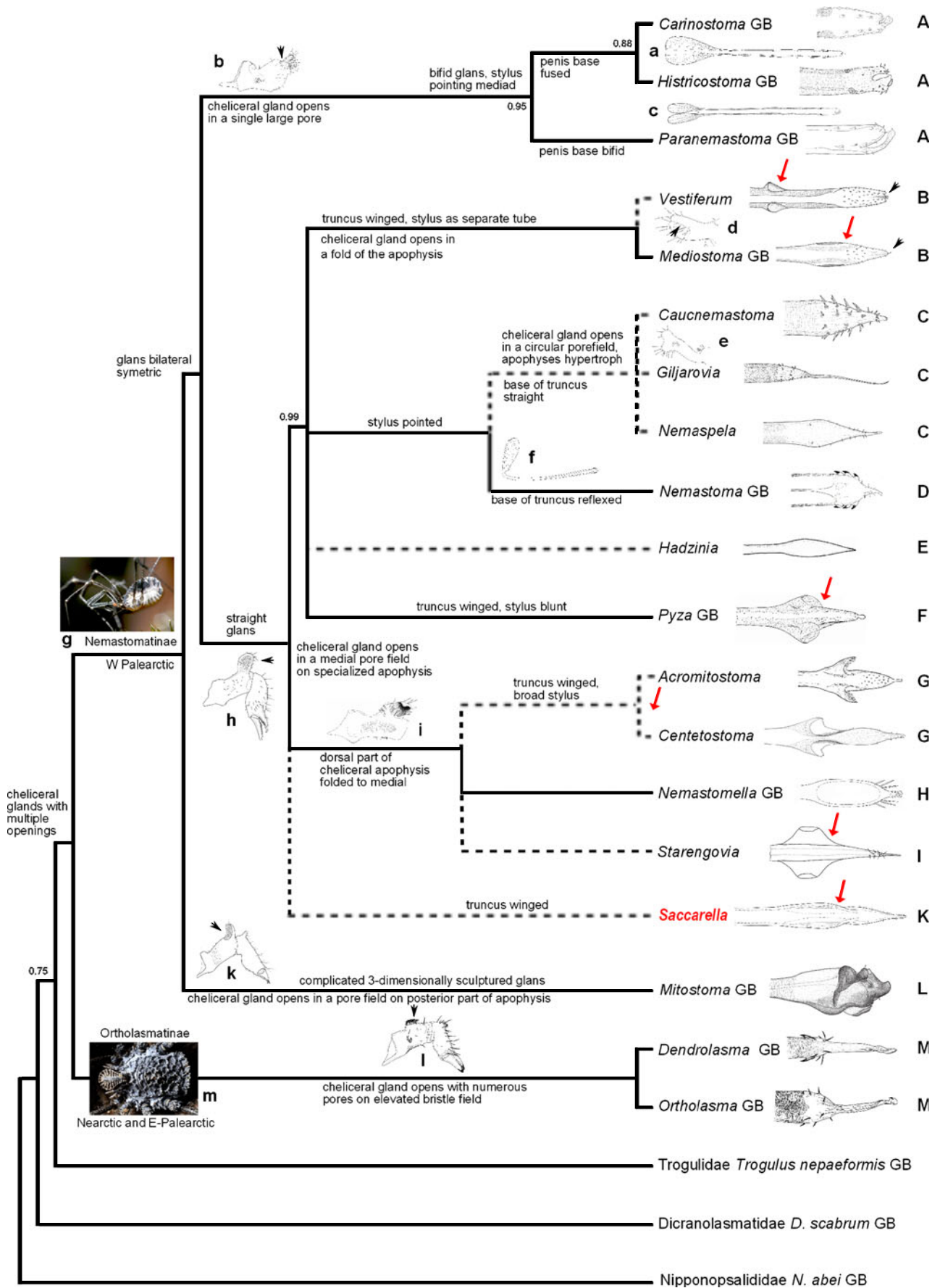
J. Martens  
Department of Systematic Zoology Institute of Zoology,  
Johannes Gutenberg University Mainz,  
Johannes-von-Müller-Weg 6,  
55099 Mainz, Germany  
e-mail: martens@uni-mainz.de

## Introduction

While studying the opilionid fauna of the South-western Alps, a number of previously collected samples within the working collection of J.M. were investigated. A single series of a hitherto unknown Nemastomatidae species was traced, apparently representing a new species. Several attempts to recollect additional specimens failed, but the present material is sufficient to describe the species and to discuss its generic status and systematic relationships. Although in external morphology superficially similar to the syntopic and widespread *Nemastoma dentigerum* Canestrini, 1873, investigation of the male genitalia precluded assignment to any nemastomatid genus presently known. The marked and unique fine structure of the distal penial truncus cane implies an exposed placement within Nemastomatidae and warrants the establishment of a novel genus. To verify the creation of a new monotypic genus, the systematic value of male genital morphological characters within the Nemastomatinae is reassessed, validated with other morphological characters and supplemented with available molecular data. Hereby, the first complete systematic framework of all described Nemastomatinae genera is provided and important character traits are mapped. The new genus and species is described in detail, and its ecology, endemism and biogeography with respect to other South-western Alpine opilionids are also discussed.

## Materials and methods

To provide a scaffold phylogeny of all Nemastomatinae and troguloidean outgroups (Fig. 1) we used available sequence data of 28S rRNA, provided mainly by Schönhofer and



**Fig. 1** Systematic framework of Troguloidea depicting development of selected character within the Nemastomatidae. *Bold branches* and *GB* (GenBank) following genus names indicate phylogenetic information based on 28S rRNA, *dashed branches* indicate tentative placement of additional genera upon outlined morphological features. Numbers at nodes indicate posterior probabilities less than 1.00 (according to Schönhofer and Martens 2010). *Black arrows* special features; *red arrows* independent evolution of wing-structures as discussed in the text. All drawings on the *right* show the distal part of the penis cane with glans and stylus; from top to bottom: *Carinostoma carinatum* (A; ventral, Martens 1978, Fig. 195); *Histicostoma caucasicum* (A; dorsal, Martens 2006, Fig. 26b); *Paranemastoma kochi* (A; ventral, Martens 1978, Fig. 169); *Vestiferum alatum* (B; dorsal, Martens 2006, Fig. 18 k); *Mediostoma variabile* (B; ventral, Martens 2006, Fig. 25o); *Caucnemastoma golovatchi* (C; dorsal, Martens 2006, Fig. 19c); *Giljarovia trianguloides* (C; ventral, Martens 2006, Fig. 7c); *Nemaspela femorecurvata* (C; ventral, Martens 2006, Fig. 14c); *Nemastoma triste* (D; dorsal, Martens 2006, Fig. 22d); *Hadzinia karamani* (E; dorsal, Šilhavý 1966, Fig. 1); *Pyza bosnica* (F; dorsal, Gruber 1979, Fig. 20); *Acromiostoma rhinocerus* (G; dorsal, Rambla 1983, Fig. 1f); *Centetostoma juberthiei* (G; dorsal, Martens 2011, Fig. 32); *Nemastomella dubium* (H; dorsal, Rambla 1969, Fig. 6); *Starengovia kirgizica* (I; dorsal, Snegovaya 2010, Fig. 7); *Saccarella schilleri* (K; dorsal); *Mitostoma gracile* (L; lateral, Martens 2006, Fig. 35c); *Dendrolasma mirabile* (M; ventral, Shear and Gruber 1983, Fig. 184); *Ortholasma coronadense* (M; ventral, Shear and Gruber 1983, Fig. 121). Within the tree (in lower case letters, including those between genera names) from top to bottom: *Carinostoma elegans* (a; penis ventral, Martens 1978, Fig. 201); *Paranemastoma quadripunctatum* (b; basal cheliceral segment lateral, Martens 1978, Fig. 156); *Paranemastoma kochi* (c; penis ventral, Martens 1978, Fig. 169); *Vestiferum funebre* (d; apophysis medial, Martens 2006, Fig. 18f); *Giljarovia vestita* (e; chelicera apophysis, medial, Martens 2006, Fig. 9k); *Nemastoma triste* (f; penis lateral, Martens 1978, Fig. 127); *Mitostoma chrysomelas* (g; body and legs; Germany, Mainz); *Saccarella schilleri* (h; chelicerae medial); *Centetostoma scabriculum* (i; apophysis medial, Martens 2011, Fig. 7); *Mitostoma chrysomelas* (k; chelicerae lateral, Martens 1978, Fig. 214); *Ortholasma coronadense* (l; chelicerae lateral, Shear and Gruber 1983, Fig. 102); *Ortholasma colossus* (m; body; Tulare, Three Rivers, CA); photos by A.S.

Martens (2010; see for accession numbers, specimen data and laboratory protocols). In addition, we used sequences of *Nipponopsalis abei* (accessions AF124948 GQ912777), *Ortholasma* sp. (accessions AF124946, GQ912775), *Nemastomella dubia* (accessions U37002, GQ912774) and *Dendrolasma parvulum* (accessions EF108574, EF108578)—all listed in Giribet et al. (2010). A Bayesian analysis was conducted using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) including a model of DNA sequence evolution (GTR+I+G) evaluated by jModelTest 0.1.1 (Posada 2008) and selected by Akaike Information Criterion. To ensure convergence, replicate analyses were run until the standard deviation of split frequencies fell below 0.01 (Ronquist et al. 2005). Clades of the resulting phylogeny were collapsed to represent only genera as terminal taxa (Fig. 1, solid branches). Genera for which molecular data were unavailable were manually grafted onto this tree (Fig. 1, dotted branches) according to characters depicted and outlined at nodes and branches, with further

elaboration in the discussion. For more detailed results on the molecular data alone, please refer to Schönhofer and Martens (2010).

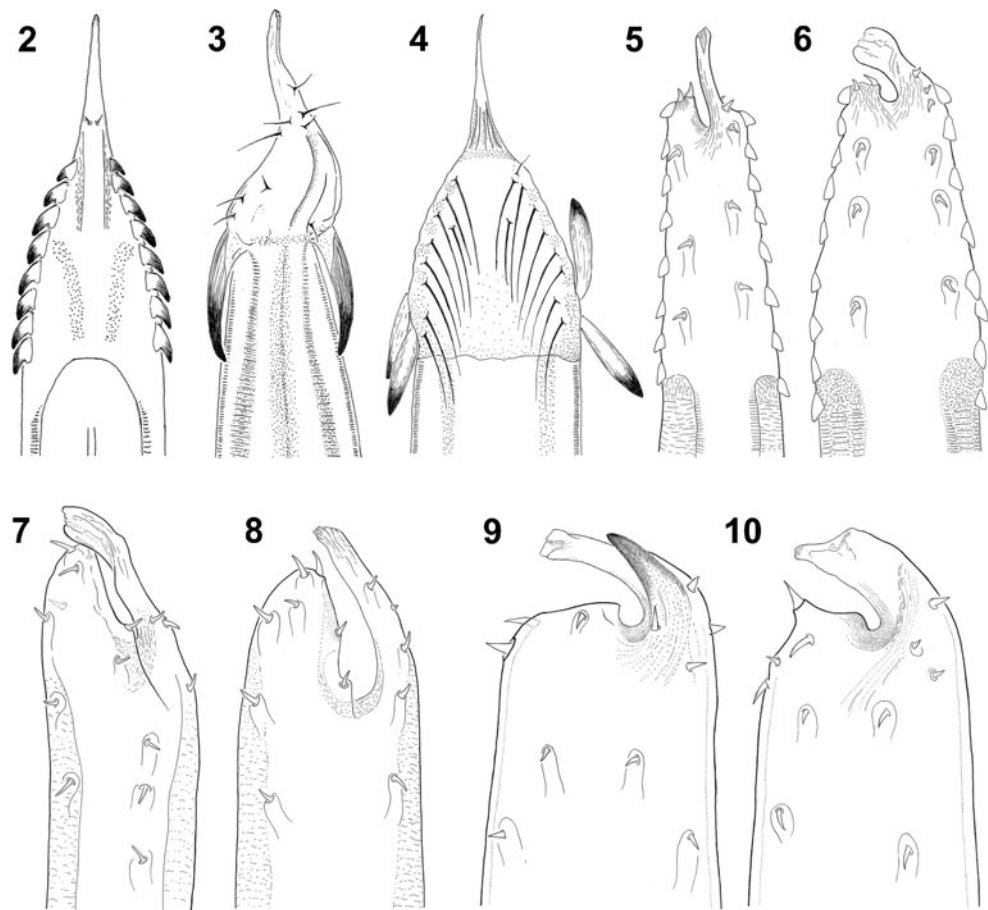
All material listed in the Taxonomy section is deposited in the working collection of J.M. in the Institute of Zoology, Mainz University, Germany (Collection J. Martens: CJM), and finally deposited with the Senckenberg Museum, Frankfurt am Main (SMF). Photographs for Figs. 11–15 were taken with a Nikon D80 attached to a Wild Heerbrugg M5A Dissecting Microscope, or with a BK Lab System (Visionary Digital; <http://visionarydigital.com>) and refined with CombineZP, Lightroom 2.0 and Photoshop CS4. Original line drawings of Figs. 16–27 were produced using a camera lucida attached to the M5A or a Leitz Laborlux Microscope. Drawings were vectorized using a Wacom Bamboo tablet CTH-460 and Inkscape 0.48. Measurements were taken by means of a micrometer disc using the same optics and devices. All measurements are given in millimeters.

## Results

The Bayesian analysis provided a topology (Fig. 1) of eight genera within the Nemastomatinae identical to that of Schönhofer and Martens (2010, plus more detail on topology and posterior probabilities [pp]). In addition, genetic data grouped Nemastomatidae, Nemastomatinae and Ortholasmatinae with 1.00 pp support within the Troguloidea (comprising all taxa in Fig. 1). All species were assigned to their proposed genera, and genera received at least 0.99 pp (e.g., species shown in Figs. 2–10). Inter-generic placement shows less support compared to the results of Schönhofer and Martens (2010), because cytochrome *b* sequence data was not included.

The novel species under discussion is peculiar in several morphological respects. Most noteworthy are characters of male genital morphology. The truncus cane of the penis is extremely slender (Figs. 19–21), its three main parts, a muscle-bearing basis, truncus cane and glans, are situated in a straight line; no part is angular. The distal part of the truncus forms a marked lateral fold, i.e., the dorsal part of this truncus section is markedly extended laterally. The opposite ventral part is slightly constricted; both parts, ventral and dorsal, form a narrow furrow with an additional lateral truncus constriction (Figs 16–18, 22; position of the cross-section of the truncus is indicated by “x”; indication of furrow by an arrow in Fig. 16). Furthermore, the truncus base is bipartite (Figs. 19–20), the individual parts each carry a muscle portion (as in all Nemastomatidae species), which extends to an elongated tendon and reaches the basal part of the ventral truncus fold (Figs. 19–20, tendons indicated as parallel dotted lines in truncus cane). As an additional remarkable character, the apophysis of the basal

**Figs. 2–10** Generic differences versus interspecific differences in male genital morphology of Nemastomatinae showing penial glans and stylus. Species shown have been assigned to their “correct” respective genus in a molecular phylogenetic analysis including 28S rRNA and cytochrome *b* (see Schönhofer and Martens 2010); all Figs from Martens (1978; respective Fig.-no. in parentheses); 1–2: dorsal; 3–9: ventral; 2: *Nemastoma bimaculatum* (Fig. 124); 3: *Nemastoma lugubre* (Fig. 136); 4: *Nemastoma bidentatum* (Fig. 147); 5: *Carinostoma carinatum* (Fig. 195); 6: *Carinostoma elegans* (Fig. 202); 7: *Paranemastoma silli* (Fig. 177); 8: *Paranemastoma quadripunctatum* (Fig. 155); 9: *Histicostoma argenteolunulatum* (Fig. 190); 10: *Histicostoma dentipalpe* (Fig. 184)



segment of the male chelicerae is large, pronouncedly dorso-distally, elongated and disposes of a large medial extrusion area for the secretion of the cheliceral gland (Figs. 25–27). This area consists of numerous fine and evenly distributed pores (Fig. 27). Such morphological details of the male genitalia and cheliceral apophysis are peculiar and unknown in other nemastomatids.

## Taxonomy

*Saccarella* gen. n.

**Diagnosis:** A new genus delineated by male genital morphology (dorsal and ventral lateral folds in distal part of truncus penis), truncus and glans straight, not bent (from dorsal/ventral view), weak glans armament (inconspicuous minute bristles), male cheliceral apophysis (large in terms of nemastomatid morphology, extended medial secretion field of minute pores), armament of dorsal side of scute (without noticeable single thorns, spines or rows of thorns); leg morphology (femur to tibia of leg I markedly inflated, short in terms of nemastomatid morphology); coloration (black, without silvery spots on dorsal scute). Presently one species known.

**Type species:** *Saccarella schilleri* sp. n. (by monotypy and original designation).

**Derivatio nominis:** The name is derived from Monte Saccarello at the western edge of the Italian Ligurian Alps; gender is female.

*Saccarella schilleri* sp. n.; Figs. 11–27.

The new species is described under the biological species concept (Mayr 1942 and exemplified for Opiliones by Martens 1969) based on unique morphological characters suggesting reproductive isolation.

**Holotype:** m#, Italy, Liguria, Prov. Imperia, Monte Saccarello, close to village Monesi di Triora, N: 44.071° E: 7.749°; 1,475 m, W. Schiller leg. 30.05.1986 (CJM 7006; ex CJM 3112).

**Paratypes:** 6 m#, 1 f#, same data as holotype (CJM 3112).

**Distribution:** The species has been collected in the Italian South-western Alps, a hotspot of alpine arthropod biodiversity and endemism (Isaia et al. 2011; Vigna Taglianti et al. 1999). Despite several attempts to relocate the species also in the frame work of the EDIT project (see Acknowledgments), it remains known only from one narrowly circumscribed locality.

**Diagnosis:** *Saccarella schilleri* sp. n. differs from all Nemastomatidae by its contrasting genital morphology, with folds alongside the distal truncus and a blunt stylus,

otherwise refer to genus diagnosis. While close relatives of *Saccarella schilleri* sp. n. are not discernible, it is discriminate from other syntopic nemastomatids. To aid determination: *Centetostoma centetes* (Simon, 1881) is much smaller, *Histicostoma dentipalpe* slightly larger, and both exhibit elongated spines on the dorsal opisthosoma, whereas *Nemastoma dentigerum* is of the same size and coloration and not discernible in the field. Males of *Saccarella schilleri* sp. n. lack the palpal apophyses present in males of *Nemastoma dentigerum*. The shape of the cheliceral apophyses in *Nemastoma dentigerum*, *Centetostoma centetes* and *Saccarella schilleri* sp. n. is superficially similar.

**Derivatio nominis:** The species' epithet honours Wolfgang Schiller (Grenzach-Whylen, Germany), a distinguished specialist of carabid Coleoptera and sophisticated collector of soil arthropods, who provided the only series of this unexpected species.

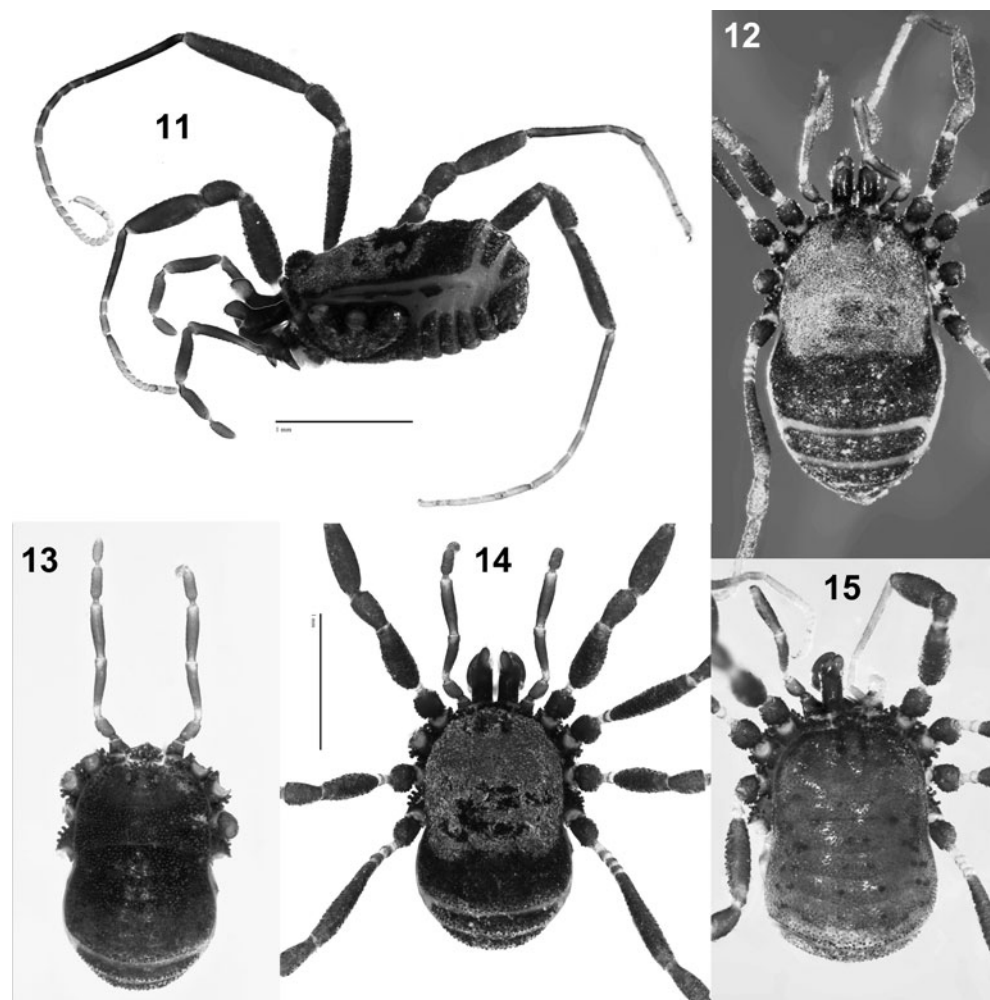
**Description:** *Measurements* Leg II (holotype m#, f# in parentheses): Femur 1.2 (1.1), Patella 0.4 (0.4), Tibia 1.0 (0.9), Metatarsus 1.5 (1.4), Tarsus 1.4 (1.3). Length of dorsal scute: 1.4–1.6 (1.6).

**Body** (Figs. 11–15) Coloration: body and legs deep black several weeks after final moult, without silvery or golden markings. A thin layer of agglutinated secretion covers the dorsal scute; thus older specimens appear with a greyish to whitish dorsum after fixation in alcohol (Figs. 11–12, 14, removed in 13); in males the area of secretion is restricted to prosoma and opisthosomal areae I and II (Figs. 11–12), in the female extended to area III (Fig. 12).

**Dorsal side:** All scutal areae and free tergites covered densely with fine acute granules, spaced about their own size, largest near frontal end of scute close to tuber oculorum, on areae I–V of the dorsal scute one pair each of larger and markedly higher tubercles, their inter-distances enlarging towards the rear areae (Fig. 15), free tergites I–III with a row of slightly more pronounced granules at rear end.

**Tuber oculorum** (Figs. 11–15): slightly elevated, rising from frontal margin of scute, height about two-thirds of length, as long as wide, irregularly covered with tubercles, increasing in size from posterior to anterior margin; eyes prominent, their diameter about half the size of the height of the tuber. Supracheliceral lamellae consisting of four small

**Figs. 11–15** *Saccarella schilleri* gen. n. sp. n., 11: lateral view; 12–15: dorsal view; 11, 13–15: males; 12: female; 11–14: paratypes; 15: holotype; 13: individual of picture 11 and 14, cleaned from soil and secretion; 15: freshly moulted and untreated specimen. Bars all 1 mm, in 11 for 11–12, 15; in 14 for 13–14



sclerite plates, with distally pointing mushroom- to ambos-shaped tubercles.

Ventral side: genital operculum and free sternites with scattered small tubercles, inconspicuous on the sternites and on corona analis; coxae pro- and retro-laterally with a scattered row of 6–12 blunt or ambos-shaped tubercles each.

*Chelicerae* (Figs. 25–27): Males with a large dorso-distal apophysis on basal cheliceral segment, laterally compressed forming a flat, irregularly spoon-shaped form (medial and lateral views); apophysis slightly inclined distally, longer than wide at basis, broadening distally (medial and lateral views), dorsally slightly rounded (medial and lateral views), anterior edge higher than posterior one (medial and lateral view), medial part of apophysis slightly concave, entirely covered with an extrusion area of minute pores for secretion produced in the cheliceral gland; pore area interspersed with medium-sized, more slender hairs.

*Pedipalp* (Fig. 23): Moderately compact; femur slightly enlarged towards distal end, patella ventrally slightly thickened. Femur to tarsus covered with sparse (femur) to denser (patella, tibia, tarsus) array of bristles, most of them of the clavate glandular type; in both sexes no patella spur armament.

*Legs* (Figs. 11–12, 14–15, 24): Short and stout in terms of nemastomatid morphology. Femur, patella and tibia of leg I and III markedly inflated, leg IV most slender; femur to tibia partly covered by two types of distinct microstructures (Fig. 24): (1) rounded tubercles, as high as broad, spaced about their diameter and irregularly scattered; (2) considerably smaller scales in the inter-distances; trochanter with tubercles dorsally, on femur throughout; on patella and tibia tubercles restricted to dorsal side, otherwise segments densely covered with scales, causing a finer and more regular appearance; metatarsus and tarsus without granules and scales but densely and regularly covered with short hairs on small tubercles; few longer hairs interspersed. Pseudo-articulations of femora: I–IV (all m#, f# in parentheses): I 0 (0), II 1–2 (2), III 1 (legs missing), IV 2–3 (2–3). In femora IV, number always differs on left and right femur.

*Male genital morphology* (Figs. 16–22): Penis straight, extremely slender (dorsal/ventral/lateral view), nearly parallel-sided (dorsal and ventral view), slightly and gradually widening toward distal end, in lateral view slightly curved. Glans symmetrical, in straight prolongation of truncus. Broadened truncus base deeply split into two elongated, muscle-bearing portions (Figs. 19–20). Ventral side of truncus (Fig. 17) sub-distally forming a slightly widened wing-like structure, markedly tapering toward basis of glans. Dorsal side of truncus slightly constricted forming a narrow connection, bridging sub-distal part of truncus and basis of glans (Fig. 16); at both lateral sides below the connection the truncus is slightly excavated forming a shallow furrow (Figs. 16, 18, 22); truncus wing slightly longer than glans

(Figs. 16–17, 19–20). Armament of glans and stylus sparse, consisting of few minute bristles mainly on lateral and ventral side, glans tapering into short stylus, opening of sperm duct at distal end.

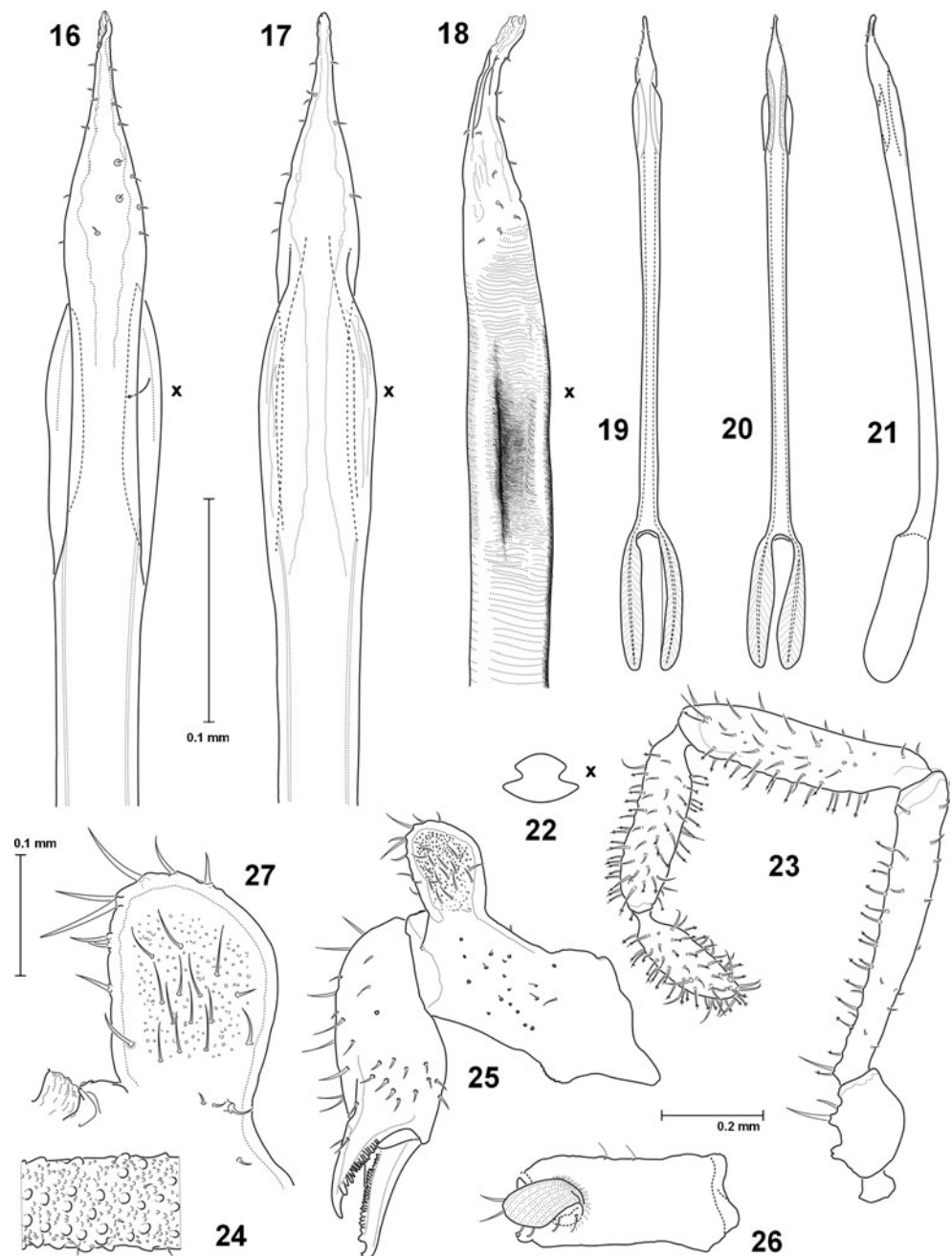
## Discussion

Current Opiliones systematics is based mainly on male genital morphology, which contributes to differentiate various taxonomic levels, that of species, genera and families (Martens 1969, 1976, 1986). This is also true within the Nemastomatidae, where genital morphology was first applied in a larger context by Šilhavý (1956, 1966) to indicate evolutionary lineages. However, it is most important to understand the significance of these structures and their contribution to functionality to infer their value for taxonomy and systematics. Within the well studied Nemastomatidae, these questions have been tackled partially by a variety of authors, namely Gruber (1976, 1979), Gruber and Martens (1968), Martens (1976, 1986, 2006, 2011), Šilhavý (1956, 1966) and Starega (1976, 1978), all of whom contributed substantially to modern understanding of nemastomatid systematics. Still, information is scattered and a summarizing approach or a comprehensive molecular phylogenetic framework to test genera and species hypothesis is currently unavailable. In the course of describing a new genus and species from the South-western Alps, questions of generic and species limits within Nemastomatidae needed to be checked; the following discussion of nemastomatid phylogeny is based on the available morphological and molecular characters.

## Functionality and the value of general penial organization for higher systematics

Within the opilionid suborder Dyspnoi, molecular systematics support the previous morphological division into superfamilies and families based on the main organisation of male genitalia (Martens 1976, 1986; Giribet et al. 2010). The superfamilies Ischyropsalidoidea and Troguloidea differ in the number of penial muscles, one in Ischyropsalidoidea, two in Troguloidea. Within the latter superfamily, the Nemastomatidae are unique in having the glans firmly attached to the truncus, which disables the independent movement of the glans and truncus while this movement is possible in the other families by means of membranous areas acting as a joint between glans and truncus (Martens 1976). Consequently, Nemastomatidae need to apply different mechanisms for penial movement than other Troguloidea, and they also differ in many other respects from the remainder of the superfamily. Most Nemastomatidae (except for

**Figs. 16–27** *Saccarella schilleri* gen. n. sp. n.: 16–22: penis; 16–18: penis tip and distal truncus; 19–21: penis; 16, 20: ventral view; 17, 19: dorsal view; 18, 21: lateral view; 22: cross-section through Fig. 17 at cross; 23: palpus, medial view; 24: central part of femur II, lateral view; 25–27: chelicerae; 25, 27: medial view; 26: dorsal view on basal segment; 27: apophysis; *Bar* 0.1 mm for 16–19; *Bar* 0.2 mm for 20–26; *Bar* 0.1 mm for 27



*Mitostoma*) have their muscles concentrated within the bulb-like base of the penis (Gruber 1976; Martens 1976, 2006), while in the other families of Trogluioidea the muscles fill most of the truncus cane (Martens 1978). The penial truncus in Nemastomatidae is mostly very thin; elongated and extended muscular tendons span the distance between these basal muscles and the glans. The tendons attach below or within the glans section and muscle contraction may enable deformation of the truncus as a whole to move the glans in various directions and stabilize the long and slender penis tube during mating (Martens 1976; 1986), perhaps the movement of the glans is also used to enhance accuracy of aiming during copulation. These structural peculiarities are

found throughout the Nemastomatidae and are easily acceptable as family characteristics.

### Morphological characters within Nemastomatidae

Attempts to classify the diversity within the family have utilized a multitude of morphological characters whose value for systematics and taxonomy have changed in the course of ongoing study of the family. External morphological features, like bridgethorns and armament with cone-like spines of the body used in earlier classifications (Roewer 1923, 1951; Kratochvíl 1958), were soon outlined as too

variable or identified as too convergent and alterable developments to aid as sole generic characteristics. Respective groupings appeared heterogeneous in terms of other characters and were subsequently disbanded, while many of the newly proposed generic names persisted but lacked a solid phylogenetic background. An exception is the subfamily classification Nearctic / Eastern Palearctic Ortholasmatinae, with their external ornamentation with anvil-shaped tubercles and a characteristic hood protruding over the chelicerae, and the less ornamented predominantly Western Palearctic Nemastomatinae (Shear and Gruber 1983). Regarding the latter, the focus is on the following.

Within the Nemastomatinae, Šilhavý (1966) was the first to establish a system based on genital morphology; he focused on differences in stylus form and glans armament to group species into genera. Subsequent research based on his system was applied to most other nemastomatid groups under revision. However, with a better understanding of nemastomatid diversity, the questions to what extent genital morphological characters are able to resolve phylogenetic relationships, and how to determine what their value as generic characters may be, were again asked.

#### Value of penial characters for systematics within Nemastomatinae

Within this subfamily, there exist three general penial glans forms, which are corroborated by molecular data to belong to different phylogenetic lineages (Schönhofer and Martens 2010). *Mitostoma* Roewer, 1951 exhibits a highly structured three-dimensionally organised glans (Fig. 1L) and is sister to all other Nemastomatinae, which, without exception, exhibit dorso-ventrally flattened and bilaterally symmetric glandes (Fig. 1a–k). Within the latter group, most species exhibit an undivided glans and the stylus is more or less pointed (Fig. 1B–K). But a group comprising *Carinostoma* Kratochvíl, 1958, *Histicostoma* Kratochvíl, 1958 and *Paranemastoma* Redikorzev, 1936 shows a bifid glans with a stylus pointing mediad (Fig. 1A). These three genital morphological groups also coincide with molecular data. Below these phylogenetic splits, molecular data is too scarce at present to test further division into genera, especially within the large group of genera comprising species with undivided glans. According to the traditional genital morphological concept in Nemastomatinae, genera are defined as natural groups of related species. These genera are outlined by similarities of stylus, glans and its armament with spines and the basal and distal part of the truncus. This basic organization of male genitalia does not change within a genus, and species level differences are obvious in the number, size and position of spines, as well

as the finer shape of the glans and stylus (Figs. 2–10 provide examples for inter-specific and inter-generic differences of glandes and styli of the sequenced species of four different genera). A well-studied example is the genus *Nemastoma* C. L. Koch, 1836, exhibiting in several cases a short and compact glans, a hooked and relatively short stylus and a bent penial base, while spination and proportions of the glans and spine armament varies considerably between species but is constant within species (Fig. 1D, Figs. 2–4). This holds true for other well defined nemastomatid genera, and molecular data based on 28S rRNA and cytochrome *b* support this generic concept (Figs. 5–10; Schönhofer and Martens 2010). Species pre-assigned to *Paranemastoma*, *Carinostoma*, *Histicostoma*, *Mediostoma* Kratochvíl, 1958 or *Nemastoma* were grouped by molecular data as monophyletic in their designated genera to support this traditional morphological discrimination of genus and species level (see Schönhofer and Martens 2010, described species included therein are depicted in Figs. 2–10).

Presently there is a good understanding of the species-delineating characters and which characters basically outline genera. Solid proof is still lacking if characters presently used for generic subdivisions further outline systematic groups within Nemastomatinae. This lack of solid proof holds especially true for the majority of traditional genera with a bilateral symmetric and straight glans. In search of “good” generic characters, special structures of the distal part of the truncus are obvious in a number of genera. As previously discussed, the movement of the glans in nemastomatids is achieved by deformation of the long and slender penial shaft. The muscular tendons enabling this movement need to be attached to the distal part of the truncus or the glans, which is reinforced for this purpose. Nemastomatids have accomplished a stabilizing construction in the distal part of the truncus and of the glans in different ways, as unique laterally extended wing-like structures. These structures are most frequent in *Vestiferum* Martens, 2006, *Pyza* Starega, 1976, *Acromistostoma* Roewer, 1951, *Centetostoma* Kratochvíl, 1958, *Mediostoma* and *Starengovia* Snegovaya, 2010 (see large red arrows in Fig. 1). The wings act as attachment points for the muscular tendons and as stabilizing elements in this section of the truncus. Other genera lack such structures and apparently their glandes present sufficient attachment points and are thus reinforced (e.g., *Nemastoma*, *Nemastomella* Mello-Leitao, 1936). However, this is harder to perceive, as the glans is a clearly separated structure in most Opiliones. *Saccarella* gen. n. stands out within the Nemastomatidae by reinforcing the distal penial truncus by longitudinal folds, which are only distantly wing-like. Its functionality is revealed by a cross-section forming almost an “H” shape, comparable to an I-beam which is a structure designed to withstand strong forces (Fig. 12).



### Systematic significance of wing structures and comparison with other characters

By their fine structure these distal stabilizing elements and “wings” differ considerably from each other in proportion and position. Thus they are presumed to be of independent origin. Furthermore, species sharing similar fine structure are traditionally united as distinct genera. One may ask the question, why not group all genera exhibiting these unique and possibly apomorphic wings together and unite their species within one genus only? Molecular data does not present two reciprocally monophyletic groups—winged species versus un-winged species. Additionally, there are a number of other morphological traits that contradict such a systematic treatment. For example, the structure of the penial stylus differs considerably: it can be simple and pointed (Fig. 1C–E), blunt and more inflated (Fig. 1F; G–H) or be set on the truncus tip as a small separate tube (Fig. 1B, arrow at tip). Groupings additionally based on these characters also show a certain geographic cohesiveness. Yet, none of these groups exhibit exclusively winged or un-winged genera.

Presuming them as natural groups, another important character trait within Nemastomatinae is the presence of large glandular apophysis on the chelicerae in males that show group-specific morphology coinciding with the form of the penial stylus. This character trait has been mapped on the cladogram (Fig. 1) and a few of these groups are outlined to explain their gland characteristics. The *Carinostoma-Histricostoma-Paranemastoma* group completely encloses the glands deeply in the prosoma and even partly into the distal parts of the opisthosoma. Only a single duct protrudes to the basic cheliceral segment and opens in a single large pore on the cheliceral surface (Fig. 1b; Martens and Schawaller 1977). Species of all other genera have the gland localized partly within the apophysis and partly in the first cheliceral segment. The secretion is extruded to the surface of the apophysis through a large number of minute channels concentrated in a compact area (Martens 1973). The apophysis itself displays various genus-typical characteristics. In the *Mediostoma-Vestiferum* group, the pore-field sinks into a deep fold within the medial part of the apophysis (Fig. 1d); the *Acromitostoma-Centetostoma-Nemastomella-Starengovia* group have a hook-like apophysis that shields the pore field (Fig. 1i). These groupings are also supported partly by available molecular data (like for group Fig. 1A). Again, penial wing structures are distributed unevenly within these groups, are of different fine structure or are absent. This disentangles them as independently evolved structures. However, they are useful as additional generic characters rather than supporting monophyletic sub-groupings within Nemastomatinae.

### The placement of *Saccarella* gen. n.

Using the preliminary phylogenetic framework shown in Fig. 1, *Saccarella* gen. n. remains difficult to place. Although placement within the Nemastomatinae with undivided glans of penis is straightforward, the unique lateral truncus folds suggest an isolated position. The cheliceral apophyses show no derived structures that would assign them to one of the genera that are outlined by specific characters. *Saccarella* gen. n. can hardly be attached to the *Mediostoma-Vestiferum* group with their unique offset stylus (Fig. 1B). A relationship is possible within the group including *Nemastoma* that share relatively simple styli (Fig. 1C, D). However, the blunt stylus and geographic proximity to the Iberian Peninsula might point to *Acromitostoma*, *Centetostoma* and *Nemastomella* as closest relatives to *Saccarella* gen. n. (Fig. 1G, H) as proposed here.

At this point it is important to note that the phylogenetic framework provided is of course simplified. Several genera are known to be heterogeneous (see statements for: Pyza, Gruber 1979, *Vestiferum*, *Mediostoma*, both Martens 2006; *Nemastomella*, Prieto 2004) and molecular genetic investigations are necessary to clarify generic and species borders within and/or between these genera. In addition, the external morphological characters outlined above can be lost in cave-adapted species, making them hard to place within a system based upon morphology alone; so far they belong to genera with rather simple genitalia (*Nemaspela* Šilhavý, 1966, *Hadzinia* Šilhavý, 1966; Fig. 1C, E). Other characters like the bisection of the truncus basis, dorsal armature of body or ornamentation of legs contribute to genus delineation but do not seem useful in a discussion of phylogenetic signals. Finally, many species, especially from the Iberian Peninsula and North Africa are still listed under the original generic placement, *Nemastoma*; this genus has been redefined for a narrow set of Central European species. Based on external or genital morphology, *Saccarella* gen. n. does not show affinities to any of these species, nor can a placement within one of the valid nemastomatid genera be verified. The discussed phylogenetic framework outlines *Saccarella* gen. n. as a unique and isolated morphological lineage. Placing *Saccarella* gen. n. anywhere but in a genus of its own would clearly conflict with the monophyly of other genera under the discussed concept.

### Endemism and biogeographic implications with focus on the opilionid fauna

Within the distribution area of *Saccarella schilleri* sp. n., the South-western Alps, a number of other Opiliones species with remarkable small distributional ranges occur. These species can be divided roughly into paleo-endemic species that exhibit no close relatives within their group, and neo-

endemic species that are perceivable as part of a recent radiations and/or have closely related but largely allopatric sister species. This side-by-side presence of paleo-endemics and neo-endemics has been shown for plants and indicates long-lasting glacial refuges in this area (Pawłowski 1970; Diadema et al. 2005). In addition, the South-western Alps show an extreme level of endemism for which a special Italian chorotype has been defined ('Alps South West': ALSW; Stoch and Vigna Taglianti 2005). While there are numerous analyses of plant diversification, no comprehensive analysis on arthropod diversity and endemism exists for that area except for troglobitic arachnids (Isaia et al. 2011), yet hundreds of endemic species from various taxa can be estimated from numerous scattered descriptions (e.g., Martens 1978 for Opiliones; Maurer and Thaler 1988 for Araneae). This rich diversity is caused by complex patterns of repeated glaciations (Diadema et al. 2005; Casazza et al. 2008; and literature cited therein) and to some extent is mirrored by the distribution of harvestman species. For example *Holoscotolemon oreophilum* Martens, 1978 (Erebomastriidae) and *Ischyropsalis pyrenaea alpinula* Martens, 1978 are present only on the Italian side of the main crest of the Maritime and Ligurian Alps (Isaia et al. 2011), *Trogulus cristatus* Simon, 1879 (Trogulidae) is confined to the French side of the mountain chain, and *Anelasmacephalus tenuiglandis* Martens and Chemini, 1988 (Trogulidae) overlaps the distribution area of these species in the southern part. *Sabacon simoni* Dresco, 1952 (Sabaconidae) and *Centetostoma centetes* (Nemastomatidae) are species that probably represent older faunal elements because they are isolated morphologically and geographically from their closest relatives (cf. Martens 1983, 2011). *Saccarella schilleri* sp. n. most likely falls in this group of South-western Alpine paleo-endemics because of its systematically isolated position.

## Ecology

The single available *Saccarella* series was extracted by using Berlese funnels from leaf litter gathered from riverine *Alnus* bushes alongside a dry avalanche incision close to a narrow, deeply incised valley, bordered by alpine meadows. The leaf litter was collected along a transect of about 100 m (W. Schiller, personal communication 2010). Further information on microhabitat conditions can only be retraced by the presence of associated species collected from this very spot. Syntopic occurrence with *S. schilleri* is stated for three trogulid species, all from the same Schiller collection which belong to the genus *Anelasmacephalus* Simon, 1879, namely *A. cambridgei* (Westwood, 1874), *A. rufitarsis* Simon, 1879 and *A. tenuiglandis*. These species outline a humid and well structured soil litter

habitat. A subsequent, but unsuccessful, search (by A.S., J.M. and S. Huber, independently in different years) for *Saccarella* revealed a rich opilionid fauna within a distance of only a few hundred meters from the type locality [*Holoscotolemon oreophilum*, *Sabacon simoni*, *Centetostoma centetes*, *Nemastoma dentigerum*, *Histricostoma dentipalpe* Ausserer, 1867 (Nemastomatidae), to mention only species from leaf litter soil cover]. The whole faunal setting at around 1,500 m is clearly subalpine.

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No ethic standards were violated.

## References

- Ausserer, A. (1867). Die Arachniden Tirols nach ihrer horizontalen und verticalen Verbreitung. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, 17, 137–170.
- Casazza, G., Zappa, E., Mariotti, M. G., Médail, F., & Minuto, L. (2008). Ecological and historical factors affecting distribution pattern and richness of endemic plant species: the case of the Maritime and Ligurian Alps hotspot. *Diversity and Distributions*, 14, 47–58.
- Diadema, K., Bretagnolle, F., Affre, L., Yuan, Y. M., & Médail, F. (2005). Geographic structure of molecular variation of *Gentiana ligustica* (Gentianaceae) in the Maritime and Ligurian regional hotspot, inferred from ITS sequences. *Taxon*, 54, 887–894.
- Dresco, E. (1952). Étude du genre *Sabacon* (Opiliones). *Annales de la Société Entomologique de France, série 6*, 121, 117–126.
- Giribet, G., Vogt, L., Pérez González, A., Sharma, P., & Kury, A. B. (2010). A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. *Cladistics*, 26, 408–437.
- Gruber, J. (1976). Ergebnisse zoologischer Sammelreisen in der Türkei: Zwei neue Nemastomatidenarten mit Stridulationsorganen, nebst Anmerkungen zur systematischen Gliederung der Familie (Opiliones, Arachnida). *Annalen des Naturhistorischen Museums in Wien*, 80, 781–801.
- Gruber, J. (1979). Ergebnisse zoologischer Sammelreisen in der Türkei. Über Nemastomatiden-Arten aus der Verwandtschaft von *Pyza* aus Südwestasien und Südosteuropa (Opiliones, Arachnida). *Annalen des Naturhistorischen Museums in Wien*, 82, 559–577.

- Gruber, J., & Martens, J. (1968). Morphologie, Systematik und Ökologie der Gattung *Nemastoma* C. L. Koch (s. str.) (Opiliones, Nemastomatidae). *Senckenbergiana biologica*, 49, 137–172.
- Huelsenbeck, J. P., & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.
- Isaia M., Paschetta, M., Lana, E., Pantini, P., Schönhofer, A.L., Christian, E., & Badino, G. (2011). *Aracnidi sotterranei delle Alpi Occidentali italiane (Arachnida: Araneae, Opiliones, Palpigradi, Pseudoscorpiones)/ Subterranean Arachnids of the Western Italian Alps (Arachnida: Araneae, Opiliones, Palpigradi, Pseudoscorpiones)*. Monografie del Museo Regionale di Scienze Naturali, Torino, Italy.
- Koch, C. L. (1836). *Die Arachniden getreu nach der Natur abgebildet und beschrieben* (Vol. 3). Nürnberg: C. H. Zeh'schen Buchhandlung.
- Kratochvil, J. (1958). Höhlenweberknechte Bulgariens (Palpatores—Nemastomatidae). *Práce Brněnské základny Československé akademie věd, Brno*, 30(12), 523–576.
- Martens, J. (1969). Die Abgrenzung von Biospezies auf biologisch-ethologischer und morphologischer Grundlage am Beispiel der Gattung *Ischyropsalis* C. L. Koch 1839 (Opiliones, Ischyropsalididae). *Zoologische Jahrbücher Abteilung für Systematik*, 96, 133–264.
- Martens, J. (1973). Feinstruktur der Chelieren-Drüse von *Nemastoma dentigerum* Canestrini (Opiliones, Nemastomatidae). *Zeitschrift für Zellforschung und mikroskopische Anatomie*, 136, 121–137.
- Martens, J. (1976). Genitalmorphologie, System und Phylogenie der Weberknechte (Arachnida: Opiliones). *Entomologica Germanica*, 3(1/2), 51–68.
- Martens, J. (1978). Spinnentiere, Arachnida—Weberknechte, Opiliones. *Die Tierwelt Deutschlands*, 64, 1–464.
- Martens, J. (1983). Europäische Arten der Gattung *Sabacon* Simon 1879 (Arachnida: Opiliones: Sabaconidae). *Senckenbergiana biologica*, 63(3/4), 265–296.
- Martens, J. (1986). Die Grossgliederung der Opiliones und die Evolution der Ordnung (Arachnida), in: Barrientos, J.A. (Ed.), *Actas del X Congreso Internacional de Aracnologia (Jaca, Spain)*, vol. 1 (pp. 289–310), Barcelona.
- Martens, J. (2006). Weberknechte aus dem Kaukasus (Arachnida, Opiliones, Nemastomatidae). *Senckenbergiana biologica*, 86(2), 145–210.
- Martens, J. (2011). The *Centetostoma scabriculum* complex – a group of three cryptic species (Arachnida: Opiliones: Nemastomatidae). *Zootaxa*, 2783, 35–51.
- Martens, J., & Chemini, C. (1988). Die Gattung *Anelasmacephalus* Simon, 1879. Biogeographie, Artgrenzen und Biospezies-Konzept (Opiliones: Trogludidae). *Zoologische Jahrbücher Systematik*, 115, 1–48.
- Martens, J., & Schawaller, W. (1977). Die Cheliceren-Drüsen der Weberknechte nach rasteroptischen und lichtoptischen Befunden (Arachnida: Opiliones). *Zoomorphologie*, 86, 223–250.
- Maurer, R., & Thaler, K. (1988). Über bemerkenswerte Spinnen des Parc National du Mercantour (F) und seiner Umgebung (Arachnida: Araneae). *Revue Suisse de Zoologie*, 95, 329–353.
- Mayr, E. (1942). *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. New York: Columbia University Press.
- Mello-Leitao, C. (1936). Les Opiliones de Catalogne. *Treballs del Museo de Ciències Naturals, Barcelona (ser. Entomol.)*, 11(9), 1–18.
- Pawlowski, B. (1970). Remarques sur l'endémisme dans la flore des Alpes et des Carpates. *Vegetatio*, 21, 181–243.
- Posada, D. (2008). jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, 25, 1253–1256.
- Prieto, C. E. (2004). El género *Nemastomella* Mello-Leitão 1936 (Opiliones: Dyspnoi: Nemastomatidae) en la Península Ibérica, con descripción de la primera especie de Andalucía. *Revista Ibérica de Aracnología*, 9, 107–121.
- Rambla, M. (1969). Una n. sp. del gen. *Nemastoma*, grupo *bacilliferum* de la Península Ibérica (Opiliones, Fam. Nemastomatidae). *Publicaciones del Instituto de Biología aplicada*, 47, 89–96.
- Rambla, M. (1983). Sobre los Nemastomatidae (Arachnida, Opiliones) de la Península Ibérica. VI. *Acromitostoma rhinoceros* y *Acromitostoma hispanum* (nueva combinación). *Speleon*, 26(27), 21–27.
- Redikorzev, V. V. (1936). Materialy k faune Opiliones SSSR - Beiträge zur Opilioniden-Fauna von U.S.S.R. *Trudy Zoologicheskogo*, 3, 33–57.
- Roewer, C. F. (1923). *Die Weberknechte der Erde Systematische Bearbeitung der bisher bekannten Opiliones*. Fischer: Jena.
- Roewer, C. F. (1951). Über Nemastomatiden. Weitere Weberknechte XVI. *Senckenbergiana*, 32(1/4), 95–153.
- Ronquist, F., & Huelsenbeck, J. P. (2003). MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
- Ronquist, F., Huelsenbeck, J.P. & van der Mark, P. (2005). MrBayes 3.1 Manual, Draft 5/26/2005, online at <http://mrbayes.csit.fsu.edu/manual.php>. Accessed 20 August 2011).
- Schönhofer, A. L., & Martens, J. (2010). Hidden Mediterranean diversity: Assessing species taxa by molecular phylogeny within the opilionid family Trogludidae (Arachnida, Opiliones). *Molecular Phylogenetics and Evolution*, 54(1), 59–75.
- Shear, W. A., & Gruber, J. (1983). The opilionid subfamily Ortholasmatinae (Opiliones, Troguloidea, Nemastomatidae). *American Museum Novitates*, 2757, 1–65.
- Šilhavý, V. (1956). Sekáci [Harvestmen - Opilionidea]. *Fauna ČSR*, 7, 1–272.
- Šilhavý, V. (1966). Über die Genitalmorphologie der Nemastomatidae (Arach., Opiliones). *Senckenbergiana biologica*, 47(1), 67–72.
- Simon, E. (1879). *Les Arachnides de France. Contenant les ordres des Chernetes, Scorpiones et Opiliones*. Paris: Librairie Encyclopédique de Roret, Tome 7.
- Simon, E. (1881). Arachnides nouveaux ou rares de la faune française. *Bulletin de la Société Zoologique de France*, 6, 82–91.
- Snegovaya, N. Y. (2010). New Harvestman Genus and Species from Kyrgyz Republic (Kyrgyzstan) (Arachnida: Opiliones: Nemastomatidae). *Acta Zoologica Bulgarica*, 62(3), 351–354.
- Starega, W. (1976). Die Weberknechte (Opiliones, excl. Sironidae) Bulgariens. *Annales Zoologici (Polska Akademia Nauk)*, 33(18), 287–433.
- Starega, W. (1978). Katalog der Weberknechte (Opiliones) der Sowjet-Union. *Fragmenta Faunistica*, 23(10), 197–234.
- Stoch F., & Vigna Taglianti, A. (2005). I corotipi della fauna italiana, in: Ruffo, S., Stoch, F. (Eds.), *Checklist e distribuzione della fauna italiana. Memorie del Museo Civico di Storia Naturale di Verona, 2. serie, Sezione Scienze della Vita*, 16, 25–28.
- Vigna Taglianti, A., Audisio, P. A., Biondi, M., Bologna, M. A., Carpaneto, G. M., De Biase, A., Fattorini, S., Piattella, E., Sindaco, R., Venchi, A., & Zapparoli, M. (1999). A proposal for a chorotype classification of the Near East fauna, in the framework of the Western Palearctic region. *Biogeographia*, 20, 31–59.
- Westwood, J. O. (1874). *Thesaurus Entomologicus Oxoniensis or, Illustrations of new, rare, and interesting insects*. Oxford: Clarendon.