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Redescription of *Tapinesthis inermis* (Araneae, Oonopidae), with detailed information on its ultrastructure

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Abstract. *Tapinesthis inermis* Simon, 1882, the only species in the genus, is widely distributed in western Europe. This redescription provides the first information on the ultrastructure of the species using SEM. The morphology of the spinnerets, tarsal claws and tarsal organs, and the internal structure of the female genitalia and the male palp are described and illustrated in detail. The combination of these structures is very similar to those encountered in some dysderoid spiders and supports the basal placement of *Tapinesthis* among Oonopinae. The phylogenetic relationships of the species are discussed. The only female among the three syntypes is designated as the lectotype.

Key words. Female genitalia, male palp, organ receptors, spinnerets, systematics

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Introduction

The spider genus *Tapinesthis* Simon, 1914 is monospecific, containing the single species *T. inermis* (Simon, 1882), widely distributed in Europe (Le Peru 2011; Platnick 2013). This rare species is often found in houses or in the neighbourhood of habitations (Kraus 1967; Heimer & Nentwig 1991; Lazarov *et al.* 2001; Korenko *et al.* 2007; Van Keer *et al.* 2006). *Tapinesthis inermis* thus appears to be strongly synanthropic, as it is often found in urban areas. Saaristo & Marusik (2009) even employed the term “hemisynanthropic” to describe its habitat preference. However, it has also been collected in natural habitats such as forests (Dalmas 1920; Le Peru 2007), garrigues and dry grasslands (Le Peru 2011) or near cliffs with a dense cover of ivy (e.g., Rochers de Marches les Dames in Belgium, this study). In Belgium, *T. inermis* appears to be abundant in litter and among ivy (Van Keer *et al.* 2006; pers. obs.).

The species is often found together with *Oonops domesticus* and *O. pulcher* (Van Keer *et al.* 2006, 2010), and, at least in Belgium, also with *Harpactea hombergi* (Scopoli, 1763) (pers. obs.).

Tapinesthis inermis is easy to identify and has been reviewed by many authors (see Platnick 2013). Originally, the species was described as *Oonops inermis* and only the female was known (Simon 1882). Later, Simon (1914) created the genus *Tapinesthis* for this species and described both sexes.

A remarkable redescription of both males and females was provided by Kraus (1967), with detailed drawings of the genitalia and other body parts. Other significant illustrations and photos have been published by Korenko *et al.* (2007) (female prosoma, vulva) and by Saaristo & Marusik (2009) (male and female habitus, male palp, female genitalia). However, this is the first detailed morphological study of *T. inermis* using SEM images, providing detailed information about the ultrastructure of the female genitalia, the spinnerets, mouthparts and legs. We also compare the genitalia with those of related taxa and discuss the relationships of this species with other oonopids.

The results of this work have previously been used for the polarization of characters in a phylogenetic study of Afrotropical *Orchestina* Simon, 1882 (Henrard & Jocqué 2012). However, one particular character, the number of tarsal organ receptors, is updated here and the consequences are dealt with in the discussion.

Material and methods

Specimens were observed with a Zeiss Stemi 2000 stereo microscope. Measurements and photographs of the habitus and details of the mouthparts and detached male palps and genitalia were taken with a Leica MZ16 using the LAS automontage software (ver. 3.8). Female genitalia were dissected, digested with pancreatin and then immersed in 75% ethanol. One male palp was detached and temporarily mounted in a clearing mixture of methyl salicylate and cedukol (Merck, Darmstadt), observed with a Leitz Dialux 22 microscope and subjected to automontage with the Syncroscopy software (ver. 5.03.61). For SEM photos, specimens were dried in HMDS (36 h), gold coated, and examined and photographed with a JEOL 6480 LV scanning electron microscope. All measurements are in millimetres.

This paper follows the terminology of Burger's series of papers (Burger 2009, 2011a, 2011b, 2013; Burger & Michalik 2010) with a few adaptations.

The following abbreviations are used:

ALS	=	anterior lateral spinnerets
ALE	=	anterior lateral eyes
ARe	=	anterior receptaculum
AS	=	anterior sclerite
D	=	duct
Ht	=	holotype
FA	=	flattened apodeme
MNHN	=	Muséum national d'Histoire naturelle, Paris (C. Rollard)
MRAC	=	Musée Royal de l'Afrique Centrale, Tervuren (R. Jocqué)
PBI	=	Planetary Biodiversity Inventory project
PER	=	posterior eye row
PLE	=	posterior lateral eyes
PLS	=	posterior lateral spinnerets
PME	=	posterior median eyes
PMS	=	posterior median spinnerets
Pp	=	posterior plate

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Pr	=	protrusion
PRe	=	posterior receptaculum
Pt	=	paratype
RBINS	=	Royal Belgian Institute of Natural Sciences, Brussels
V	=	vesicle
Te	=	tendon
Tw	=	thin-walled duct

Results

Class Arachnida Cuvier, 1812
 Order Araneae Clerck, 1757
 Family Oonopidae Simon, 1890

Tapinesthis Simon, 1914

Diagnosis

Soft-bodied, pale Oonopidae with strongly sloping cephalothorax provided with dark net-shaped pattern, without leg spines, with unipectinate tarsal claws; pedicel with meshed texture; male palp with short sclerified sperm duct and female genitalia with wide median T-shaped structure visible by transparency, flanked by two rounded apodemes.

Description

Male

CEPHALOTHORAX. *Carapace* in vivo pale yellowish-orange (Fig. 1A–B) to pinkish, in ethanol yellowish-white to pale orange (Figs 2A–B, 3A–D), with dark net-shaped pattern and dark margins; non-marginal pars cephalica setae present in three rows, ovoid in dorsal view, pars cephalica strongly sloping in lateral view, reaching highest point at level of second coxa (Fig. 2E), anteriorly narrowed to 0.49 times its maximum width or less, with rounded posterolateral corners (Fig. 2A–B), surface of elevated portion of pars cephalica smooth, sides smooth, with radiating patches of smooth platelets (Fig. 6A–B); thorax without depressions, fovea absent, lateral margin undulate, smooth; pars cephalica setae needle-like. *Clypeus* margin curved downwards in front view (Fig. 2G), sloping forward in lateral view (Fig. 2E), high, ALE separated from edge of carapace by their radius or more. *Eyes* (Fig. 2A, E): six, well developed, all subequal, ALE oval, PME circular, PLE circular; posterior eye row recurved from both above and front; ALE separated by their radius to diameter, ALE–PLE separated by less than ALE radius, PME touching, PLE–PME separated by less than PME radius, ALE–PME separated by less than PME radius. *Sternum* (Fig. 2C) yellowish white, with faint radiating dark stripes, longer than wide, with radial smooth furrows between coxae I–II, II–III and III–IV, anterior margin with semicircular depression on the middle half, posterior margin extending posteriorly beyond anterior edges of coxae IV as single extension, distance between coxae approximately equal; setae abundant, evenly scattered, without hair tufts. *Mouthparts:* chelicerae, endites and labium yellowish white. Chelicerae (Fig. 6F) straight; without teeth on both promargin and retromargin; fangs directed medially, paturon inner margin with scattered setae. Labium (Figs. 2C, 6C–D, F) rectangular, fused to sternum, anterior margin indented at middle, basal corners with small circular depression, sclerotization as in sternum; with 6 or more setae on anterior margin, subdistal portion with unmodified setae. Endites (Fig. 6C–G) distally not excavated, serrula present in single row, anteromedian tip unmodified, posteromedian part unmodified, sclerotization as in sternum; anterior margin with ventral row of spatulate setae and dorsal row of distally pectinate setae, median margin with finely barbed setae.

ABDOMEN (Fig. 2A–B, D–F). Ovoid, rounded posteriorly, without scuta; dorsum soft portions yellow-brown, without color pattern. Dorsum setae present, needle-like. *Epigastric area* setae uniform, needle-

like. Postepigastric area setae present, needle-like. *Pedicel* with meshed texture (Fig. 6C) as in *Orchestina* (see Henrard & Jocqué 2012, figs. 21, 113, 114, 404), abdomen extending anteriorly of pedicel. *Colulus* present (Fig. 9A), with four setae. *Spinnerets* (Fig. 9B–D): ALS with one major ampullate gland spigot emerging from cylindrical tubercle and two piriform gland spigots emerging from shallow tubercle; PMS with one minor ampullate gland spigot emerging from cylindrical tubercle; PLS with two aciniform gland spigots emerging from cylindrical tubercle.

LEGS. White, without color pattern; femur IV not thickened, same size as femora I–III, patella plus tibia I longer than carapace, tibia I unmodified, metatarsi of at least leg II in the middle and IV at basal quarter, with eye-shaped smooth gland outlet with single pore (Fig. 12C–E). *Leg spines* absent. *Tarsal claws* (Fig. 10A–F) unipectinate, tarsal proclaws and retroclaws inner face smooth; tarsus I–IV superior claws with six teeth on lateral surface of proclaw, six teeth on lateral surface of retroclaw. Tarsi claw tuft with three carpeted setae. Tarsi I to IV without inferior claw. *Trichobothria* (Fig. 12D–E) with rounded bothrium, internal texture of aperture not grate-like, hood covered by numerous low, closely spaced ridges; sometimes accompanied by eye shaped structure with unknown function (Fig. 12C–D). *Tarsal organ* (Fig. 11A–D, H–I) pear-shaped, margin raised above surroundings, with 4 receptors on legs I and II, with 3 receptors on legs III and IV. In a probably unusual case, the tarsal organ has only 1 receptor on both legs IV (Fig. 11H–I), whereas I–III of the same specimen have the usual 4-4-3 formula (not illustrated). According to observations made on other oonopids the formula appears to be 3-3-2-2, since the distalmost receptor is distally bifid, but both parts stem from a common base as in *Stenoconops* Simon, 1891 (Platnick & Dupérré 2010).



Fig. 1. *Tapinesthis inermis* photographed in vivo. **A.** ♂ (PBI 33564). **B.** Same. **C.** ♀ (PBI 33267). **D.** Same. **E.** Same. Remark color differences of cephalothorax between ♂ and ♀. For explanation, see text.

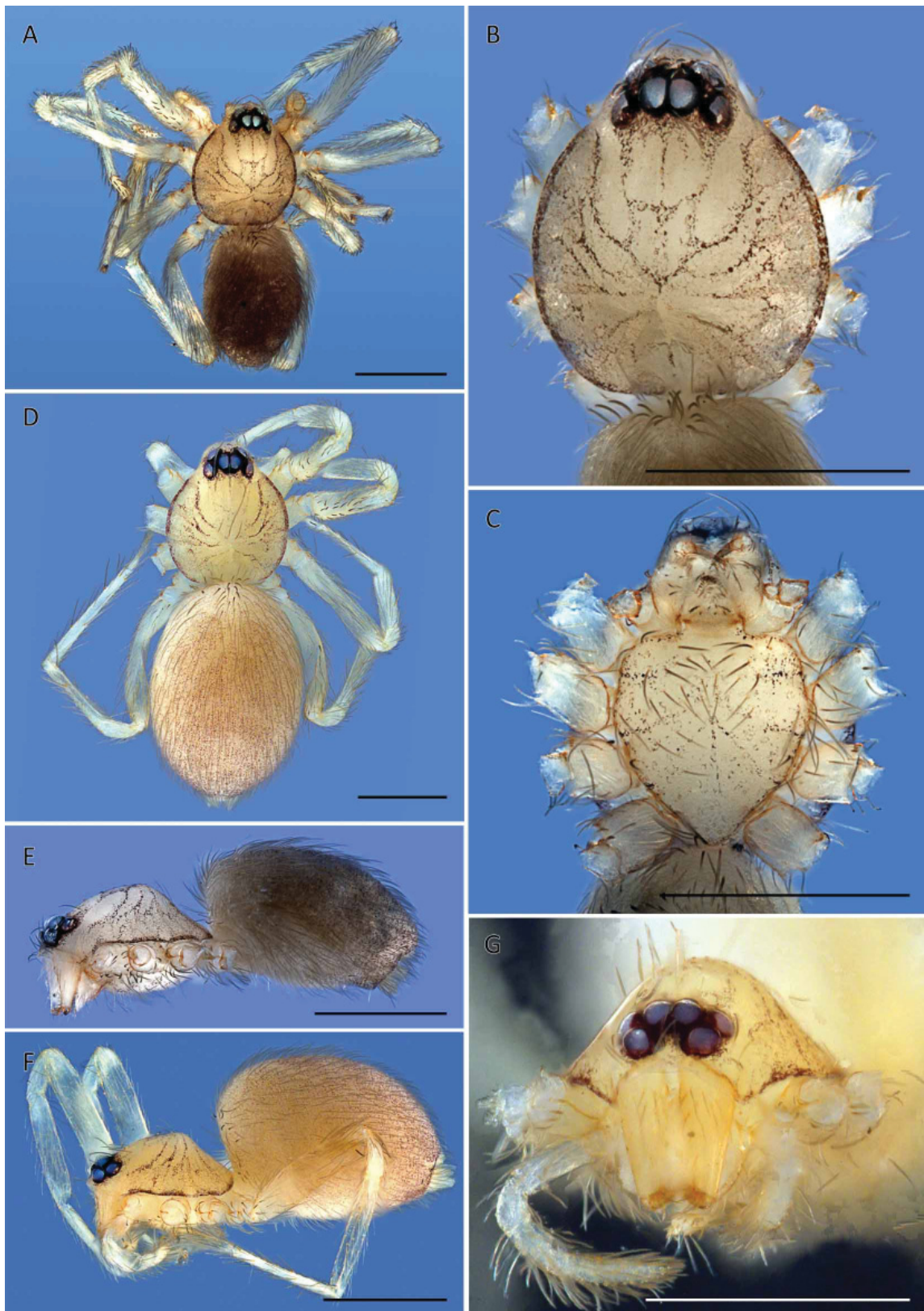


Fig. 2. *Tapinesthis inermis*. **A.** ♂ (PBI 33564), habitus, dorsal view. **B.** Same, carapace. **C.** Same, sternum, ventral view. **D.** ♀ (PBI 33267), habitus, dorsal view. **E.** ♂ (PBI 33564), habitus, lateral view. **F.** Same, ♀ (PBI 33267). **G.** ♀ (PBI 08123), carapace, anterior view. Scale bars = 0.5 mm.

GENITALIA (Figs. 4A–E, 7A–D). *Epigastric region* with sperm pore small, narrow, slit-like, situated at level of anterior spiracles. *Palp* normal size, not strongly sclerotized, right and left palps symmetrical, proximal segments white; trochanter normal size, unmodified; femur normal size, two or more times as long as trochanter, without posteriorly rounded lateral dilation, attaching to patella basally; patella shorter than femur, not enlarged, without prolateral row of ridges, setae unmodified; tibia ventral margin swollen; cymbium white, ovoid in dorsal view, not fused with bulb, not extending beyond distal tip of bulb, plumose setae absent, without stout setae, without distal patch of setae; bulb white, 1 to 1.5 times as wide as cymbium, stout, piriform with frontal margin slightly concave, tapering apically with long, medially bent embolus, distal sclerotized part of seminal duct (D) short, restricted to distal part, abruptly interrupted, internally with poorly defined vesicle (V), opening into embolus through duct with basal part thin-walled (Tw), distal part sclerotized; tendon (Te) running from base of cymbium to distal end of vesicle (V); embolus simple, dark, tube-shaped, flattened apically, tip blunt, grooved, appearing pale.

Female (Figs 1C–E, 2D, F–G)

As male except as noted.

CEPHALOTHORAX. Female palpal claw absent; spines absent. Tarsal organs (Fig. 11A–D) as in male.

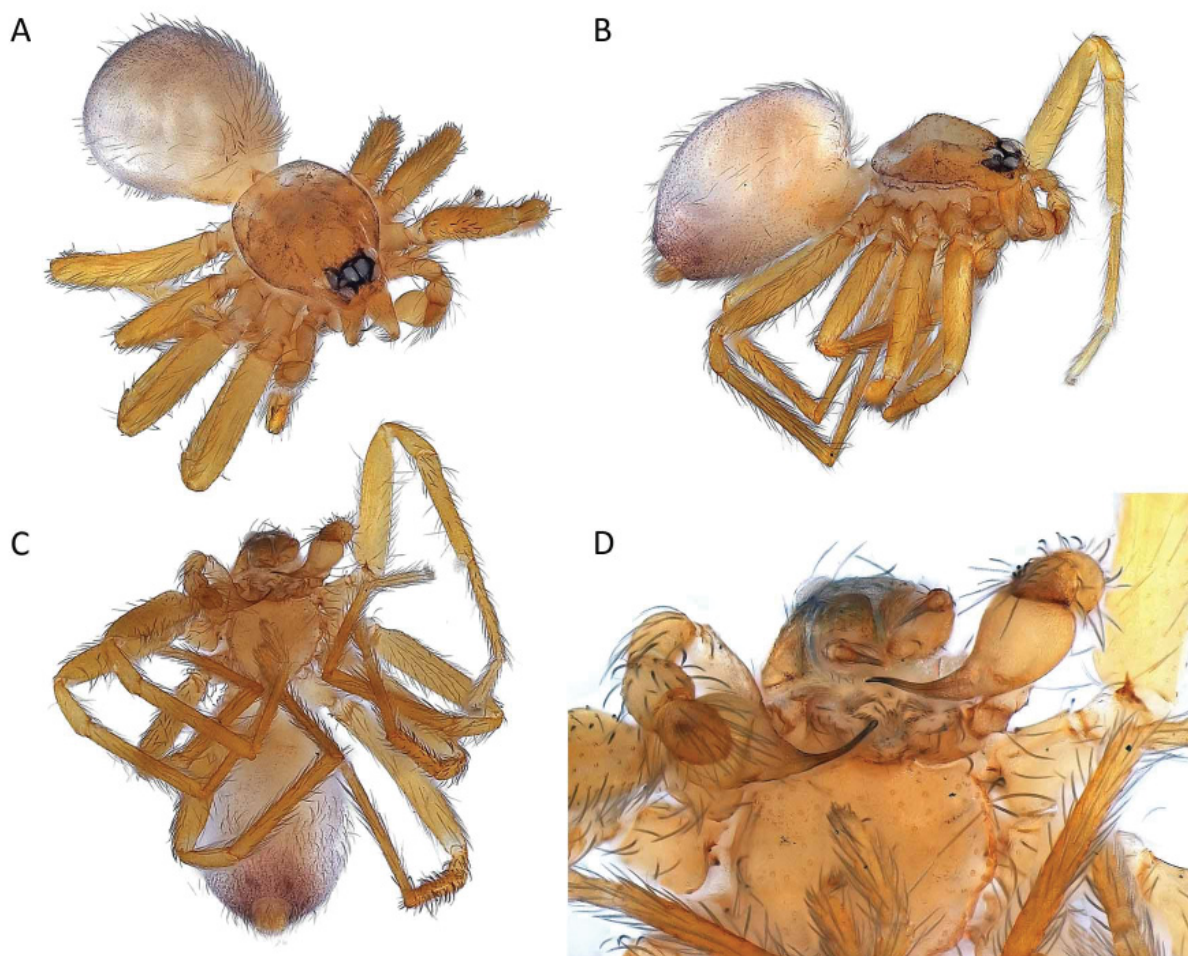


Fig. 3. *Tapinesthis inermis*, ♂ from the Czech Republic (PBI 32902). **A.** Habitus, dorsal view. **B.** Same, lateral view. **C.** Same, lateral view. **D.** Prosoma, ventral view.

ABDOMEN. *Spinnerets* (Fig. 9E–H): ALS with one major ampullate gland spigot emerging from cylindrical tubercle and three piriform gland spigots emerging from shallow tubercle; PMS with minor ampullate gland spigot and three aciniform gland spigots; PLS with six aciniform gland spigots.

GENITALIA (Figs 5A–D, 8A–G). Shape: anterior epigastric margin strongly sclerotized, preceded by T-shaped structure visible in transparency (AS), with larger, square part (ARe) in between, the latter provided at base with fine transverse sclerite (T) ending in two faint procurved lobes (FA) extending as far as lateral protrusions (Pr) of frontal T-shape (AS). SEM view, details: anterior sclerite (AS) short, T-shaped, with lateral protrusions (Pr) well developed and provided with ramified ridges on anterior side and dorsally near extremities; AS connected with anterior receptaculum (ARe) antero-ventrally; ARe about half as wide as AS including Pr, square, provided dorsally and apically with rows of gland ducts (GD) confined in frontal groove; ARe adjacent to transverse sclerite (T) ending laterally in well developed,

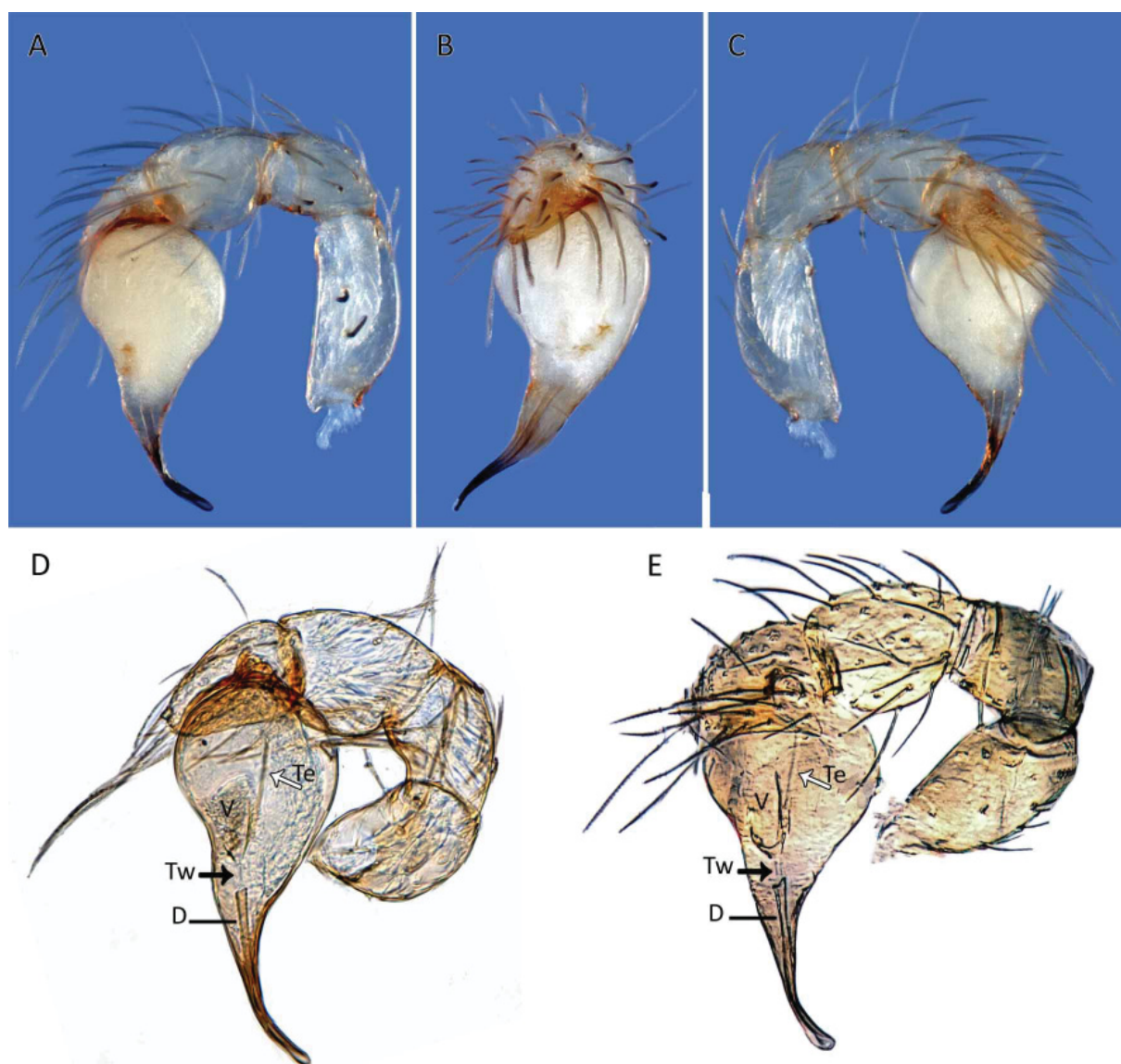


Fig. 4. *Tapinesthis inermis*. – A–C. ♂ (PBI 33564), palp. A. Retrolateral view. B. Same, frontal view. C. Same, prolateral view. – D. ♂ (PBI 09021), palp, prolateral view, transmitted light. – E. ♂ palp, lateral view after Saarisalo & Marusik, 2009 (modified). – D: duct; Te: tendon; Tw: thin-walled duct; V: vesicle.

bilobed, flattened apodeme (FA), its dorsal extremity anchoring into the posterior receptaculum (PRe); PRe well developed, egg-shaped, emerging from base of ARe. Uterus externus not visible.

Tapinesthis inermis (Simon, 1882)

Oonops inermis Simon, 1882: 240.

Tapinesthis inermis. – Simon 1914: 88, 90. — Kaston 1948: 61, figs 4–6. — Kraus 1967: 382, figs 1–10. — Heimer & Nentwig 1991: 52, fig. 110. — Lazarov, Deltchev & Blagoev 2001: 8, figs 5–6. — Trotta 2005: 170, figs 369–370. — Van Keer 2006: 36, fig. 3. — Korenko, Rezac & Pekár 2007: 6, figs 1–3. — Saaristo & Marusik 2009: 64, figs 11–14, 23, 27. — Le Peru 2011: 307, fig. 537.

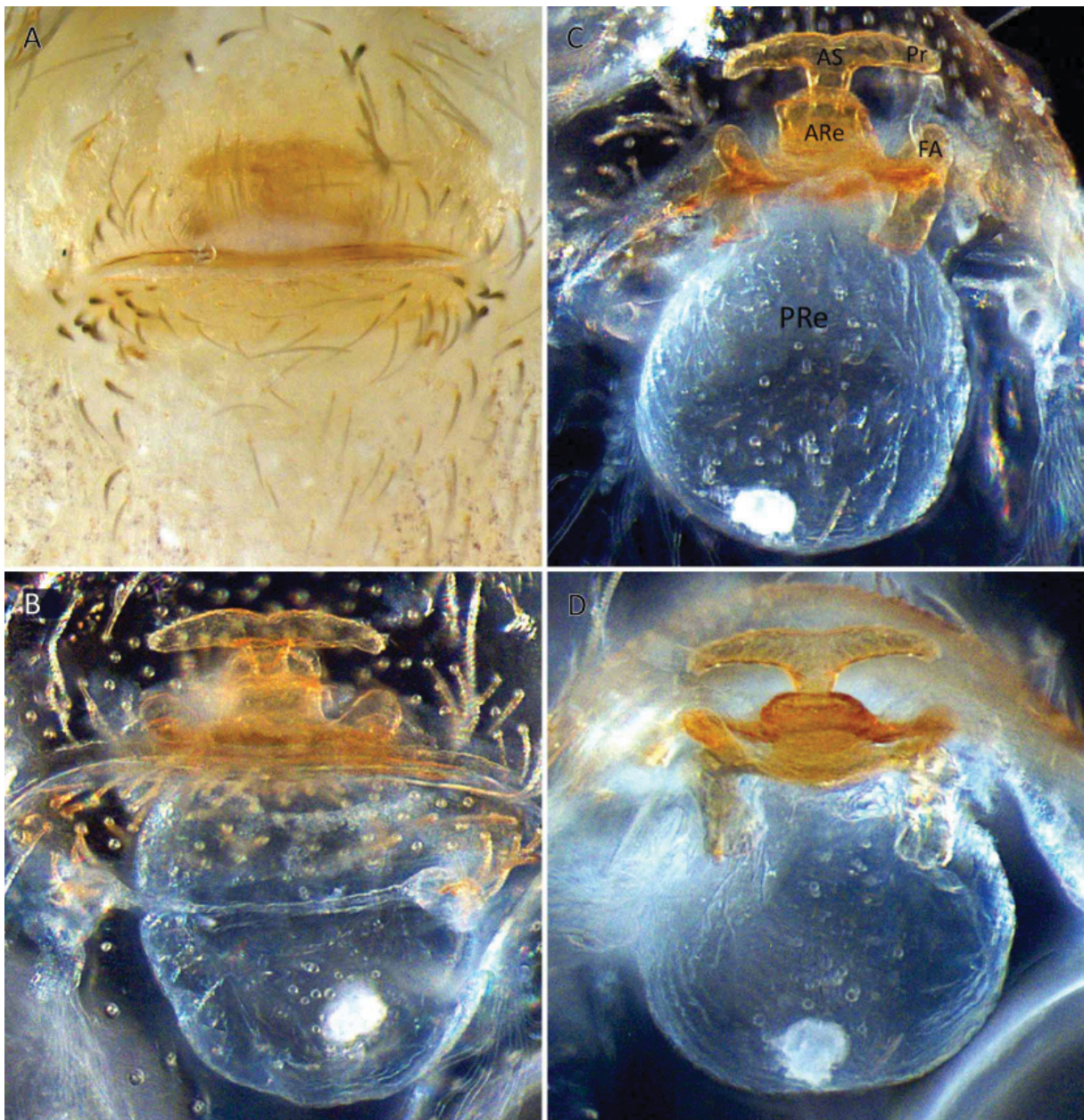


Fig. 5. *Tapinesthis inermis*, genitalia of ♀ (PBI 33267) **A.** Genital area, ventral view. **B.** Same, after digestion, ventral view. **C.** Same, dorsal view. **D.** Same, anterior view. – ARe: Anterior Receptaculum; AS: Anterior Sclerite; FA: Flattened Apodeme; Pr: lateral Protrusion; PRe: Posterior Receptaculum.

Material examined

Lectotype (here designated)

♀, *Oonops inermis* E.S. [= E. Simon], Gall. m. [= Gallia mediterranea?], MNHN AR1468 *pars* (PBI OON 6262 *pars*).

Paralectotypes

2 ♂♂, *Oonops inermis* E.S. [= E. Simon], Gall. m. [= Gallia mediterranea?], MNHN AR1468 *pars* (PBI OON 6262 *pars*, PBI OON 6263).

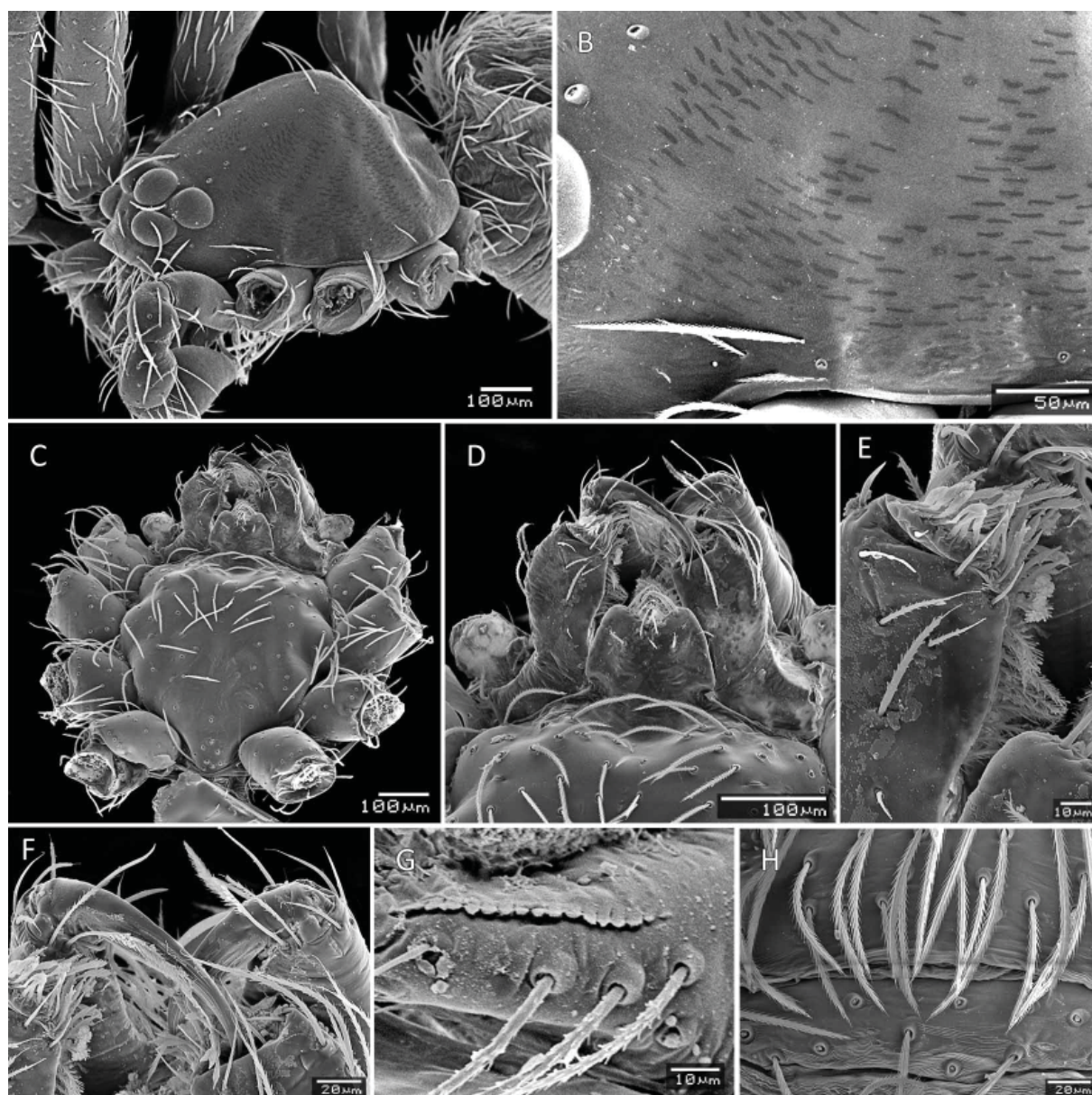


Fig. 6. *Tapinesthis inermis*, SEM views. **A.** ♂ (PBI 08123), carapace, antero-lateral view. **B.** Same, close up on the distribution of the smooth platelets. **C.** ♂ (PBI 33564), sternum, ventral view. **D.** Same, mouthparts. **E.** Same, close up of endite setae. **F.** Same, cheliceral fangs. **G.** ♂ (PBI 08123), endites, anterior view with detail of serrula. **H.** ♂ (PBI 33564), genital region, ventral view.

Other material

BELGIUM: Antwerpen, Turnhout, forest remnant, under liana, 27 m, 51.31666° N, 4.93333° E, 19 Oct. 2006, H. De Coninck, 5 ♂♂, RBINS I.G.32708 *pars* (PBI OON 8123 *pars*), 3 ♀♀, RBINS I.G.32708 *pars* (PBI OON 8123 *pars*). Namur, Marche-les-Dames, 50.48250° N, 4.94917° E, 25 May 2010, A. Henrard, 1 ♀, RBINS I.G.32708 *pars* (PBI OON 33267); Marche-les-Dames, understory, litter among ivy, 50.48250° N, 4.94917° E, 7 Aug. 2011, A. Henrard, 1 ♂, RBINS I.G.32708 *pars* (PBI OON 33564).

CZECH REPUBLIC: Zlínský Kraj, Lhota u Vsetina, Lhotské Paseky Sklep, building, 545 m, 49.324528° N, 17.936269° E, 8 Aug. 2010, coll. Andrej Mácháč, det. Jørgen Lissner, 1 ♂ (leg. J. Lissner, collection (V), 6821) (PBI OON 32902).

Description

Male (PBI OON 33564)

As for the genus except as noted. Total length 2.02.

Female (PBI OON 6262)

As male except as noted. Total length 2.21.

Distribution

Austria, Belgium, Bulgaria, Czech Republic, France, Germany, Italy, Netherlands, Spain, Switzerland (after Le Peru 2011, extended).

Remarks

It was the count de Dalmas (1916), and then Kaston (1948), who pointed out that the specimen mentioned in Emerton's note on the New England spiders (Emerton 1909) was not *Orchestina saltitans* but *Tapinesthis inermis*. This single specimen is the only one ever recorded from the United States and was found in the cellar of the Boston Society of Natural History building, probably hidden in a package shipped from Europe to the Society (Kaston 1948). The mention 'introduced in USA' is therefore not valid as no further specimens were found, which indicates that no viable population of this species persists in the USA.

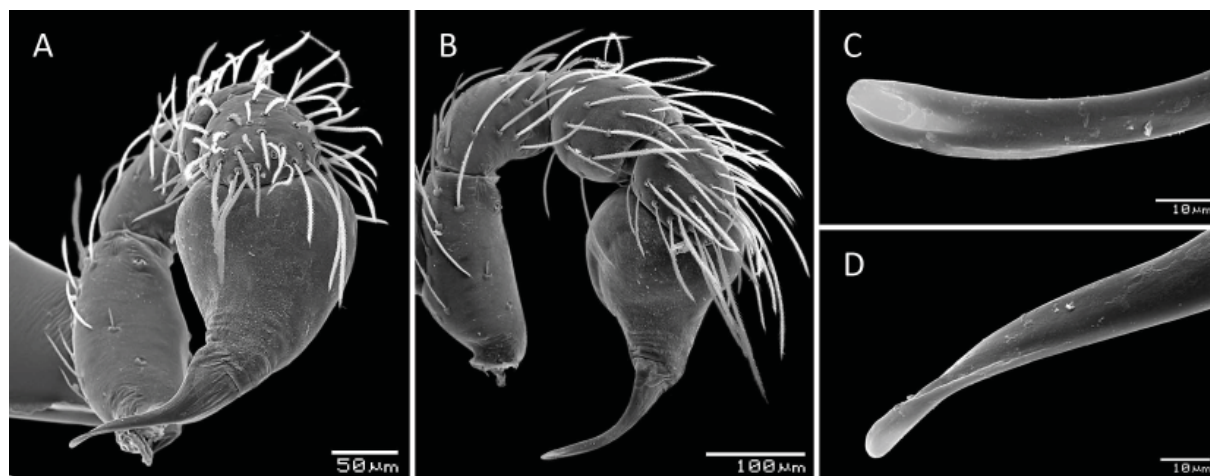


Fig. 7. *Tapinesthis inermis*, SEM views of ♂ (PBI 33564). **A.** Palp, frontal view. **B.** Same, prolateral view. **C.** Tip of embolus, ventral view. **D.** Same, retrolateral view.

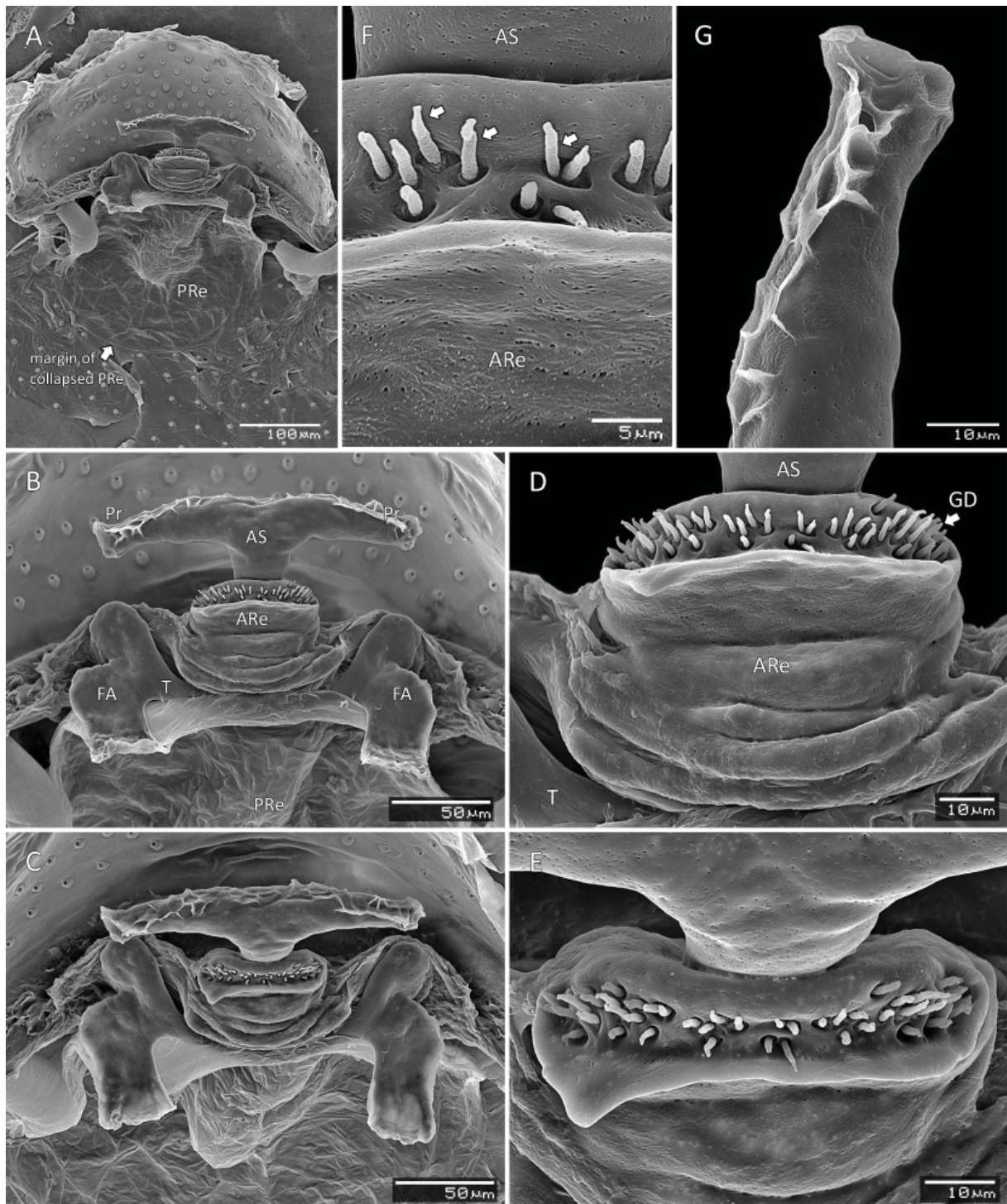


Fig. 8. *Tapinesthis inermis*, SEM views of ♀ genitalia (PBI 33267). **A.** Overview of genital area, dorsal view. **B.** Same, close up. **C.** Same, view slightly anterior. **D.** Anterior receptaculum (ARe), close up, arrow indicates gland ducts (GD). **E.** Same, anterior view. **F.** Same, detail of gland ducts (arrows). **G.** Lateral protrusion (Pr), detail, dorsal view. – ARe: Anterior Receptaculum; AS: Anterior Sclerite; FA: Flattened Apodeme; GD: Gland Duct; Pr: lateral Protrusion; PRe: Posterior Receptaculum; T: transverse sclerite.

Discussion

Tapinesthis inermis is perhaps one of the easiest oonopid species to identify. This spineless “molles” oonopid, without abdominal scuta, can easily be recognized by the absence of ventral spines on the first tibiae, the net-shaped pattern on the carapace, the clumped eyes with slightly recurved PER and by the plesiomorphic aspect of the male palp and the female genital organs. Although this species is not easily seen, it cannot be considered as “rare”. However, in the Czech Republic for instance, it is rarely found and only females were caught before this study (J. Král, pers. comm.; see also Korenko *et al.* 2007).

Dalmas (1916) mentions the occurrence of two adult seasonal forms, one in spring and one in summer, differing by the colouration and the hair cover. This observation is of interest since it is the only spider

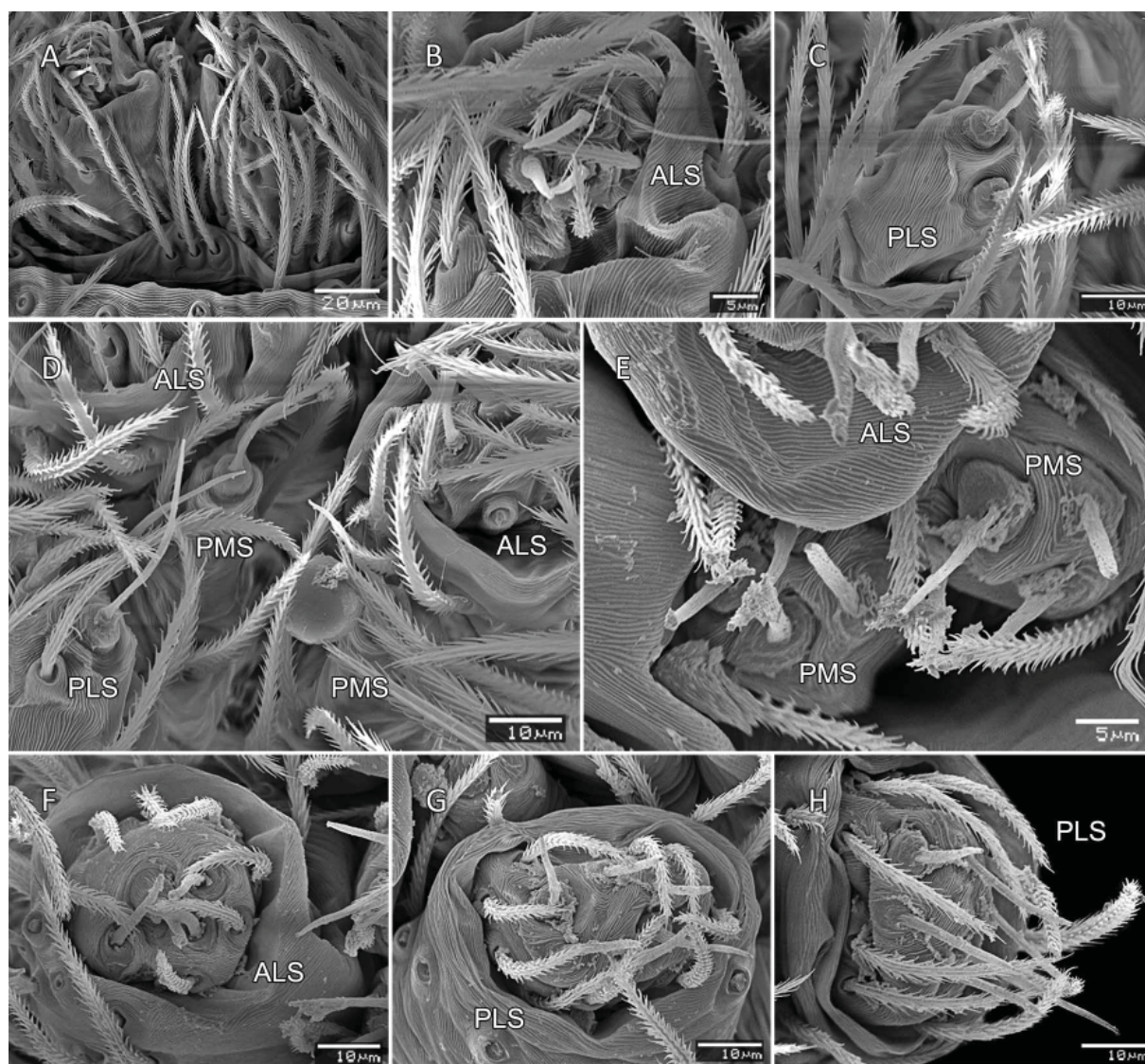


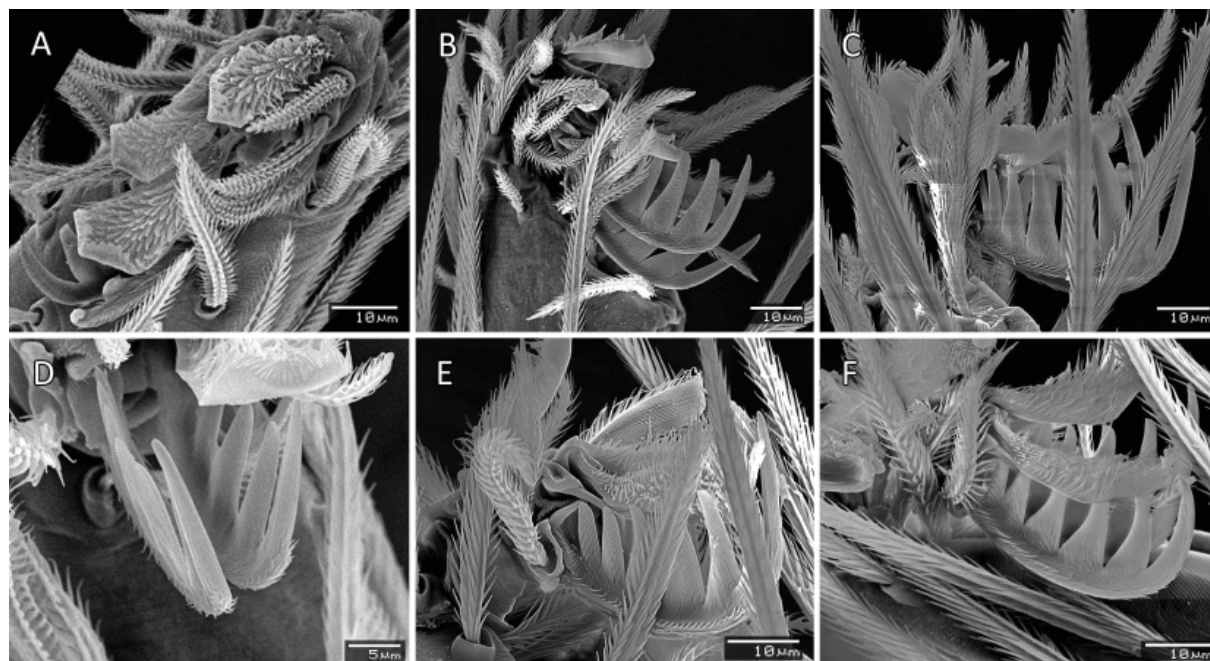
Fig. 9. *Tapinesthis inermis*, SEM views of spinneret area of ♂ (PBI 33564) and ♀ (PBI 33267). **A.** ♂, colulus, ventral view. **B.** Same, anterior lateral spinnerets, ventral view. **C.** Same, posterior lateral spinnerets. **D.** Same, focus on posterior median spinnerets. **E.** ♀, posterior median spinnerets, ventral view. **F.** Same, anterior lateral spinnerets. **G.** Same, posterior lateral spinnerets. **H.** Same, lateral view. – ALS: anterior lateral spinnerets; PLS: posterior lateral spinnerets; PMS: posterior median spinnerets.

species for which seasonal forms have been recognized. However, our observations do not point in the same direction. The illustrations of Fig. 1 clearly show the colour differences between a specimen caught in summer (Fig. 1A–B) and another one photographed in spring (Fig. 1C–E). The spring specimen (female) is pale, whereas the one from August (male) is orange. The hair cover is similar in both cases. Since we know that the differences do not depend on the sex, we assume that the two forms are simply specimens of different age: they become darker, possibly by incorporating pigment from their prey, and might in some cases lose part of the hair cover. Dalmás (1916) possibly observed dark specimens that were born in autumn and had passed the winter, which, in the Mediterranean area where he made his observations, might have been perfectly possible.

Genitalia, male palp

The male palp of *T. inermis* is an excellent example of the basic plesiomorphic structure of the haplogyne palp: a piriform bulb with a simple tubular embolus, without appendage as found in some segestriids. The latter character is the main difference with *Oonopinus angustatus* Simon, 1882, another spineless species (Simon 1882; Saaristo & Marusik 2009; Le Peru 2011).

A number of features of the male palp can only be seen when it is cleared. The seminal duct has apparently two parts: a short, well sclerotized part leading into the embolus and a thin-walled part connecting to the faintly delimited, vesicle-like reservoir. Next to the latter, a thin linear structure runs from the base of the bulb to the distal end of the sperm reservoir. This structure is also visible in *Spinestis nikita* Saaristo & Marusik, 2009 and *Megaoonops avrona* Saaristo, 2007 (Saaristo & Marusik 2009) and some other oonopids. Saaristo and Marusik (2009) regard the linear structure adjacent to the sperm reservoir as a sclerite, but Grismado & Ramirez (2013) and Grismado *et al.* (in press) clearly showed that this is a tendon, which is in accordance with the findings of Huber (2004).



Figs. 10. *Tapinesthis inermis*, SEM views of tarsal claws of ♂ (PBI 33564). **A.** Leg I, anterior view. **B.** Same, lateral view. **C.** Leg II, lateral view. **D.** Same, anterior view. **E.** Leg III, lateral view. **F.** Leg IV, lateral view.

Female genitalia

It is now well established that the internal genital structures of some haplogynes are highly diverse and can be remarkably complex (Uhl 2000; Huber 2002; Burger *et al.* 2003, 2006; Burger 2007). According to some authors, the complexity of the female genital organ may be correlated to its function for postcopulatory female choice (Burger *et al.* 2003; Burger 2011a, 2011b, 2011c).

The female genitalia of *Tapinesthis inermis* are characterized by the presence of a large T-shaped anterior sclerite (AS) based antero-ventrally to the anterior receptaculum (ARe), associated with gland ducts dorsally and apically to the ARe, strong, flattened apodemes and a large, egg-shaped membranous posterior receptaculum.

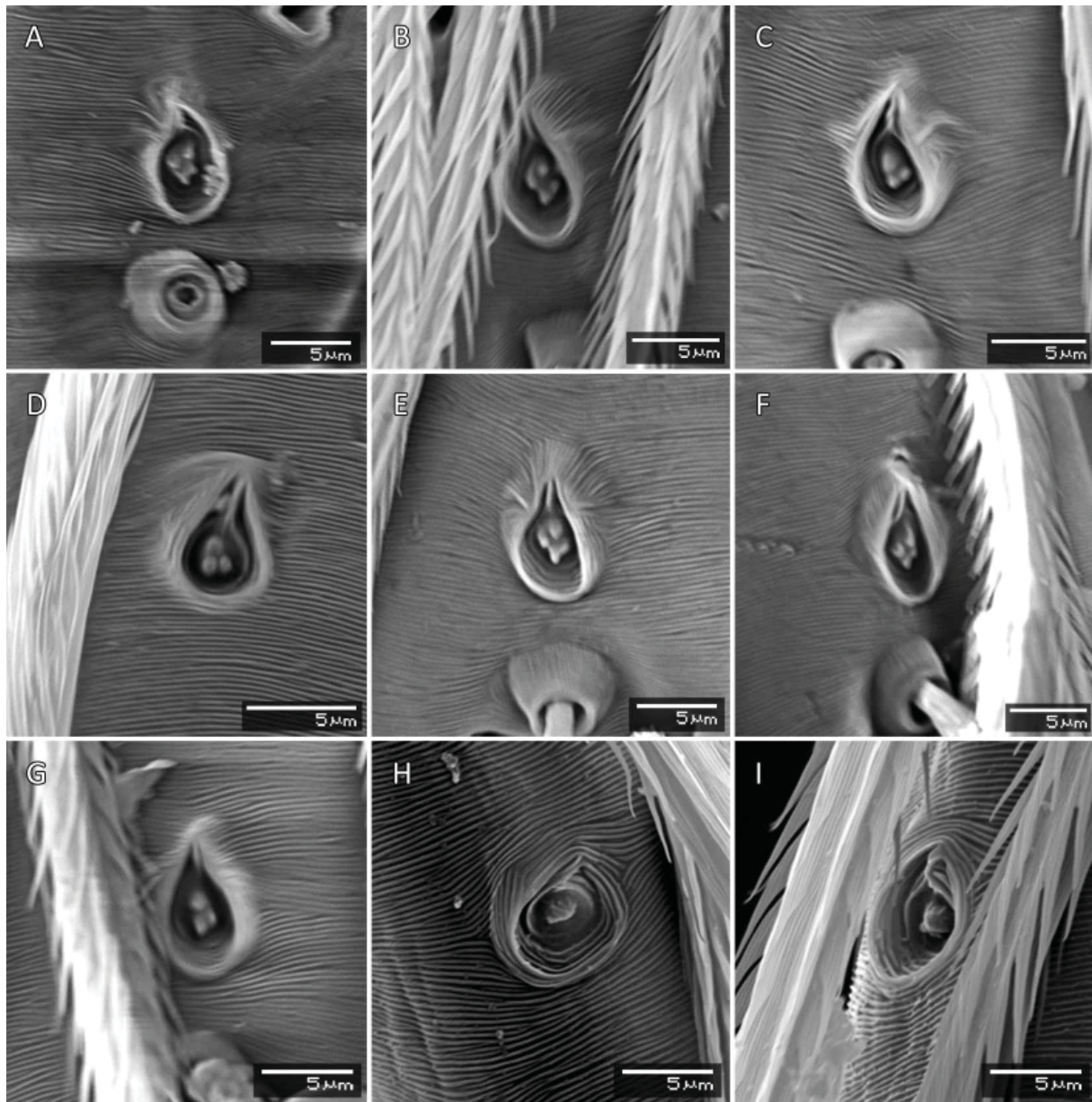


Fig. 11. *Tapinesthis inermis*, SEM, A–H dorsal views, I lateral view. – A–D. ♂ (PBI 33882). A. Leg I. B. Leg II. C. Leg III. D. Leg IV. – E–G. ♀ (PBI 33883). E. Leg I. F. Leg II. G. Leg III. – H–I. ♂ (PBI 33564). H. Leg IV. I. Tarsal organ, leg IV.

The combination of these structures is very similar to the one encountered in many dysderoid spiders such as Dysderidae (Forster & Platnick 1985; Uhl 2000; Burger & Kropf 2007), Segestriidae (Brignoli 1976), Orsolobidae (Forster & Platnick 1985; Izquierdo & Labarque 2010) and some basal Oonopidae such as *Puan chechehet* Izquierdo, 2012 (Izquierdo *et al.* 2012) and *Unicorn catleyi* Platnick & Brescovit, 1995 (Izquierdo & Rubio 2011). It thus supports the basal placement of *Tapinesthis* among Oonopinae.

Burger's terminology for receptacula is based on sections. If a sclerite anterior of the uterus didn't contain sperm in one of the different females analyzed, the use of the term "receptaculum" was considered ambiguous and the term "anterior sclerite" was preferred over "anterior receptaculum". Burger (2010, 2011a, 2013) assumes that in "higher" oonopids, the receptacula are reduced to sclerites and that sperm is stored only in the uterus in order to improve the control over fertilization processes through cryptic female choice (Burger *et al.* 2003; Burger 2011a, 2011b, 2011c).

In the present work, no sections were made to verify the presence of sperm in those sclerites. However, the use of "ARe" for this sclerite was preferred to differentiate the upper part, i.e., the T-shaped structure

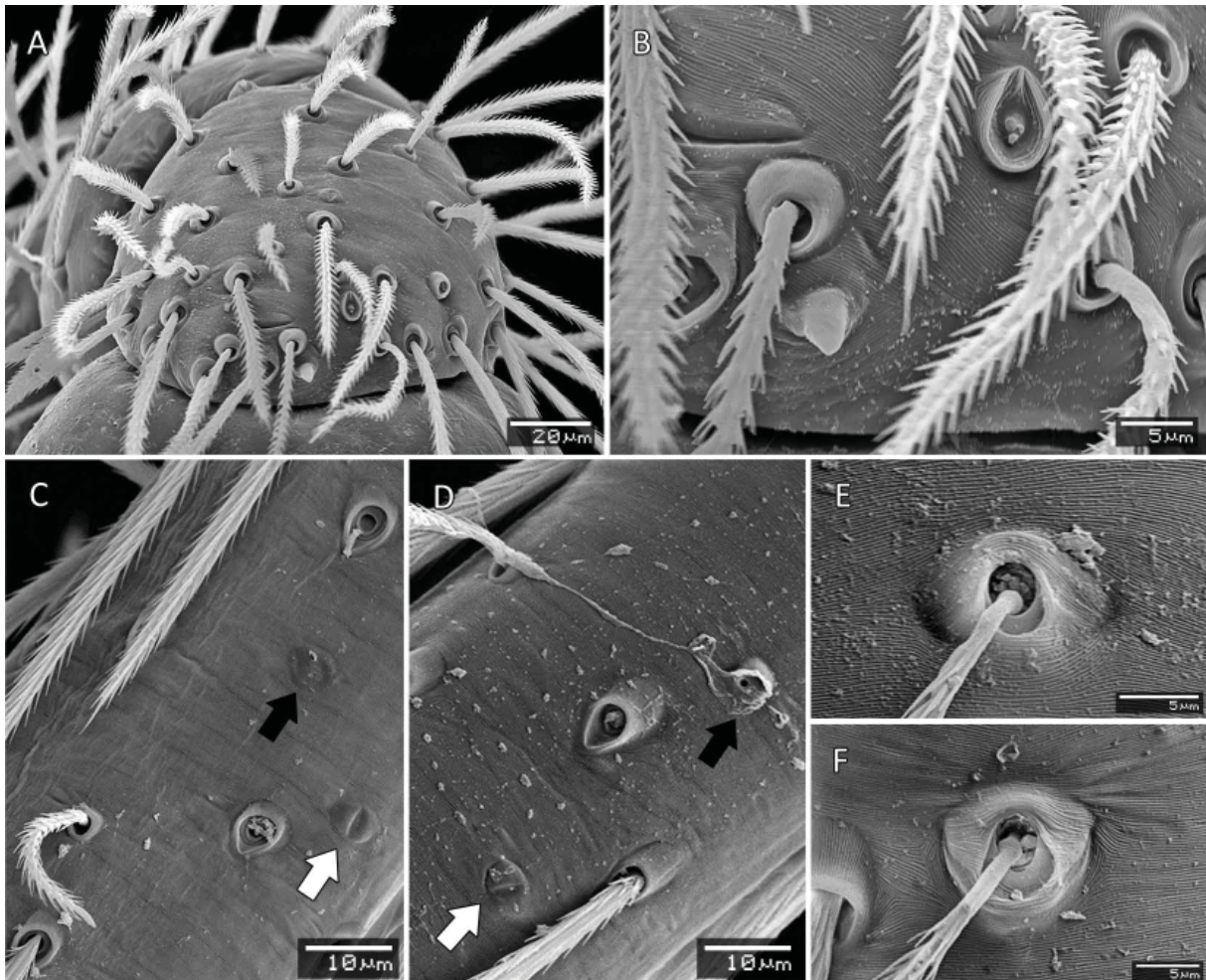


Fig. 12. *Tapinesthis inermis* ♂ (PBI 33564), SEM views. **A.** Cymbium, frontal view. **B.** Same. **C.** Metatarsus II, dorsal view, black arrow showing pore and white arrow indicating eye-shaped structure. **D.** Metatarsus IV, black arrow as in C. **E.** Trichobothrium, dorsal view of bothrium on tibia IV. **F.** Dorsal view of bothrium on metatarsus.

called here anterior sclerite (As), which has a different function (muscle attachment, see Izquierdo & Rubio 2011).

It was not possible to observe the uterus externus (UE). The tissue of that organ typically appears as a very flat, membranous structure on SEMs and the opening for the UE is supposed to be somewhere between the ARe and the PRe (M. Burger, pers. comm.). Again, cross sections are needed to certify the position of the UE. We therefore avoid the term ‘Anterior Uterine Sclerite (AUS)’ used by Fannes (2010) and Henrard & Jocqué (2012) for what is called here the AS (e.g.). The term ‘uterine’ can indeed be confusing, especially since we do not know the position of the uterus on SEMs.

In *Tapinesthis*, gland ducts are confined to a frontal groove on the apical part of the ARe. In other oonopids, GD are located in the middle of the AS (e.g., *Puan chechehet*, see Izquierdo *et al.* 2012) or at the base of the AS (e.g., *Heteroonops spinimanus*, see Burger 2011a; *Oonopinus kilikus*, see Burger 2013). Note that GD are also present on the AS in other dysderoid genera of the families Orsolobidae (Izquierdo & Labarque 2010), Segestriidae (Brignoli 1976; Forster & Platnick 1985) and Dysderidae (Uhl 2000). According to Burger (2011b), gland ducts associated with the anterior sclerites may produce part of the secretion surrounding the spermatozoa in the posterior receptacula. This secretion may either serve to store and fix the spermatozoa within the receptaculum or provide nutrition for the spermatozoa (e.g., Uhl 1994, 1996).

Relationships

Simon (1893) recognized two informal groups, ‘molles’ and ‘loricatae’, based on the presence of abdominal scuta and sclerotization of the body. Petrunkevitch (1923) and subsequent authors recognized these groups as subfamilies, Oonopinae and Gamasomorphinae, respectively. Later, a third subfamily, the monotypic Orchestininae, was added for the genus *Orchestina* (Chamberlin & Ivie 1942). In a recent paper, Platnick *et al.* (2012) profoundly changed the subfamilial structure of the Oonopidae. The main characters they used were the structure of the tarsal organs and more precisely their number of receptors, the sclerotization of the spermduct in the male palp and the position of the eyes. On the basis of seven characters, the family was subdivided into three subfamilies: the Sulsulinae, Oonopinae and Orchestininae, which remained monotypic.

The three main characters on which the recent subfamilial structure is based are not straightforward in all the oonopids and may need an additional state. In *Tapinesthis*, and a few other genera, it might indeed be questioned whether the eyes are clumped and whether the male palpal bulb lacks a sclerotized sperm duct. The situation in *Tapinesthis* can be considered as intermediate between Orchestininae and Oonopinae: the eyes are not really clumped but also not as far apart as in *Orchestina* and they nearly have an H-shaped disposition with a slightly recurved PER. The absence of a clearly thick-walled, heavily sclerotized sperm duct within the male palp leaves no doubt about the placement of *Tapinesthis* among Oonopinae. The sperm duct in the bulb of *Tapinesthis* has a thin-walled part, but the distal part is still clearly sclerotized. However, this structure cannot be considered identical to the sclerotized duct as found in *Orchestina* and the outgroups used in Platnick *et al.* (2012); hence an intermediate state for this set-up would be necessary. The tarsal organ receptor pattern that gives the impression to be 4433 at a first glance turns out to be 3322, since the distalmost receptor appears to be bifid. Here again, this configuration would best be considered as a separate state different from both the “simple” 3322 without a bifid receptor and the plesiomorphic 4433 receptor formulas.

In view of these modifications, a more extensive set of characters will be needed to clarify the position of *Tapinesthis* within the Oonopinae. However, the combination of the characters discussed above supports a relatively basal placement of *Tapinesthis* in the Oonopinae. In addition, recent molecular results of De

Busschere *et al.* (submitted), which place *Tapinesthis* relatively basally among the Oonopinae, appear to corroborate our findings on the basis of morphology.

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