SOIL ORGANISMS 87 (1) · April 2015 pp. 29–49

Sensing the world without antennae and eyes: external structure and distribution of sensilla in *Eosentomon pinetorum* Szeptycki, 1984 and on the protarsus of *Acerentomon franzi* Nosek, 1965 (Hexapoda: Protura)

Christian W. Hädicke[1,*], Stephan M. Blank[2,#], Hans Pohl[3], Carsten H. G. Müller[1,4] and Andy Sombke[1,#]

[1] Ernst-Moritz-Arndt-University of Greifswald, Zoological Institute and Museum, Cytology and Evolutionary Biology, Soldmannstraße 23, 17487 Greifswald, Germany
[2] Senckenberg Deutsches Entomologisches Institut, Eberswalder Straße 90, 15374 Müncheberg, Germany
[3] Friedrich-Schiller-Universität Jena, Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Erbertstraße 1, 07743 Jena, Germany
[4] University of Arizona, Department of Neuroscience, Strausfeld Lab, 1040 E 4th Str, Tucson (AZ) 85721, U.S.A.
* Corresponding author, e-mail: christian-haedicke@gmx.de
\# Shared last authorship

Received 2 September 2014 | **Accepted** 23 January 2015
Published online at www.soil-organisms.de 1 April 2015 | **Printed version** 15 April 2015

Abstract

Protura are miniaturized soil arthropods with an enigmatic biology. Among mandibulate arthropods, Protura are outstanding due to the absence of antennae. This study provides the first detailed investigation on external cuticular sensilla in two proturan species using scanning electron microscopy. The fine structure and distribution of cuticular sensilla on the protarsus as well as putative sensory structures on the body surface are described. Distinct differences in quality and quantity are evident between different proturan taxa. Potential consequences of these observations on the proturan biology are discussed.

Keywords Protura | sensilla | SEM

1. Introduction

In arthropods, a wealth of specialized cuticular sensilla allows to receive external and internal stimuli. In particular, sensilla capable of gathering environmental information caught and still catch much attention (Zacharuk & Shields 1991, Eguchi & Tominaga 1999, Hallberg & Hansson 1999, Hallberg & Skog 2011, Müller et al. 2011, Keil 2012). The majority of sensory structures, such as compound eyes and antennae are located on the arthropod head (cephalon, cephalothorax, prosoma or caput, respectively). Commonly, a high number of sensilla can be found on the antennae of mandibulate arthropods. Their number can range from over one thousand in e.g. decapod crustaceans (Cate & Derby 2001), centipedes (Sombke et al. 2011) and ground beetles (Merivee et al. 2001), up to more than ten thousand in for example the silkmoth *Bombyx mori* (Steinbrecht 1973) or even nearly twenty thousand on the antennae of the honeybee *Apis melifera* (Esslen & Kaissling 1976). While most research focuses on this sensory appendage, studies dealing with sensilla not located on antennae are, however, few in Mandibulata. This is contrary to chelicerates, which lack (deutocerebral) antennae. Popular examples are the antenniform legs of whip spiders (Amblypygi; Foelix & Hebets 2001) and the well known Haller's organ as well

ISSN 1864-6417

as other sensilla on the first tarsomere in mites and ticks (Acari; Foelix & Axtell 1972, Talarico et al. 2006).

Examples of mandibulate arthropods lacking antennae are rare: apode larvae of apocritan Hymenoptera and Diptera as well as all developmental stages of Protura (Gillott 2005). In comparison to other hexapods, Protura have been described and investigated rather late in entomology (Silvestri 1907). They are hexapods of about one millimetre in length which inhabit leaf litter and soil. Some comprehensive monographs have dealt with the biology and taxonomy of Protura (Berlese 1909, Denis 1949, Janetschek 1970, Nosek 1973, Tuxen 1964, Yin 1999). Yet, even 44 years after Janetschek's monograph, some enigmas of proturan biology still persist. The most striking problems concern proper species identification, autecology and the sperm transfer (Pass & Szucsich 2011). Recently, Protura and other 'basal' Hexapoda gain more and more interest in different fields of biology (reviewed by van Straalen et al. 2008). For Protura, progress has been made in sperm ultrastructure (Dallai et al. 2010) and molecular genetics (Chen et al. 2011, Resch et al. 2014, Shrubovych et al. 2012, Shrubovych et al. 2014). Moreover, Protura turned out to be a key taxon in e.g. molecular systematic studies (Meusemann et al. 2010, von Reumont et al. 2012).

Nonetheless, while the interest in Protura has increased, our knowledge concerning their 'sensory equipment' stagnates since approximately 20 years. First accounts date back to Berlese (1909). External cuticular sensilla are frequently described in taxonomic literature on Protura (e.g. Bernard & Biechele 2008, Bu & Yin 2007, Bu et al. 2014, Galli et al. 2011, Nakamura 2010, Nosek 1973, Tuxen 1964, Shrubovych & Smykla 2012, Shrubovych et al. 2014). Yet, only one study dealing with this type of sensilla used scanning electron microscopy (SEM) (Sixl et al. 1974). Moreover, Janetschek (1970) and Sixl et al. (1974) assumed that additional sensory structures occur on other body parts. With the above mentioned exception, available data in cuticular sensilla in this group base on light microscopy alone. To gain more insights into the sensory world of Protura, we examined sensilla on the head, thorax, abdomen, and legs of Protura.

2. Material and Methods

2.1. Species sampling

Specimens of *Eosentomon pinetorum* were obtained from soil samples below beech trees (*Fagus sylvatica*) in a forest south of Greifswald (Germany). Each of the samples was placed in a Tullgren funnel to extract specimens (Tullgren 1918). We applied different on/off cycles of illumination to prevent rapid desiccation. The funnels were checked regularly. The extracted Protura were anaesthetized using CO_2 and subsequently fixed in 70% ethanol. The species were identified according to Nosek (1973) and Szeptycki (1984).

Overall, ten specimens were examined. Out of these specimens, all 20 prothoracic legs were examined laterally and dorsally. The medial surface was examined in two prothoracic legs from different specimens. The ventral surface was examined in three prothoracic legs. Additionally, we examined the protarsus of a single specimen of *Acerentomon franzi* Nosek, 1965.

2.2. Preparation and SEM-examination

Specimens were rinsed in a solution of dishwashing detergent and Aqua dest. for one hour to clean the body surface. Subsequently, they were dehydrated in a graded series of ethanol and critical-point-dried (BAL-TEC CPD 030, Balzers). Specimens were either attached to an adhesive copper band or glued to the tip of a fine pin. Both attempts enabled an examination from different directions. Those specimens attached to a fine pin were examined with a specialized holder device (Pohl 2010), while specimens attached to a copper band were fixed on standard SEM stubs (Plano). The specimens were sputter-coated with gold-palladium (SC7620, Quorum Technologies). Samples of *E. pinetorum* were either examined with an EVO LS10 (Zeiss) or a JSM-6060 (Jeol) scanning electron microscope. The specimen of *A. franzi* was examined with a XL30ESEM (Philips).

All measurements are based on SEM-images and the number of individually measured structures is given in brackets. Due to their small size, Protura are difficult to handle. Thus, a compromise between quality of the images and loss or damage of the specimens was necessary.

2.3. Terminology

We apply terms used by Tuxen (1964) and Nosek (1973) to mark specific cuticular sensilla (and setae) of Protura. This terminology refers to specific locations and arrangements of sensilla, which is crucial for taxonomists. The established terms are used here to allow an easier comparison with earlier descriptions of other proturan species. In our view, the alternative classification proposed by Müller (1976) is unsuitable (see discussion). Terminological synonymies from different authors are shown in Table 1.

On the dorsal site of the protarsus, the following sensilla occur: sensilla α (α-setae after Tuxen 1964), and sensilla t1–3. The ventral site bears the sensilla β (β-setae after Tuxen 1964). The lateral protarsus possesses sensilla γ (γ-setae after Tuxen, 1964) and sensilla a–g. On the medial site of the protarsus sensilla δ (δ-setae after Tuxen 1964) and sensilla a'–c' can be found. While this distribution applies for *Acerentomon* sp., additional sensilla are present in *Eosentomon* sp. On the dorsal site, an additional sensillum α3' and sensilla x, y, z, b2' and f2 occur. Medially, additional sensilla δ3' and δ4' are located on the protarsus of *Eosentomon* sp.

Apart from these terms (which refer primarily to the location) we group the sensilla according to morphological criteria as proposed by Schneider (1964) and Altner (1977), while the respective prefix is noted in brackets.

Reliable statements on potential functions are not possible based on external morphology alone. Therefore, we introduce the term 'tentative sensilla' (ts) for exoskeletonal structures which likely are sensilla, in shape of the shaft or socket.

On the proturan body surface, additional setae occur. Following Tuxen (1964), only setae located on the anterior (a-setae) and posterior (p-setae) margin of tergites and sternites are provided with specific prefixes. Terms used to describe sclerites of thorax and abdomen refer to Janetschek (1970), Nosek (1973) and François (1996). The terminology for the abdominal appendages corresponds to Rusek (1974).

3. Results

3.1. *Eosentomon pinetorum*

The length of examined specimens ranges from 800 to 900 µm. Three distinct tagmata can be distinguished: head, thorax and abdomen (Fig. 1). The head appears cone-shaped. The thorax comprises three metameres each bearing a pair of five-articulated appendages. The abdomen consists of eleven metameres plus telson. The first three abdominal metameres bear abdominal appendages (Fig. 1A–B).

3.1.1. Head

The head exhibits a distinct clypeo-labral suture (Fig. 1B) and an indistinct occipital suture (Fig. 2G, arrow). No further external demarcations are recognizable. Accordingly, three regions can be distinguished: (1) clypeolabrum, (2) epicranium, and (3) postocciput (Fig. 1B and 2A). Some superficial furrows occur on the ventral portion of the epicranium (not shown). In some specimens, the occipital suture appears as a ridge rather than as a furrow (Fig. 2G). The pseudoculi are located antero-lateral on the epicranium (Fig. 2A, B). They are ellipsoid in shape and surrounded by a thin furrow. There is no external trace of a cuticular bracelet on the pseudoculus (Fig. 2B). Ventrally, the linea ventralis extends from the proximal base of the labium to the posterior margin of the head (Fig. 2D). Both, the maxillary and labial palps are externally visible, while the mandibles and maxillae are concealed (Fig. 2C, F). The maxillary palps consist of four visible palpomeres (Fig. 2D); the labial palps of three (Fig. 2E).

Tentative sensilla

The first maxillary palpomere is devoid of tentative sensilla (ts). The second palpomere bears a stout ts (ca. 8 µm in length, n = 4). A socket could not be identified. The third palpomere bears some shorter ts with sockets. A tuft of ts (3–4 µm long, n = 6) is located distally on the fourth palpomere (Fig. 2D).

The labial palps show a similar pattern. The proximal palpomere bears two ts with sockets (ca. 4 µm in length, n = 4; Fig. 2E). The medial palpomere possesses two ts with sockets (similar length), while the distal palpomere bears 5–6 ts (ca. 3 µm long, n = 2). In one specimen, two ts on the labial palp exhibit a dark apical spot (Fig. 2F), which could be a hint for a terminal pore.

On the epicranium, ts are arranged in transverse and longitudinal rows (Fig. 1A), ts on the clypeolabrum in one transverse row (Fig. 2A). The length of these ts ranges from 9–14 µm (n = 5).

3.1.2. Thorax

In contrast to the succeeding metameres, the prothorax shows certain characteristics. The pronotum is of oval shape and measures approximately one fourth of the length and one half of the width of the mesonotum (Fig. 1A). The sternal sclerites of all three thoracic segments are of similar size (not shown). Meso- and metathorax are similar in dimension. Both nota are ellipsoid and occupy the whole length of the metamere (Fig. 1). Spiracles are located at the antero-lateral margin of the tergites (Fig. 1A and 3D).

Tentative sensilla

On each lateral margin of the pronotum, a pair of tentative sensilla is located, thus, forming a single row of four ts (not shown). Thereby, the medial ts (ca. 9 µm

Table 1. Summary of different terms used describing protarsal sensilla in Protura.

Silvestri (1907)	Berlese (1909)	Rimsky-Korsakow (1911)	Prell (1912)	Condé (cited in Tuxen, 1964)	Tuxen (1955)
claw	claw	claw	claw	claw	claw
—	—		empodium	empodium	empodium
claw	claw	claw	claw	claw	claw
claw	claw	claw	claw	claw	claw
—	—	—	—	—	—
—	—	—	—	—	s
long bristles	Sensilli laterali del tarso, bristle-shaped sensilla (Ssl)	—	—	—	α
long bristles	—	—	—	—	β
long bristles	—	—	—	—	γ
long bristles	—	—	—	—	δ
Sensillo breve leggei short club-shaped sensillum	Sensillo basale del tarso, short club-shaped sensillum (‘Ssb’)	Tasthaar	spatelförmige Sensillen	—	t1
long bristles	—	Tasthaar		—	t2
long bristles	Sensillo apical del tarso, similar to ‘Ssb’ (‘Ssa’)	Tasthaar	sensenförmige Sensillen	—	t3
long bristles	—	—	borstenförmige Sensillen	a’	a
long bristles	—	—	—	c	b
long bristles	—	—	—	c	c2
long bristles	—	—	—	e	e
long bristles	—	—	—	f0	f1
long bristles	—	—	—	f2	—
long bristles	—	—	—	a’	a’
long bristles	—	—	—	b’1	—
long bristles	—	—	—	b’2	b’1
long bristles	—	—	—	d	b’2
long bristles	—	—	—	c’1	c’
long bristles	—	—	—	c’2	c’
long bristles	—	—	—	—	c1
long bristles	—	—	—	—	d
long bristles	—	—	—	—	f2
long bristles	—	—	—	g	g

Tuxen (1964)	Sixl et al. (1974)	Müller (1976)	this study (*E*. cf. *germanicum*)	this study (*A. franzi*)
claw	claw	I	claw	claw
empodium	empodium	II	praetarsal sensillum	praetarsal sensillum
claw	claw	claw	claw	claw
claw	claw	IV	claw	claw
—	—	?	—	—
s	sensillum chaeticum	?	praetarsal sensillum	praetarsal sensillum
α	α	?	sensillum chaeticum	sensillum chaeticum
β	β	?	sensillum chaeticum	sensillum chaeticum
γ	γ	?	sensillum chaeticum	sensillum chaeticum
δ	δ	?	sensillum chaeticum	sensillum chaeticum
t1	t1	?	Type 1	Type 1
t2	sensillum basiconicum	?	sensillum chaeticum	sensillum chaeticum
t3	t3	?	Type 2	sensillum chaeticum
a	a	?	sensillum basiconicum	sensillum trichodeum
b	b	?	sensillum chaeticum	sensillum trichodeum
c	c	?	sensillum basiconicum	sensillum trichodeum
e	e	?	Type 1	sensillum trichodeum
f1	f1	?	sensillum basiconicum	—
f2	f2	?	sensillum basiconicum	—
a’	a’	?	sensillum chaeticum	sensillum trichodeum
b’1	b’1	?	sensillum chaeticum	sensillum trichodeum
b’2	b’2	?	—	—
d	d	?	d	sensillum trichodeum
c’	c’	?	Type 2	sensillum trichodeum
c’’	c’’	?	—	—
x	x	?	sensillum chaeticum	—
y	y	?	sensillum trichodeum	—
z	z	?	sensillum trichodeum	—
g	g	?	Type 1	sensillum trichodeum

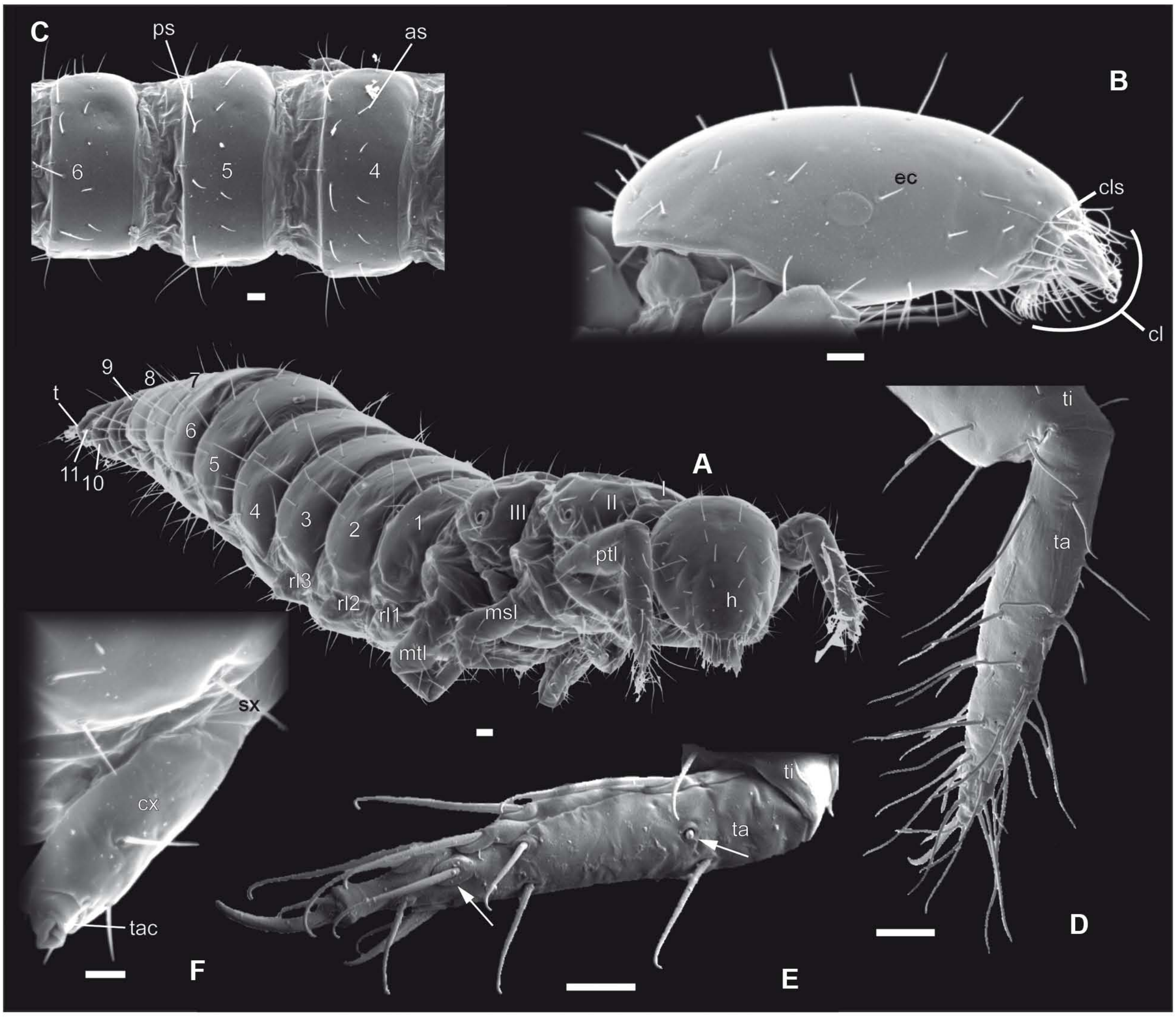


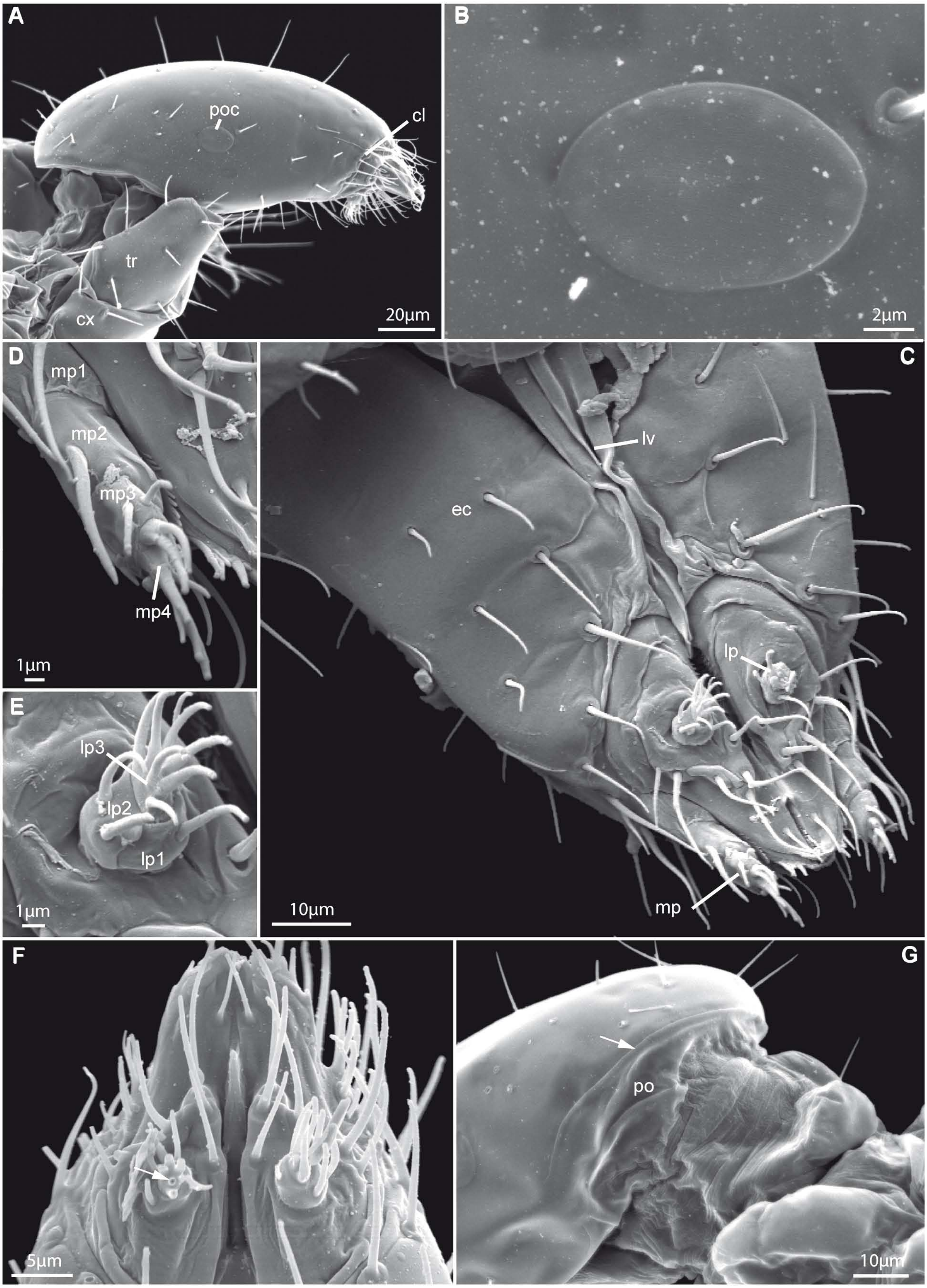
Figure 1. Habitus of *Eosentomon pinetorum* (**A**) and body parts examined in this study: head (**B**), abdomen (**C**), protarsus (**D**), meso- and metatarsus (**E**) (arrows indicate different socket types), as well as abdominal appendages (**F**).

Abbreviations: **as** – anterior setae, **cl** – clypeolabrum, **cls** – clypeo-labral suture, **cx** – coxa, **ec** – epicranium, **h** – head, **msl** – mesothoracic leg, **mtl** – metathoracic leg, **ps** – posterior setae, **ptl** – prothoracic leg, **rl** – rudimentary legs, **ta** – tarsus, **ti** – tibia, **tac** – terminal article, **sx** – subcoxa.

Scale bar: 10 µm.

► **Figure 2.** The head and mouthparts of *Eosentomon pinetorum*. (**A**) Lateral aspect of the head with pseudoculus and mouthparts flanked by some tentative sensilla (setae). (**B**) Details of pseudoculus. (**C**) Ventral view on visible mouthparts comprising maxillary and labial palps. (**D**) Left maxillary palp with maxillary palpomeres 1–4. (**E**) Left labial palp with labial palpomeres 1–3. (**F**) Ventral view on mouthparts. The arrow indicates a putative terminal pore on a single process on the labial palp. (**G**) Lateral view on the neck. The occipitial suture is indicated by a deep furrow (arrow). This furrow encircles the foramen magnum. No cervical sclerites are obvious.

Abbreviations: **cl** – clypeolabrum, **cx** – coxa, **ec** – epicranium, **lp** – labial palp, **lv –** linea ventralis, **mp** – maxillary palp, **po** – postocciput, **pso** – pseudoculus, **tr** – trochanter.


A
poc
cl
tr
cx
20µm
B
2µm
D
mp1
mp2
mp3
mp4
1µm
C
lv
ec
lp
mp
10µm
E
lp3
lp2
lp1
1µm
F
5µm
G
po
10µm

in length, n = 6) are shorter than the lateral ones (ca. 14 µm in length, n = 4; not shown). In contrast, meso- and metanotum bear setae which are arranged in distinct rows (Fig. 3B). Ventrally, the praesternit is devoid of ts, while each of the basi- and furca-spinasternites (sternellum sensu Janetschek 1970) bears some rows of ts (Fig. 3A). Anterior and posterior to the spiracle, there are short and fine ts (p3a and p4 in Fig. 3D). Anterior ts (a) of meso- and metathorax (meso: ca. 7 µm long, n = 6; meta: ca. 9 µm long, n = 5) are shorter (pa) than the posterior ones (p) (meso: ca. 11 µm long, n = 9; meta: ca. 19 µm long, n = 8). In addition, short trichoid ts are situated between the p-ts (pa), these are 3 to 5 µm long (n = 5). In all examined ts, a trichoid cuticular shaft is present. Comparing several specimens, this cuticular shaft exhibits a wide variation of deflection. Also the sockets are variably shaped. The majority of ts possesses a rounded socket with an equally elevated wall (type 1, p2a in Fig. 3C). In other ts, the sockets are bulging on the anterior or lateral margin (type 2, p2 in Fig. 3C).

3.1.3. Abdomen

All metameres comprise a tergite and a sternite and lack pleurites. Sternites of the abdominal metameres one to three show posteriorly constricted margins which leave two lateral pouches for the abdominal appendages (Fig. 1A, F).

Tentative sensilla

Abdominal tentative sensilla (ts) are arranged in distinct anterior and posterior rows (a- and p-ts). Each seta possesses a trichoid cuticular shaft with longitudinal ridges. The shaft is variably deflected. Two types of sockets can be observed: bulge-like (type 2) and rounded ones (type 1). Sensilla with a bulge-like socket always bear a ca. 30 µm long cuticular shaft (n = 4, a and p ts compare Fig. 3E). Sensilla with rounded socket bear a ca. 10 µm long cuticular shaft (n = 3, pa ts compare Fig. 3E). The anterior ts on the first eight metameres are always shorter, ranging from 8–20 µm i.l. (n = 12) in comparison to posterior ones ranging from 30–40 µm i.l. (n = 14).

3.1.4. Thoracic and abdominal appendages

Prothoracic legs

The coxa appears conical and is orientated in parallel to the body axis. The conical trochanter is articulated with the anterior margin of the coxa and lies perpendicularly to the latter. Femur and tibia are club-shaped. Distally, the tibia is articulated with the spear-shaped tarsus.

Tentative sensilla

Ts on coxa, trochanter, femur, and tibia possess a trichoid cuticular shaft and a rounded socket. The socket consists of a broad outer wall and a narrow inner ring. Among the podomeres, the length of the cuticular shaft varies (coxa: 14 µm, n = 3; trochanter: 9 µm, n = 2; femur: 13 µm, n = 4; tibia: 23 µm, n = 3). Several sensillar types can be distinguished on the protarsus: sensillum chaeticum, sensillum trichodeum, sensillum type 1-3 and tentative sensilla (ts). Their distribution is schematised in Fig. 4.

Sensilla chaetica (α, β, γ, δ, t2, d, a', b'2, c', x)

The sensilla α, β, γ, and δ are located on each site of the protarsus (Figs 5A, 7A). Two additional sensilla occur among the sensilla α (α3' is located between α3 and α4) and δ (δ4' is situated between δ4 and δ5, see Fig. 4). They show a specific arrangement: except for the sensilla δ, single sensilla are arranged in a zig-zag pattern (Fig. 4). Sensillum δ6 lies distal to sensillum δ5. Sensilla δ4 plus δ4' and δ3 plus δ3' are arranged in an oblique line, perpendicular to the longitudinal axis of the protarsus. The remaining sensilla δ are situated ventrally in an inversely orientated line (Figs 4, 8A). While s. chaetica occupy the whole length of the protarsus, their density is higher distally. They become more frequent from the middle of the protarsus. The distribution of the remaining s. chaetica is more irregular (Fig. 4). Sensillum t2 is located medially on the dorsal site of the protarsus (Fig. 5A), sensilla a', b'2, c' on the medial site (Figs 5A, 8A) and sensillum x medially on the lateral site (Fig. 7A, D). The socket of s. chaetica consists of a broad outer cuticular ring which is separated from the surrounding surface by a distinct furrow (Fig. 5B). The ring measures approximately 2 µm in diameter (n = 5). Additionally, an inner cuticular structure exists which consists of two clasps on the distal margin of the socket (in relation to the podomere). These clasps touch or overlay each other but do not form a closed ring (Fig. 5B). They are nearly 1.2 µm long and 0.2 µm broad (n = 3). The proximal diameter of the trichoid shaft measures 1 µm (n = 3). A joint membrane stretches between the cuticular shaft and the inner clasps. The sockets on the proximal (Fig. 7B) as well as on the distal portion of the tarsus are less distinctly separated from the surrounding cuticular surface (Fig. 8C), than those of the median portion (Fig. 7E). The shaft shows longitudinal ridges (Fig. 7F), pores were not observed. The length of s. chaetica varies: α: 15–26 µm (n = 4), β: 19–21 µm (n = 3), γ: 22–25 µm (n = 5), δ: 11–16 µm (n = 4), t2: 15 µm (n = 2), a': 10 µm (n = 1), b'2: 23 µm (n = 1), c': 8 µm (n = 1), b: 13 µm (n = 2), x: 19 µm (n = 3).

Sensilla trichodea (y, z)

Sensilla trichodea are exclusively located on the distal portion of the protarsus (Figs 5A, 7A, 8A). The cuticle surrounding the base of the cuticular shaft is elevated. No additional characteristics are evident (Fig. 8C). The length of the cuticular shaft of both sensilla is nearly the same (*y*: 34 µm, n = 4; *z*: 33 µm, n = 3).

Type 1 sensilla (a, c, f2, t3)

Sensilla a and c are located on the lateral site of the protarsus (Figs 4, 5A, 7A); sensilla f2 and t3 on the latero-distal site (Figs 4, 8E). Sensillum a (Fig. 7C) is located in the proximal half of the protarsus, sensillum c (Figs 5C, 6D) in the middle of the lateral portion. Both, sensillum f2 (Fig. 7H) and sensillum t3 are situated near each other on the protarsus (Fig. 8E). They are characterised by the absence of a distinct socket structure. The cuticular shaft is lance-shaped and shows an alveolar texture. Distinct shrinking artefacts are evident in sensillum f2 and t3 (compare Figs 5E, 8E). Both lateral sensilla (a and c) are 8–9 µm long and measure 1 µm in diameter (n = 4). The latero-distal pair (*f2* and *t3*) is ca. 6 µm long and 1 µm wide (n = 3).

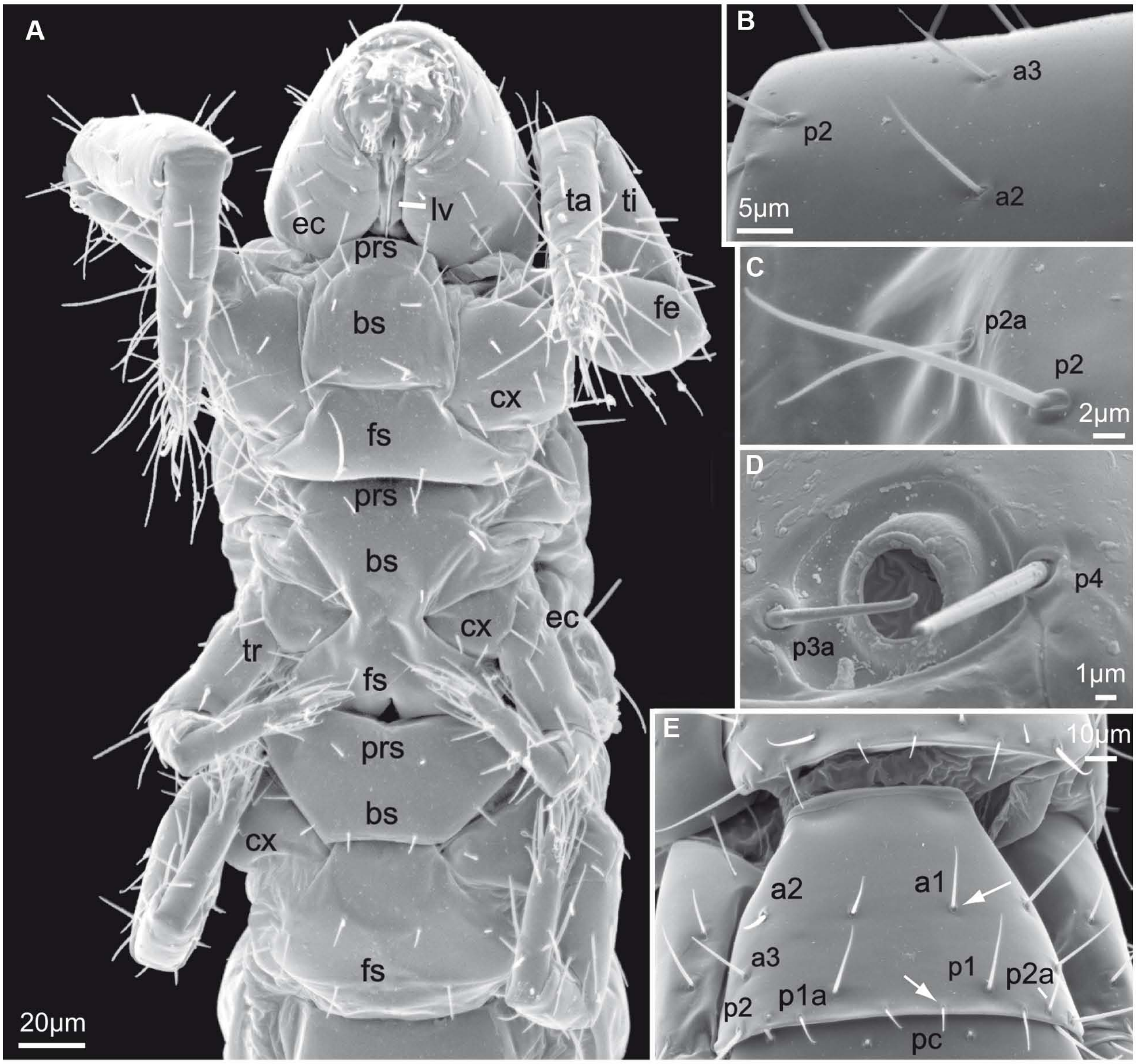


Figure 3. Arrangemente of the thoracic venter and tentative sensilla on thorax and abdomen. (**A**) Ventral view of the head and thorax of *Eosentomon pinetorum*. (**B**) Tentative sensilla (ts) on the second abdominal tergit. (**C**) Details of posterior ts showing different socket structures. (**D**) Tentative sensilla associated with the spiracles. (**E**) Tentative sensilla on the second abdominal sternum.

Abbreviations: **bs** – basisternit, **cx** – coxa, **ec** – epicranium, **fe** – femur, **fs** – furca-spinasternum, **lv** – linea ventralis, **prs** – praesternit, **ta** – tarsus, **ti** – tibia, **tr** – trochanter.

Type 2 sensilla (e, f1, g, t1)

This sensillar type can be found on different sites of the protarsus (Fig. 4). Sensillum t1 (Figs 5C–D, 7E) lies medially on the dorsal site (Fig. 5A), while the other sensilla are arranged in a triangular formation on the distal portion of the lateral site (Fig. 6A). Type 2 sensilla show a similar socket structure compared to sensilla chaetica. A broad outer cuticular ring is discernible, while an inner cuticular ring is only indicated as elevation (Fig. 5D). The cuticular shaft is characterised by a distal swelling (Figs 5C–D, 6A–B, 7E, G–H). The length/width ratio of the distal swelling ranges from 5 : 1 in sensilla e (n = 2) and g (n = 7), 4 : 1 in t1 (n = 3) and 3 : 1 in f1 (n = 3). Distally, a knob-shaped projection tops the swollen distal region of the cuticular shaft (Figs 5C–D, 6B). Flat longitudinal ridges or distinct furrows are found on the surface of sensillum t1 (Fig. 5C–D). Sensilla f1 (Fig. 5E), g and e display no surface texture. Pores are not detectable in all four sensilla. Sensillum t1 is the shortest (5 µm, n = 5), while remaining sensilla are 6 µm (f1, n = 3), 13 µm (g, n = 1), and 12 µm (e, n = 3) long, respectively.

Type 3 sensillum (b)

This sensillum type is similar to type 1 sensilla but differs in the absence of the swollen tip. It inserts medially on the ventral site of the protarsus (Fig. 4). The socket possesses an outer cuticular wall but an inner cuticular structure cannot be observed. The cuticular shaft is short (ca. 13 µm; n = 3), trichoid, and curved parallel to the protarsal surface (Fig. 5A, C). No surface texture is visible.

Praetarsal sensilla

The claw and two associated sensilla are separated from the tarsus by a distinct furrow (Fig. 8C–D). The sensilla flank the claw on its median and lateral side, respectively (Fig. 8D). They are 10–12 µm long (n = 2) while the shaft is ca. 0.7 µm wide (n = 3). Distally, these sensilla widen to a diameter of 1.1 µm (n = 4) and appear lance-shaped. This lance-shaped portion houses a longitudinal slit which is ca. 2 µm long (n = 3). The slits are orientated distally from the claw (Fig. 8F–G).

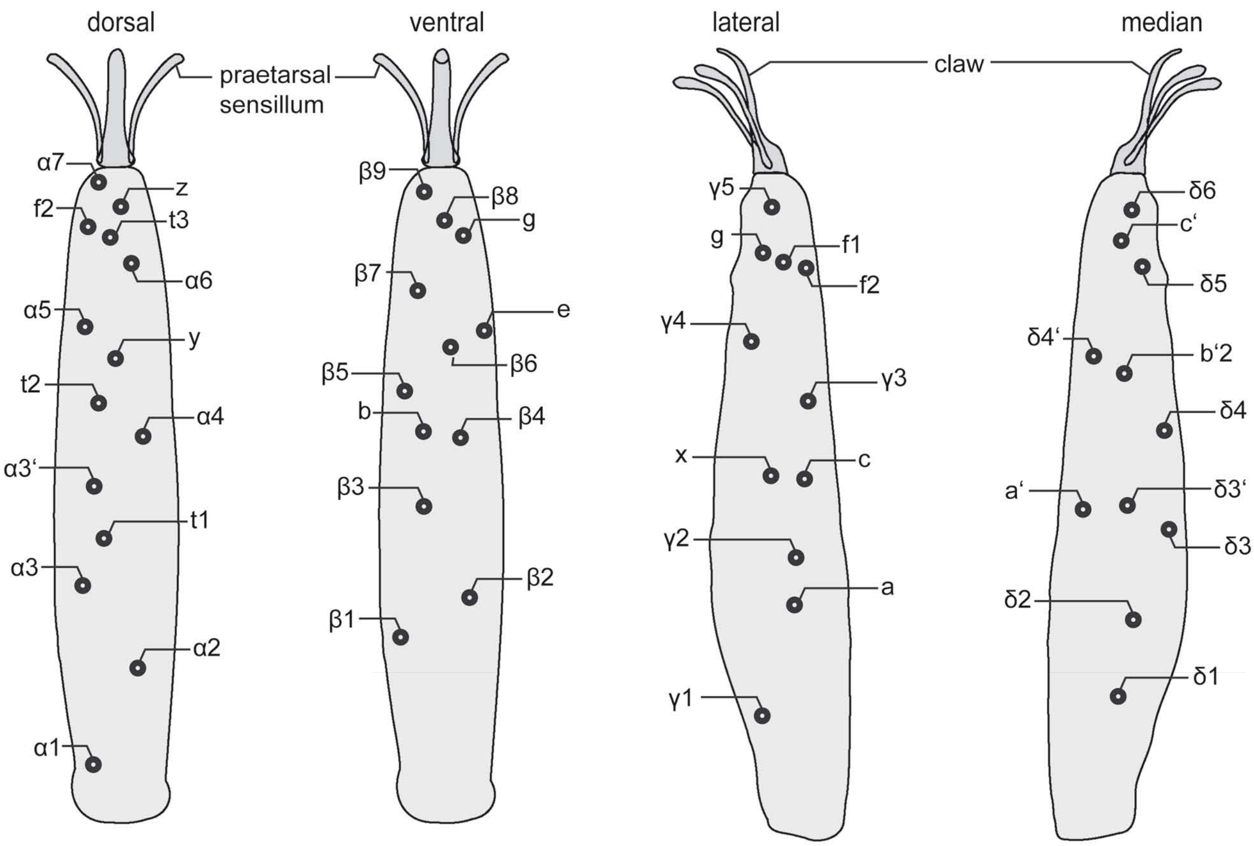


Figure 4. Schematical distribution-pattern of protarsal sensilla on the left protarsus of *Eosentomon pinetorum*. Only site-specific sensilla are shown (compare terminology).

Tarsal pores and threads

Besides cuticular protuberances, three pores are present on the dorsal site of the protarsus. One is located on the medial portion of the protarsus close to sensillum d (Fig. 5B, arrow), another lies in between α3' and γ3 (Fig. 7E), the third one lies in between γ5 and f1 (Fig. 6B, arrow).

Threads of an approximate thickness of 0.4 µm (n = 3) were observed on the distal protarsal cuticle of several specimens (Figs 6A–C, 8A–B). Such threads were not observed on other body parts. They are irregularly shaped and exhibit various lengths. They are found attached to the protarsal surface and to ts, and they bridge the space in between.

Walking legs

Both, meso- and metathoracic legs are shorter than the prothoracic legs but comprise the same number of podomeres (Fig. 1).

Tentative sensilla

Ts occur on each podomere. While all sensilla possess a socket structure, two types of elevated ts can only be

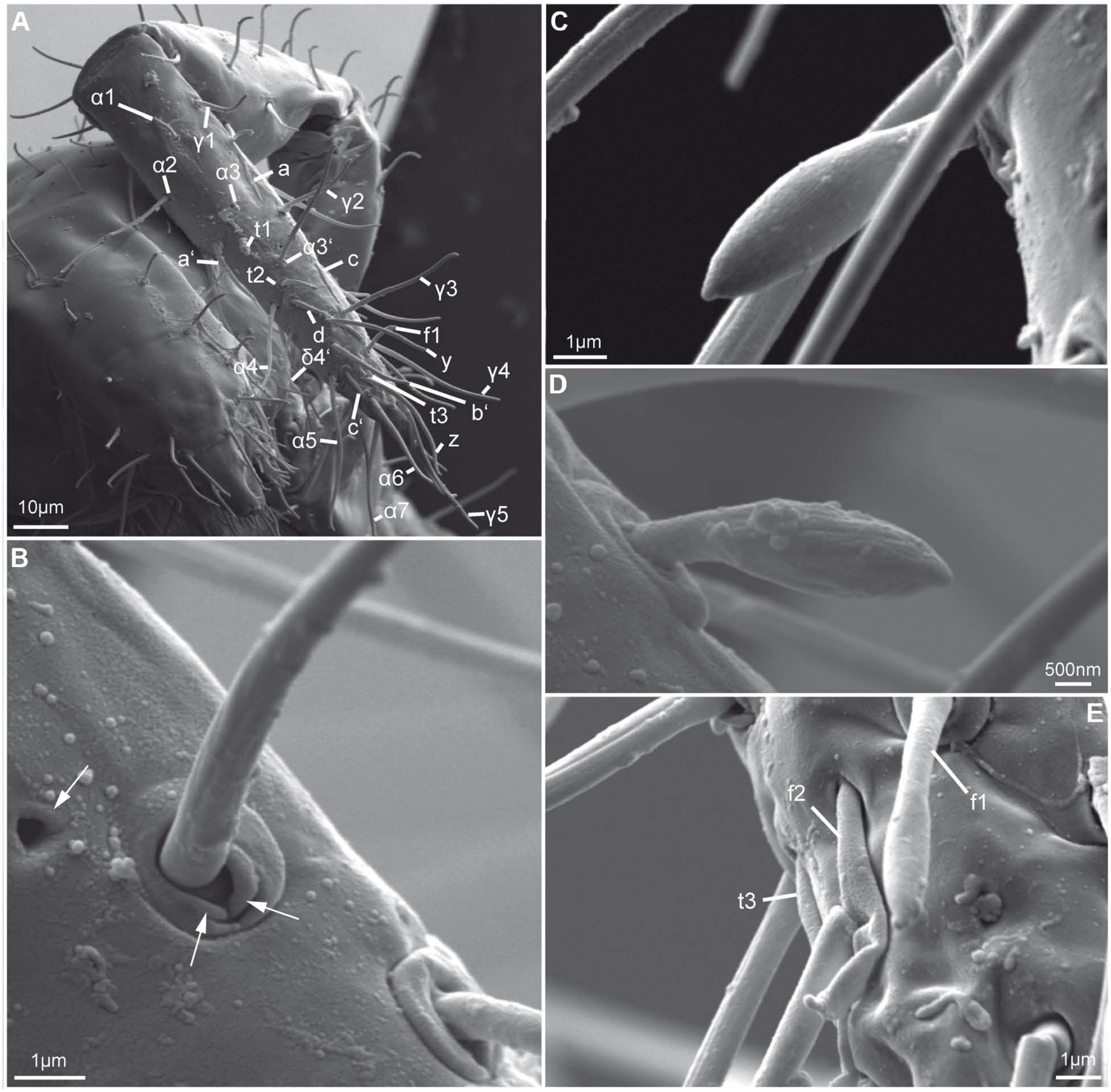


Figure 5. Protarsus of *Eosentomon pinetorum*, dorsal site. (**A**) Overview showing the diversity and distribution of sensilla. (**B**) Socket of sensillum α3', with inner cuticular clasps overlapping each other (arrows) and tarsal orifice (arrow). (**C–D**) Lateral aspects of sensillum t1 with weak (**C**) or distinct longitudinal ridges (**D**) on its surface. (**E**) Collapsed sensilla t3, f1, and f2.

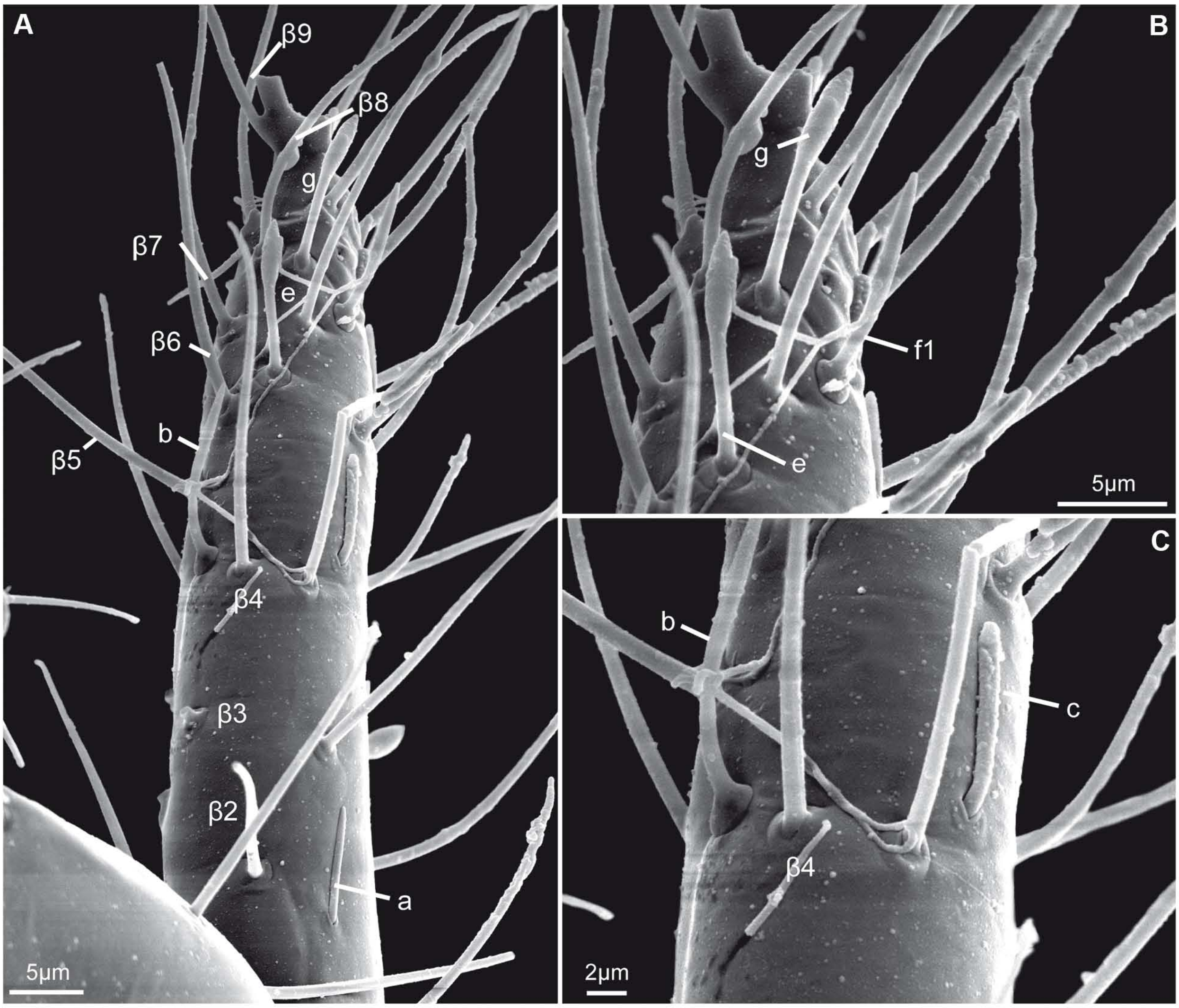
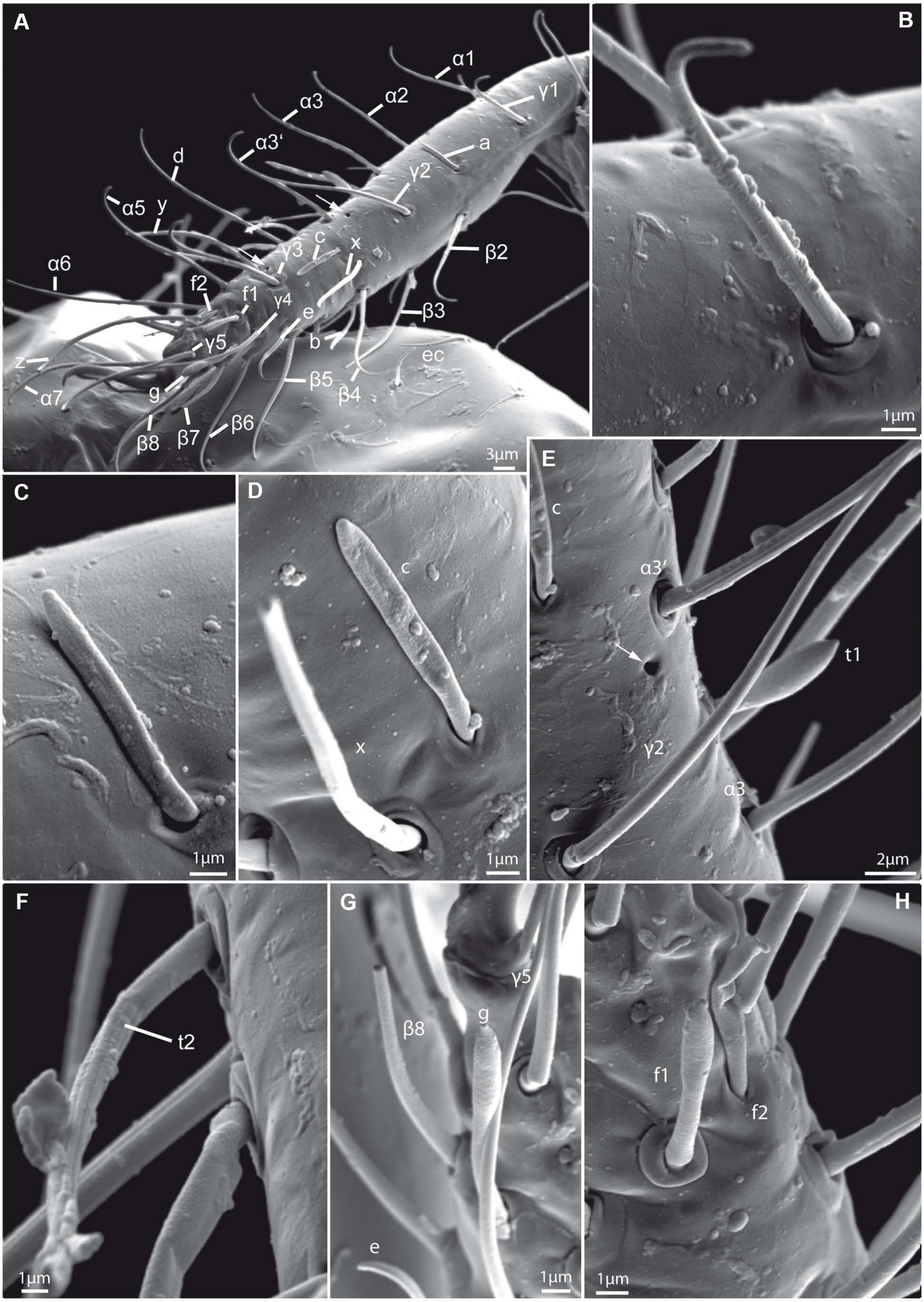


Figure 6. Protarsus of *Eosentomon pinetorum*, ventral site. (**A**) Overview showing the diversity and distribution of sensilla. (**B**) Details of sensilla e, f1 and g. Between the sensilla, tread of secretion is visible on the surface. (**C**) Sensilla b and c with broad outer ring of socket.

► **Figure 7**. Protarsus of *Eosentomon pinetorum*, lateral aspects. (**A**) Overview showing diversity and distribution of sensilla. (**B**) Sensillum γ1 with bi-partite socket (inner ring difficult to notice). (**C**) Sensillum a without inner socket structure. (**D**) Sensilla x and c with different socket structures. (**E**) Sensilla α3, t1 and y2. (**F**) Sensillum t2 with distal ridges. (**G**) Sensillum *g* with characteristically swollen tip. (**H**) Sensilla f1 (collapsed) and sensillum f2 with distinct socket structure and swollen tip.


A
α1
γ1
α3
α2
a
α3‘
d
γ2
α5
y
c
x
α6
γ3
β2
f2
f1
γ4
e
β3
γ5
b
z
ec
α7
g
β5
β4
β8
β7
β6
3µm
B
1µm
C
1µm
D
c
x
1µm
E
c
α3‘
t1
γ2
α3
2µm
F
t2
1µm
G
γ5
g
β8
e
1µm
H
f1
f2
1µm

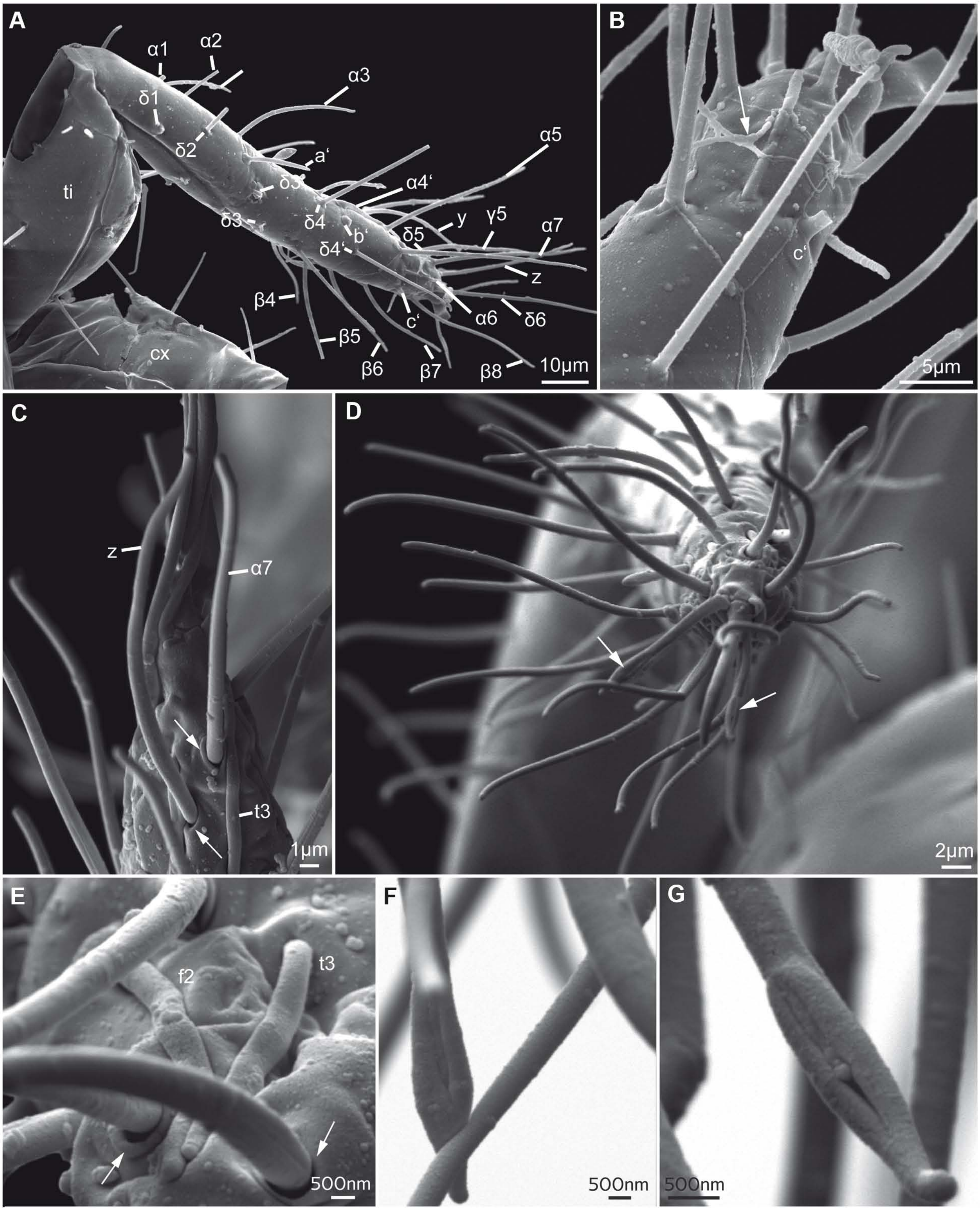


Figure 8. Medial site of the protarsus in *Eosentomon pinetorum*. (**A**) Overview showing diversity and distribution of sensilla. (**B**) Sensillum c' with threads of secretion and hardly visible socket (arrow). (**C–D**) Distal tip of the protarsus in dorso-lateral (**C**) and frontal (**D**) aspect. The Socket structure of distal sensilla chaetica sometimes is difficult to separate from those of sensilla trichodea (arrows in C). Praetarsal sensilla are mostly inclined laterally (arrows in **D**). (**E**) Sensilla f1 and t3 (collapsed). Arrows indicate socket structures. (**F–G**) Left (**F**) and right (**G**) praetarsal sensilla with slits.

observed on femur, tibia, and tarsus (Fig. 1). The first type is rounded, 3 µm in diameter (n = 3), and present on each podomere. The second type is ellipsoid, 4 µm (n = 2) long, 2 µm broad (n = 2), and exclusively located on the tarsus (Fig. 1E, arrow). The trichoid shaft shows neither a texture nor pores. On the outer margin of the mesotarsus, some ts with a thicker cuticular shaft are located (Fig. 1E). The length of the shaft varies among the podomeres: 12 µm on the coxa (n = 4), 8 µm on the trochanter (n = 1), and 10 µm on the femur (n = 3) and tibia (n = 3). On the tarsus, the cuticular shaft is distinctly longer, ranging from 13–15 µm (n = 3).

3.1.5. Abdominal appendages

Three pairs of appendages are present on the abdominal metameres 1–3 (Fig. 1A–F). They are inserted between sternites and tergites. All abdominal appendages consist of three podomeres: subcoxa, coxa, and terminal article. The proximal subcoxa is dome-shaped, the larger distal coxa is cylindrical, and the terminal article bears an eversible vesicle (Fig. 1F).

Tentative sensilla

The subcoxa bears no ts. On the distal portion of the coxa, five ts are located. Two of them are located medially on the anterior site while the remaining ts are arranged around the joint formed by the coxa and terminal article. A rounded socket structure is evident in all ts. The cuticular shaft is trichoid and shows neither a surface texture nor a pore. Ts at the tip of the coxa are 7 µm long (n = 3) while isolated ts are 9–11 µm long (n = 4; Fig. 1F).

3.2. *Acerentomon franzi*

3.2.1. Protarsus

Sensilla chaetica (α, β, γ, δ, t2, t3)

Only the distribution of the sensilla α, β and γ was documented. They are arranged in a zig-zag pattern along the protarsus (Fig. 9A–D). Sensilla t2 and t3 are only recognisable depending on the angle of view.

The socket of each s. chaeticum consists of a broad outer cuticular ring (6 µm in diameter) (n = 2) and an inner ring with a diameter of ca. 3 µm (n = 2) consisting of two clasps. These clasps overlap each other (Fig. 9B). A joint membrane extends between the inner cuticular clasps and the base of the cuticular shaft which is 2 µm in diameter (n = 3). While longitudinal ridges can be observed, no pores are evident (Fig. 9B). The length of the sensilla varies: α: 53–72 µm (n = 5), β: 38–75 µm (n = 3), γ: 56–64 µm (n = 3), and δ: 22–37 (n = 2) µm. Sensilla t2 measure 25 µm x 0.2 µm (n = 1) and t3 16 µm x 0.2 µm (n = 1) (Fig. 9A–D).

Sensilla trichodea (a–g, a', c')

S. trichodea a–g are located laterally (Fig. 9A). Sensillum a appears separated and is positioned on the proximal portion of the protarsus (Fig. 9A) while the remaining sensilla are located in closer proximity to each other. The sensilla b and c are located on the same level on the median tarsal portion (Fig. 9A), however, their sockets are widely separated (Fig. 8C). Sensilla d–g lie distinctly closer together (Fig. 9A). Sensilla a' and c' are inserted on the median site (Fig. 9D). In contrast to all other s. trichodea, the surface of sensillum b bears several longitudinal ridges (Fig. 9C). No pores are noticeable on any sensilla. The cuticular shaft in all s. trichodea is 13 µm long (n = 2) and 2 µm broad (n = 3).

Type 1 sensillum (t1)

This sensillum possesses a distinct socket. The cuticular shaft is short and swollen distally. A slit is present at the base of this swelling (Fig. 9E). The shaft is 14 µm long (n = 2), the swollen tip measures nearly 8 µm x 3 µm (n = 2). Distally, the diameter decreases resulting in a nipple-shaped tip with a diameter of ca. 60 nm (n = 1) (Fig. 9E–F).

Praetarsal sensilla

Two sensilla are inserted close to the claw: the first one is ca. 56 µm long and located on the dorsal site of the praetarsus, the second one is ca. 5 µm long and is located ventrally. Both sensilla possess a trichoid cuticular shaft.

Tarsal pores

Two protarsal pores were observed. One is located median near sensillum b and c, and one distally near sensillum t3 (Fig. 9D, median one not shown).

4. Discussion and conclusion

4.1. The sensillar equipment of Protura

The present extern-morphological investigation provides the first detailed documentation of cuticular sensilla on the entire body of *Eosentomon pinetorum* and the protarsus of *Acerentomon franzi*. Sixl et al. (1974) provided the first SEM study on sensory structures of Protura. However, the authors only mentioned one sensillum basiconium (t3) and one s. chaeticum (praetarsal sensillum). Additional sensilla are solely mentioned but

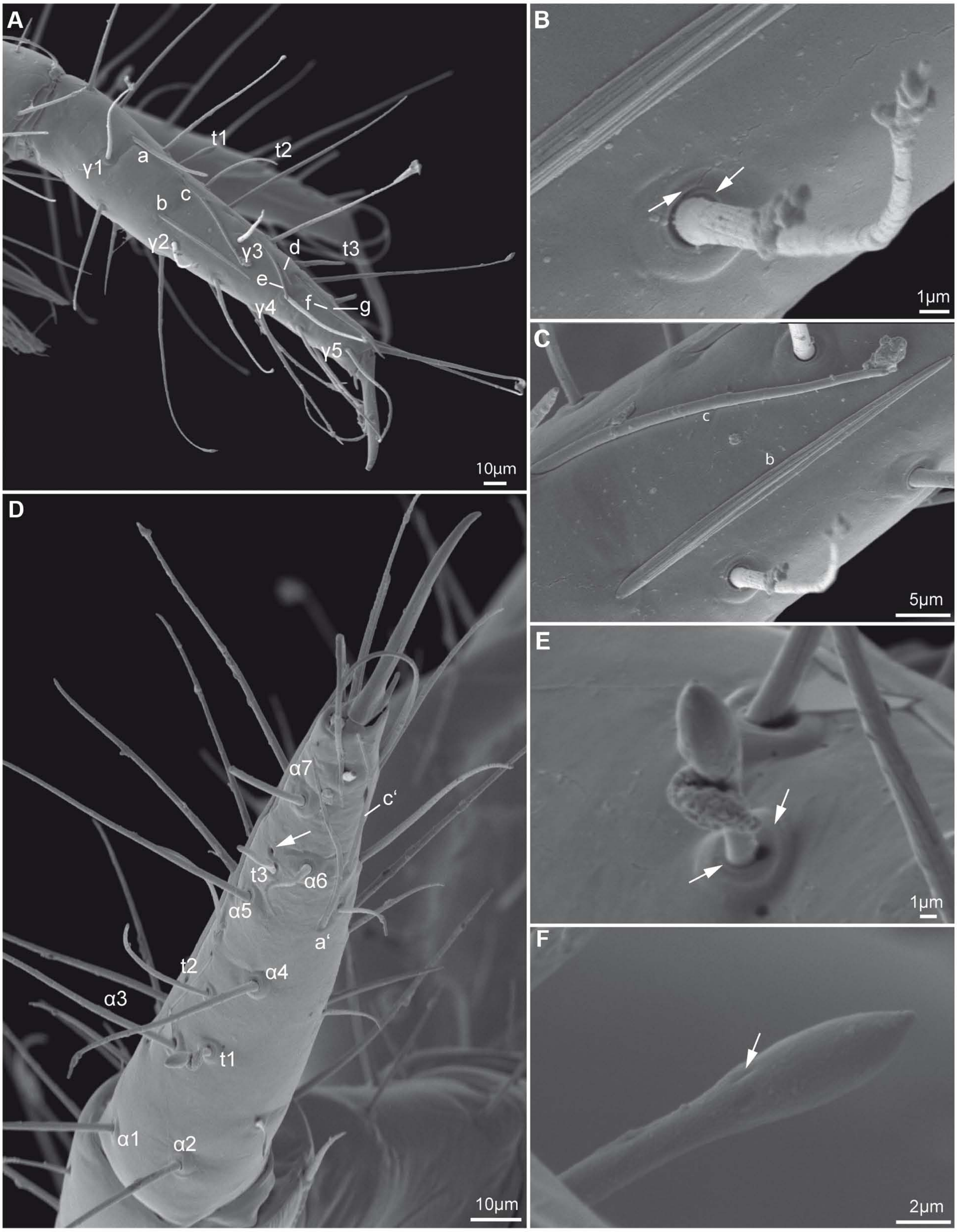


Figure 9. Protarus of *Acerentomon franzi*. (**A**) Lateral site. Only terms of unambiguously identified sensilla are given. (**B**) Sensillum γ2 with overlapping inner clasps of the socket (arrows). (**C**) Sensilla c and b. Sensillum b with ridges. (**D**) Dorsal site. Only the names of unambiguously identified sensilla are given. The arrow indicates the pores of protarsal glands. (**E**) Sensillum t1 with bi-partite socket (arrows indicate the outer and inner ring structure). (**F**) Sensillum t1 with slit (arrow).

not described in detail. The first anatomical examination of tarsal sensilla including transmission electron microscopy (TEM), was conducted by Müller (1976) on *Protentomon* sp. For two reasons, these results are not applicable to the present description. Firstly, Müller (1976) used a Roman and an Arabic numbering for claw and tarsal sensilla, which does not correspond to the classification of other authors (e.g. Tuxen 1964, Nosek 1973). Secondly, his scheme of sensillar distribution on the protarsus (see his Fig. 4, p. 157 in Müller 1976) is not in concordance with the descriptions provided by other authors (e.g. Tuxen 1964, Nosek 1973). Single sensilla were examined by Dallai & Nosek (1981) in *Acerentomon maius* Berlese, 1908 using TEM. A wealth of taxonomic papers includes descriptions and figures of proturan protarsal sensilla, but these are mainly line drawings (e.g. Tuxen 1964, Nosek 1973, Bernard & Biechele 2008, Bu et al. 2014, Shrubovych et al. 2014). SEM images, if at all available, only provide an overview (e.g. Tuxen 1986). Most recently, Böhm et al. (2011) explore how useful confocal laserscanning microscopy is for determing proturan species. However the resolution is not sufficient for examinations of sensillar fine structures.

As up to now, the lack of suitable data on sensilla in Protura hampers a comparison beyond species level and, therefore, also impede evolutionary morphological considerations. The present study may help to make terminology of proturan sensilla more consistent.

Prothoracic legs

Sensilla chaetica are predominant on the protarsi as well as on the whole body surface of the here examined species of Protura. The remaining sensillar types are located exclusively on the protarsus. Besides differences in the number of sensilla, the protarsus of the examined proturan species also shows differences in sensillar types and their distribution.

In *Eosentomon pinetorum* and in *Acerentomon franzi,* sensilla chaetica on the dorsal, ventral, and lateral site of the protarsus are longer than those on the median site. Among sensilla other than s. chaetica, type 1 sensilla are restricted to *E. pinetorum*. Perhaps, type 1 sensilla are more widespread throughout Protura. However, the available light microscopic descriptions do not allow any comparison.

Sensillum t2 and t3 differ in length in both examined species. These sensillar subtypes exhibit some variation in the shape of the cuticular shaft (e.g., Tuxen 1964, Nosek 1973). Apart from protarsal s. chaetica, all tentative sensilla (ts) described as tentative sensilla correspond to the s. chaetica. The presence of a distinct socket as well as the shape of the cuticular surface supports this interpretation.

The two examined species also exhibit differences in respect to sensilla trichodea. In *E. pinetorum* they are exclusively located dorso-distally, but occur on the lateral and median site of the protarsus in *A. franzi*. In *E. pinetorum,* sensilla with a corresponding location show distinct morphological differences. Thus, these sensilla are here classified as type 1 sensilla (sensilla a and c, compare Fig. 7C and D). Actually, type 1 sensilla occur only in *E. pinetorum*. This sensillar type corresponds to sensilla basiconica by the alveolate texture and the lower ratio of length to diameter of the cuticular shaft. Sixl et al. (1974) considered the t1 sensillum as s. basiconicum, however, Schneider (1964) defined s. basiconicum also on the absence of a socket. Altner (1977) classified sensilla with socket as s. basiconicum, but these are setiform and possess a terminal pore. Thus, t1 differ from this sensillar type, leading us to create a new type (i.e. type 2 sensilla). The type 2 sensillum includes sensilla previously considered as separate types (club-shaped and spatulate cuticular shaft). The t1 sensilla of *A. franzi* and *E. pinetorum* show some differences: ridges were found only in *E. pinetorum* confirming the observation of Dallai & Nosek (1981). A slit at the base of the swollen tip is only present in *A. franzi* (compare Fig. 9F). To our knowledge, this slit was never been mentioned in any previous study.

The type 3 sensillum only differs to t1 sensilla by the absence of a swollen tip. It is only present in *E. pinetorum*; the sensillum b in *A. franzi* represents a s. trichodeum.

Praetarsal sensilla

Taxonomic literature distinguishes a praetarsal ‘empodium’ and praetarsal sensillum (e.g., Tuxen 1964). TEM-data, however, show sensory neurons supplying both ‘empodium’ and sensillum (Müller 1976; his ‘sensillum III’ = empodium and ‘sensillum 1’ = praetarsal sensillum). While praetarsal sensilla are commonly considered to be located dorsally and ventrally, our observations in *E. pinetorum* suggest a rather lateral position. On the other hand, the dorsal-ventral arrangement in *A. franzi* corresponds to the drawings of Tuxen (1964).

We show that *E. pinetorum* possesses two praetarsal sensilla as already noted by Müller (1976) for another proturan genus. Thus, the question arises to what extend a separation into ‘empodium’ and sensillum is reliable. According to Snodgrass (1935), an empodium arises from the distal portion of the unguitractor plate. Yet, detailed descriptions of the praetarsus in Protura is solely based on light microscopy and the praetarsus was described as a ring equipped with claw and a dorsal and ventral process (‘empodium’ and ‘sensillum’) (Janetschek 1970). Our data confirm the praetarsal arrangement as described by Janetschek (1970) and show no trace of an unguitractor plate (see Fig. 8D). Both processes originate at the same level as the claw. Therefore, they do not correspond to any sensillar type introduced above.

Mouthparts

As we did not examine any details of sensillar equipment of the mouthparts in *A. franzi*, in the following we only discuss data for *E. pinetorum*. In contrast to Tuxen (1964) and Imadate (1994), there is more than one seta located on the maxillary and labial palpomeres. Each of them is equipped with a socket. Thus, they presumably represent sensilla chaetica. The distal tufts of both palps correspond to 'microtrichia on setae' sensu Richards & Richards (1979) (compare Sixl et al. 1974; Fig. 1D p. 110). Apart from that, our data suggest that the labial palp possesses three proximal palpomeres (Fig. 2E). This observation is in contrast to previous authors (Tuxen 1964, Janetschek 1970, Nosek 1973).

Tarsal pores and threads

Several tarsal pores as well as threads were observed. Among Protura, the distribution of pores on other body parts is of importance for taxonomy (`porotaxy` sensu Szeptycki 1988; see also Rusek et al. 2012, Shrubovych & Smykla 2012, Bu et al. 2014). Condé & François (1962) and Dallai (1991) provide some information on the ultrastructure of these associated glands, but their function remains dubious. In the proturan protarsus, Müller (1976) mentioned huge epidermal glands and Dallai & Burroni (1976) provided ultrastructural descriptions and assumed defence or lubrication as possible function. Tarsal pores have been described for several proturan species (Bernard 1985, Bernard & Biechele 2008, Bu et al. 2012, Shrubovych & Rusek 2010, Shrubovych et al. 2012).

Occasionally, we found irregularly shaped threads of variable length on the protarsus. Since we never observed threads immediately associated with gland pores, a contamination cannot be excluded definitely. Still, the exclusive presence of threads on the distal part of the protarsus implies a functional relation to this podomere and we assume that these threads represent the secretion released by protarsal glands. Due to the position of the protarsus, being comparatively close to the mouth, it appears also conceivable that the secretion is involved in capturing prey. The sensilla aggregated close-by the protarsus may be involved in this behaviour by receiving stimuli produced by potential prey. But a predatory scenario appears ambiguous given the fungivory suggested by Sturm (1959). Otherwise, the secretion might be used to create cocoons or galleries as in Embioptera (Edgerly et al. 2012). Yet, detailed anatomical and behavioural examinations as well as biochemical analyses are necessary to clarify the function of the secretion.

4.3. Sensory ecology of Protura

Although no fossil record of Protura is known (e.g. Janetschek 1970), the systematic position suggests a phylogenetic age similar to that of their putative sistergroup, the Collembola (see Grimaldi & Engel 2005, von Reumont et al. 2012). Thus, Protura likely live successfully without antennae since the Devonian (ca. 360 mya). It is consensus that the proturan protarsi replace the antennae functionally (Gillott 2005, Koch 2009). As we could demonstrate, s. chaetica, s. trichodea and three other sensillar types (Type 1 to 3) occur on the proturan protarsus. Regarding the habitat, in the soil, we consider mechanical (including vibrations), chemical (volatile and non-volatile substances), and physical factors (humidity, temperature) to be relevant for the proturan sensory ecology (compare Bowdan & Wyse 1996).

The protarsi of *E. pinetorum* and *A. franzi* differ in both quantity and quality of sensilla. It is obvious to ask, whether these differences reflect different ecological preferences. Observations on proturan food sources are available for several species (Sturm 1959, Pass & Szucsich 2011). All notes are in favour of fungivory. Sturm (1959) pointed out that the gut content is either brownish (*Eosentomon* sp.) or whitish (*Acerentomon* sp.), which might also indicate different food preferences. On the other hand, the abundance of different *Eosentomon* and *Acerentomon* species correlates with that of mycorrhiza-mycelia (Stumpp 1990), indicating a primary dependence. Paired spiracles are present on the meso- and metanotum of *Eosentomon* spp., but are absent in representatives of *Acerentomon* sp. One might expect that the presence of spiracles is correlated with living in humid habitats. However, such assumptions seem premature, as *Sinentomon erythranum* also possesses spiracles, but inhabits environments with lower humidity (Yin 1965). Judging from a drawing of Yin (1965; Fig. 4 and 5 p. 187), this species exhibits a minor density of protarsal sensilla than *E. pinetorum*. Therefore, it appears doubtful whether the presence of spiracles corresponds to a higher density of sensilla.

The proturan biology is full of enigmas (compare Pass & Szucsich 2011), but information on the proturan autecology are crucial for sound conclusions on the sensory ecology in this group. The present study of external cuticular sensilla by SEM shows that sensilla in Protura are capable to receive different environmental stimuli. But to clarify functional modalities of individual sensilla additional ultrastructural and physiological examinations are necessary.

5. Acknowledgement

We like to acknowledge Birgit Balkenhol (Görlitz, Germany) for useful suggestion concerning collection and extraction techniques as well as Wolf Sixl (Graz, Austria) for kindly providing rare literature. Furthermore, we like to thank Steffen Harzsch (Greifswald, Germany) for his support. We are grateful to Rabea Schlüter, Lara Lopardo and Gabriele Uhl (all Greifswald) for their support in specimen preparation, critical-point-drying and technical questions. This study was supported by a fellowship of the Landesgraduiertenstiftung Mecklenburg-Vorpommern to CWH.

6. References

Altner, H. (1977): Insektensensillen: Bau- und Funktionsprinzipien. – In: Rathmayer, W. (ed.): Verhandlungen der Deutschen Zoologischen Gesellschaft. – Gustav Fischer Verlag, Stuttgart: 139–153.

Berlese, A. (1909): Monografia dei Myrientomata. – Redia **6**: 1–182.

Bernard, E. C. (1985): Two new species of Protura (Insecta) from North America. – Proceedings of the Biological Society of Washington **98**: 72–80.

Bernard, E. C. & L. T. Biechele (2008): *Nipponentomon pembertonense*, n. sp. (Protura: Acerentomidae) from Maryland. – Proceedings of the Biological Society of Washington **121:** 438–444.

Böhm, A., D. Bartel, N. U. Szucsich & G. Pass (2011): Confocal imaging of the exo- and endoskeleton of Protura after non-destructive DNA extraction. – Soil Organisms **83**: 335–345.

Bowdan, E. & G. A. Wyse (1996): Sensory Ecology: Introduction. – Biological Bulletin **191**: 123–124.

Bu, Y. & W. Y. Yin (2007): Two new species of *Hesperentomon* Price, 1960 from Qinghai Province, Nortwestern China (Protura: Hesperentomidae). – Acta Zootaxonomica Sinica **32**: 508–514.

Bu, Y. & D. H. Wu (2012): Revision of Chinese *Yamatentomon* (Protura: Acerentomata: Acerentomidae), with description of one new species, redescription of *Yamatentomon yamato*, and key to world species. – Florida Entomologist **95**: 839–847.

Bu, Y., M. B. Potapov & W. Y. Yin (2014): Systematic and biogeographical study of Protura (Hexapoda) in Russian Far East: new data on high endemism of the group. – ZooKeys **57**: 19–57.

Cate, H. S. & C. D. Derby (2001): Morphology and distribution of setae on the antennules of the Caribbean spiny lobster *Panulirus argus* reveal new types of bimodal chemo-mechanosensilla. – Cell and Tissue Research **304**: 439–454.

Chen, W.-J., Y. Bu, A. Carapelli, R. Dallai, S. Li, W.-Y. Yin & Y.-X. Luan (2011): The mitochondrial genome of *Sinentomon erythranum* (Arthropoda: Hexapoda: Protura): an example of highly divergent evolution. – BMC Evolutionary Biology **11**: 246.

Condé, B. & J. François (1962): Prèsence de glandes tégumentaires unicellulaires chez les Protoures. – Bulletin de la Société Zoologique de France **87**: 221–225.

Dallai, R. (1991): Are Protura really Insects? – In: Simonetta, A. M. & S. C. Morris (eds): The early evolution of Metazoa and the significance of problematic taxa. Cambridge University Press, Cambridge: 263–269.

Dallai, R. & D. Burroni (1976): La struttura delle ghiandole tegumentali delle zampe anteriori dei Proturi (Insecta). – Redia **64:** 165–172.

Dallai, R. & J. Nosek (1981): Ultrastructure of sensillum t1 on the foretarsus of *Acerentomon majus* Berlese (Protura: Acerentomidae). – International Journal of Insect Morphology and Embryology **10**: 321–330.

Dallai, R., D. Mercati, Y. Bu, Y. W. Yin, G. Callaini & M. G. Riparbelli (2010): The spermatogenesis and sperm structure of *Acerentomon microrhinus* (Protura, Hexapoda) with considerations on the phylogenetic position of the taxon. – Zoomorphology **129**: 61–80.

Denis, J. R. (1949): Ordre des protoures. – In: Grassé, P.-P. (ed.), Traité de Zoologie. – Masson et Cie, Paris: 186–207.

Edgerly, J. S., S. Büsse & T. Hörnschemeyer (2012): Spinning behaviour and morphology of the spinning glands in male and female *Aposthonia ceylonica* (Enderlein, 1912) (Embioptera: Oligotomidae). – Zoologischer Anzeiger **251**: 297–306.

Eguchi, E. & Y. Tominaga (1999): Atlas of artrhopod sensory receptors: dynamic morphology in relation to function. – Springer, Tokyo: 200pp.

Esslen, J. & K. Kaissling (1976): Zahl und Verteilung antennaler Sensillen bei der Honigbiene (*Apis mellifera* L.). – Zoomorphologie **83**: 227–251.

Foelix, R. F. & R. C. Axtell (1972): Ultrastructure of Haller's organ in the Tick *Amblyomma americanum* (L.). – Zeitschrift Für Zellforschung und Mikroskopische Anatomie **124:** 275–292.

Foelix, R. & E. Hebets (2001): Sensory biology of whip spiders (Arachnida, Amblypygi). – Andrias, **15**: 129–140.

François, J. (1996): Squelette et musculature thoraciques des protoures. – Annales de la Société Entomologique de France **32:** 233–249.

Galli, L., M. Capurro & C. Torti (2011): Protura of Italy, with a key to species and their distribution. – Zookeys **67**: 19–67.

Gillott, C. (2005): Entomology – Springer, Dordrecht: 831pp.

Grimaldi, D. & M. S. Engel (2005): Evolution of the Insects. – Cambridge University Press, New York: 772pp.

Hallberg, E. & B. S. Hansson (1999): Arthropod sensilla: morphology and phylogenetic considerations. – Microscopy Research and Technique **47**: 428–439.

Hallberg, E. & M. Skog (2011): Chemosensory sensilla in Crustaceans. – In: Breithaupt, T. & M. Thiel (eds): Chemical Communication in Crustacea. – Springer, New York: 103–121.

Imadate, G. (1994): A new *Eosentomon* (Protura, Eosentomidae) from Yonaguni island, southwest Japan. – Japanese Journal of Entomology **62** 309–313.

Janetschek, H. (1970): Protura. – In: Helmke, J.-G., D. Stark, & H. Wermuth (eds), Handbuch der Zoologie IV. Band: Arthropoda-2. Hälfte: Insecta. – de Gruyter, Berlin: 1–72.

Keil, T. A. (2012): Sensory cilia in arthropods. – Arthropod Structure and Development **41**: 515–534.

Koch, M. (2009): Protura. – In: Resh, V. H. & R. T. Cardé (eds), Encyclopedia of Insects. – Elsevier, Burlington: 855–858.

Merivee, E., A. Ploomi, A. Luik, R. T. Rahi & V. Sammelselg (2001): Antennal sensilla of the Ground Beetle *Platynus dorsalis* (Pontoppidan, 1763) (Coleoptera, Carabidae). – Microscopy Research and Technique **55**: 339–349.

Meusemann, K., B. M. Reumont, S. Simon, F. Roeding, S. Strauss, P. Kück, P. Kück, I. Ebersberger, M. Walzl, G. Pass, S. Breuers, V. Achter, A. von Haeseler, T. Burmester, H. Hadrys, J. W. Wägele & B. Misof (2010): A phylogenomic approach to resolve the arthropod tree of life. – Molecular Biology and Evolution **27**: 2451–2464.

Müller, H. (1976): Feinbau der Sensillen an den Vorderbeinen der Proturen. – Zoologischer Anzeiger **197**: 151–178.

Müller, C., A. Sombke, G. Hilken & J. Rosenberg, (2011): Chapter 12. Sense organs. – In: Minelli, A. (ed.): Treatise on Zoology - Anatomy, Taxonomy, Biology - The Myriapoda. – Brill, Leiden: 235–278.

Nakamura, O. (2010): Taxonomic revision of the family Eosentomidae (Hexapoda: Protura) from Japan. – Magnolia Press, Auckland: 109 pp.

Nosek, J. (1973): The European Protura, their taxonomy, ecology and distribution, with keys for determination. – Muséum d'histoire naturelle, Geneva: 345 pp.

Pass, G. & N. U. Szucsich (2011): 100 years of research on the Protura: many secrets still retained. – Soil Organisms **83**: 309–334.

Pohl, H. (2010): A scanning electron microscopy specimen holder for viewing different angles of a single specimen. – Microscopy Research and Technique **73**: 1073–1076.

Prell, H. (1912): Beiträge zur Kenntnis der Proturen. III. Gliederung und eigene Muskulatur der Beine von Acerentomon und Eosentomon. – Zoologischer Anzeiger **40**: 33–50.

Resch, M. C., J. Shrubovych, D. Bartel, N. U. Szucsich, G. Timelthaler, Y. Bu, M. Walzl & G. Pass (2014): Where taxonomy based on subtle morphological differences is perfectly mirrored by huge genetic distances: DNA barcoding in Protura (Hexapoda). – PLoS One **9**: e90653.

von Reumont, B. M., R. A. Jenner, M. A. Wills, E. D. Ampio, I. Ebersberger, B. Meyer & B. Misof (2012): Pancrustacean Pancrustacean phylogeny in the light of new phylogenomic data: support for Remipedia as the possible sister group of Hexapoda. – Molecular Biology and Evolution **29**: 1031–1045.

Richards, G. & P. A. Richards (1979): The cuticular protuberances of insects. – International Journal of Insect Morphology and Embryology **8**: 143–157.

Rimsky-Korsakow, M. (1911): Über die Organisation der Protura Silvestri. – Travaux de la Société des Naturalistes de St. Pétersbourg **52**: 2–24.

Rusek, J. (1974): Zur Morphologie und Phylogenesis der Abdominalbeine der Protura. – Pedobiologia **14**: 134–137.

Rusek, J., J. Shrubovych & A. Szeptycki (2012): Head porotaxy and chaetotaxy of order Acerentomata (Protura). – Zootaxa **3262**: 54–61.

Schneider, D. (1964): Insect antennae. – Annual Review of Entomology **9**: 103–122.

Shrubovych, J. & J. Rusek (2010): *Sugaentulus andrzeji* sp. nov. from Siberia, Russia (Protura: Acerentomidae: Acerentominae) and key to Acerentominae genera. – Zootaxa **2720**: 59–68.

Shrubovych, J. & J. Smykla (2012): Review of the genus *Paracerella* Imadaté (Protura: Acerentomidae, Nipponentominae) with identification key and description of a new species. – Zootaxa **3509**: 69–76.

Shrubovych, J., C. Schneider & C. A. D'Haese (2012): Description of a new species of *Acerentulus* Berlese 1908 (Protura: Acerentomata: Acerentomidae) with its barcode sequence and a key to the confinis group. – Annales de la Société Entomologique de France **48**: 1–7.

Shrubovych, J., C. Schneider & C. A. D'Haese (2014): Revision of the genus *Andinentulus* (Protura: Acerentomidae: Berberentulinae), with a key to South and Central American Acerentomidae Species. – Annals of the Entomological Society of America **107**: 567–574.

Silvestri, F. (1907): Descrizione di un nuovo genere di Insetti Apterigoti, rappresentante di un nuovo ordine. – Bollettino del Laboratorio di zoologia generale e agraria della R. scuola superiore d'agricoltura in Portici **1**: 296–311.

Sixl, W., J. Nosek & H. Waltinger (1974): Sensory hairs and tegument in Protura. – Pedobiologia **14**: 109–112.

Snodgrass, R. E. (1935): Insect morphology. – McGraw-Hill Book Company, New York: 667

Sombke, A., Rosenberg, J., Hilken, G., Westermann, M. & A. Ernst (2011): The source of chilopod sensory information: external structure and distribution of antennal sensilla in *Scutigera coleoptrata* (Chilopoda, Scutigeromorpha). – Journal of Morphology **272**: 1376–87.

Steinbrecht, R. A. (1973): Der Feinbau olfaktorischer Sensillen des Seidenspinners (Insecta, Lepidoptera). – Zeitschrift Für Zellforschung und Mikroskopische Anatomie **139**: 533–565.

Stumpp, J. (1990): Zur Ökologie einheimischer Proturen (Arthropoda: Insecta) in Fichtenforsten. – Zoologische Beiträge **33**: 345–432.

Sturm, H. (1959): Die Nahrung der Proturen. – Naturwissenschaften **46**: 90–91.

Szeptycki, A. (1984): Three new species of *Eosentomon* Berlese, 1909, from Poland with redescription of *Eosentomon germanicum* Prell, 1912 (Protura). – Polskie Pismo Entomologiczne **54**: 195–213.

Szeptycki, A. (1988): New genera and species of Protura from the Altai Mts. – Acta Zoologica Cracoviensia **31**: 297–362.

Talarico, G., M. F. Silva & G. Alberti (2006): Ultrastructure of tarsal sensilla and other integument structures of two *Pseudocellus* species (Ricinulei, Arachnida). – Journal of Morphology **267**: 441–463.

Tullgren, A. (1918): Ein sehr einfacher Ausleseapparat für terricole Tierformen. – Zeitschrift für Angewandte Entomologie **4**: 149–150.

Tuxen, S. L. (1955): The first record of Canadian Protura. With systematic notes on *Acerentulus*. – Entomologiske Meddelelser **27**: 113–128.

Tuxen, S. L. (1964): The Protura. A revision of the species of the world with keys for determination. – Hermann, Paris: 360pp.

Tuxen, S. L. (1986): Protura (Insecta), no. 9 – Fauna of New Zealand, Wellington: 52pp.

van Straalen, N. M., Timmermans, M. J. T. N., Roelofs, D. & M. P. Berg (2008): Apterygota in the spotlights of ecology, evolution and genomics. – European Journal of Soil Biology, **44**: 452–457.

Yin, W. Y. (1965): Studies on Chinese Protura II. A new family of the suborder Eosentomoidea. – Acta Entomogica Sin. **14**: 186–195.

Yin, W. Y. (1999): Arthropoda. Protura. Fauna Sinica. – Science Press, Beijing: 510pp.

Zacharuk, R. Y. & V. D. Shields (1991): Sensilla of immature insects. – Annual Review of Entomology **36**: 331–354.