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ORIGINAL PAPER

A scanning electron microscopic survey of the cuticle in Cyphophthalmi (Arachnida, Opiliones) with the description of novel sensory and glandular structures

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Abstract The cuticular surfaces of Cyphophthalmi (Opiliones) were studied in detail, covering a wide range of their taxonomic diversity. Previously unknown structures are described, including a sexually dimorphic row of spines and glandular openings on leg I of *Fangensis cavernarum*. Scanning electron micrographs of the prosomal paired hairs and the subapical process are provided for the first time. Evidence for the multi-pored nature of the shaft of solenidia as well as the hollowed nature and absence of wall pores of sensilla chaetica are also shown for the first time using scanning electron microscopy. The prosomal paired hairs may constitute a novel autapomorphy for Cyphophthalmi, as they are absent in all studied members of the other species of Opiliones. Finally, the variation in shape of some of the structures examined may be of great taxonomic value.

Keywords Glands · Sensilla · Sensory structures · Sexual dimorphism · Taxonomy

Introduction

The arthropod cuticle is the substrate to structures of great importance for obtaining environmental information (Keil and Steinbrecht 1984; Chapman 1998) and for the production of visual, acoustical, and chemical signals (Bradbury and Vehrencamp 1998; Greenfield 2002). Comprehensive knowledge of the sensory structures present in animals is the very first step toward understanding the sensory modalities to which they respond, a main goal of sensory ecology. Recognizing, for example, patches of setae used in courtship displays, stridulatory organs, or glandular openings, might be of great importance for studying signaling. For evolutionary biologists, cuticular structures may unravel relationships between taxa and have been of great use in systematics in a number of arthropod taxa (e.g., Arachnida: Zhang et al. 2004; Crustacea: Grygier and Ohtsuka 2008; Chilopoda: Edgecombe and Koch 2008; Hexapoda: Schuh et al. 2008).

Cyphophthalmi is the sister group to all other Opiliones, including 174 named species and subspecies of minute (<6 mm) mite-like animals inhabiting caves and the most superficial regions of soil, litter, and the underside of logs or rocks (http://giribet.oeb.harvard.edu/Cyphophthalmi/; Berland 1932; Juberthie 1964; Shear 1980). Behavioral data are scarce (e.g., Juberthie 1964, 1965; Schwendinger and Giribet 2005; Karaman 2005; Novak 2005), and few articles make inferences about the function of their cuticular structures, both sensory and glandular. However, systematists have long been using cuticular structures to infer phylogenies (e.g., Shear 1980; Giribet and Boyer 2002; de Bivort and Giribet 2004; Boyer and Giribet 2009; Clouse et al. 2009) which eventually help toward understanding important biogeographic patterns (e.g., Boyer et al. 2007b; Boyer and Giribet 2009).

Herein, we further explored the cuticular structures of this clade of harvestmen, aiming at unraveling additional

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taxonomic characters and at providing basic information for sensory ecologists. In addition to describing setae and trichomes shared with species of the other three groups of Opiliones (Eupnoi, Dyspnoi, and Laniatores), we report on previously undescribed spines, glandular openings, and slit sensilla and provide the first electron micrographs of two sensory structures, first described by Hansen and Sørensen (1904). We also provide evidence of the multi-pored nature of the shaft of solenidia and of the absence of wall pores and the hollowed nature of sensilla chaetica.

Material and methods

Bodies and appendages of cyphophthalmid specimens were coated with an Au–Pd film using a Denton Desk II sputter coater and then photographed on an FEI Quanta 200 scanning electron microscope (SEM). In addition to studying the hundreds of SEM images of adult Cyphophthalmi available in the database of the Department of Invertebrate Zoology at the Museum of Comparative Zoology, Harvard University, we produced 407 new SEM micrographs of seven focal species, including immature specimens, males and females. The species used for the micrographs were *Rakaia magna australis* Forster, 1952 (Pettalidae), *Ogovea cameroonensis* Giribet and Prieto 2003 (Ogoveidae), *Fangensis cavernarum* Schwendinger and Giribet 2005, *F. insulanus* Schwendinger and Giribet 2005, *F. leclerci* Rambla, 1994, *F. spelaeus* Schwendinger and Giribet 2005, *Stylocellus globosus* Schwendinger and Giribet, 2004, and an undescribed species of *Leptopsalis* from Bantimurung Bulusaraung N.P., Sulawesi Selatan, Indonesia (specimen voucher MCZ DNA101938) (Stylocellidae).

Results

Hansen’s organ

Multiple organs, measuring from ~30 to 45 μm in diameter, can be found on the cuticular surface of male and female specimens of the genus *Ogovea*, recognized by their circular shape, the several protuberances with rounded borders, and the few glandular openings among them. Herein, we present a SEM micrograph of a Hansen′s organ in the leg IV of *Ogovea cameroonensis* (Fig. 1a).

Prosomal paired hairs

We present for the first time a SEM micrograph of such structures (Figs. 1b, c) in immature *Rakaia magna australis*. It is a pair of frontal setae, close to each other, slightly posterior to the anterior margin of the prosoma. These hairs are almost cylindrical, tapering gradually and are shorter and thicker than the setae that surround them (*sensilla chaetica*). The shaft has a rough texture and is not striated like some *sensilla chaetica* (see below). The shaft measures from 28 to 32 μm.

Fig. 1 **a** Hansen’s organ in female *Ogovea cameroonensis*, leg IV. ► **b**, **c** Prosomal paired hairs; immature *Rakaia magna australis*. **b** Dorsal scutum, anterior region; *arrows* mark prosomal paired hairs. **c** Single hair. **d** Sensillum chaeticum (*Sc*) with shaft broken, showing its hollow nature and absence of wall pores; adult male *Rakaia magna australis*. **e**, **f** **Slit sensilla**; *Rakaia magna australis*. **e** Immature specimen. Latero-dorsal region of right leg I; *arrow* marks slit sensillum (*asterisk* shows the subapical process). **f** Adult male. Slit sensillum on the latero-dorsal region of right leg I (exact same region of 1e). Two glandular pores can be seen on the *bottom*. *AMP* anterior margin of the prosoma, *Chel* chelicera, *So* solenidium, *Tr* trichome

Sensilla chaetica

The shaft of the *sensilla chaetica* inserts on the leg within a basal membrane, forming an angle, in the cyphophthalmid species studied so far, of 70°–90°. The shaft is between 40 and 100 μm in length. We found clear evidence that the shaft is hollow and that the wall is not multi-perforated (Fig. 1d), as in those of Eupnoi and Laniatores. The sensilla chaetica may bear longitudinal ridges separated by narrow grooves along their length.

Slit sensilla

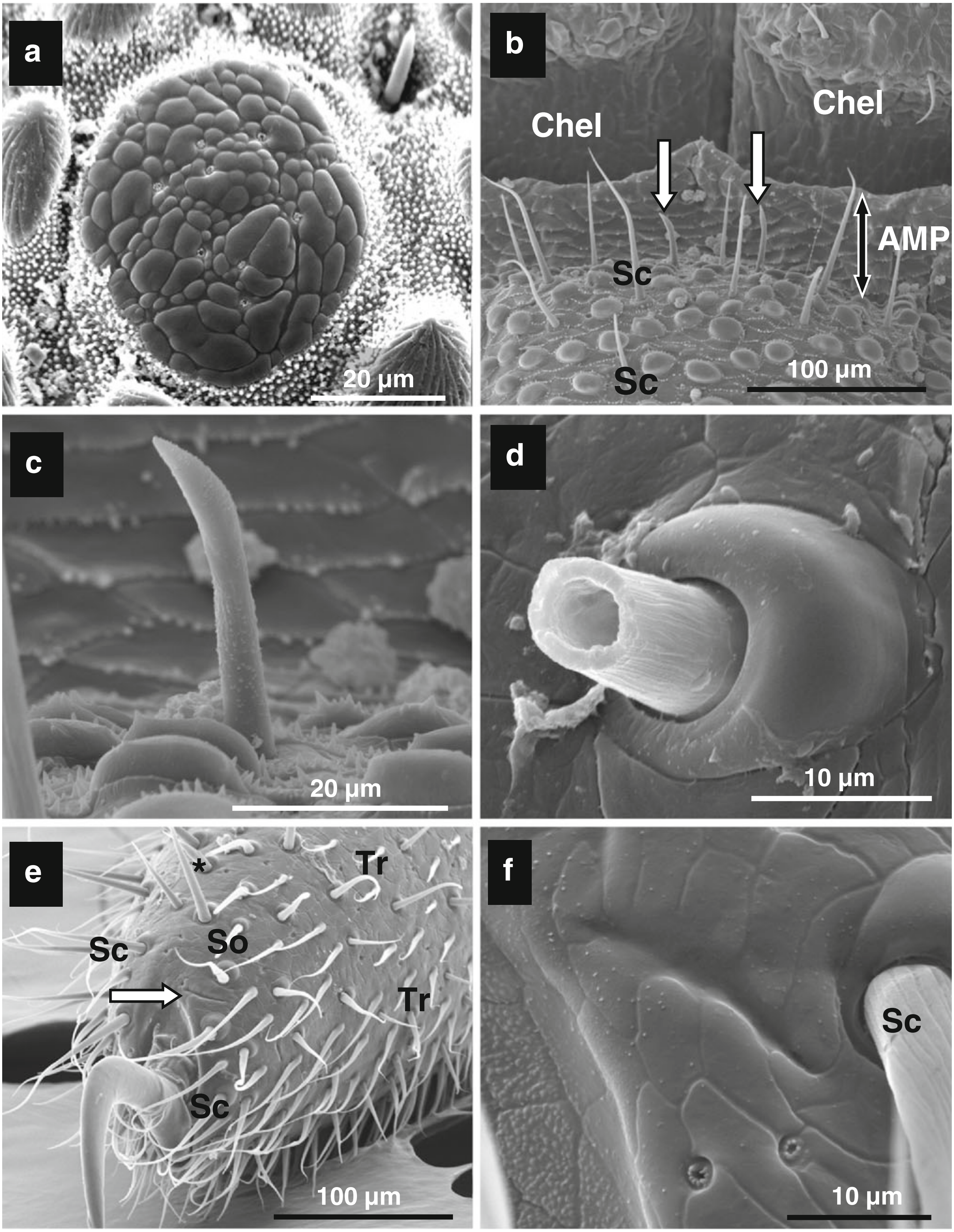
We found specific slit sensilla present on the latero-dorsal region, distally, on all four leg-pairs, both in the retro and prolateral regions of immature, males and females of *Rakaia magna australis* (Figs. 1e, f). They form a depression of elongated shape. The slits presented here measure between 15 and 16 μm. We did not find clusters of slits (lyriform organs).

Solenidia

These setae are defined by their obtuse end (Figs. 1e, 2a–d, 3a–c). Though there is variation among species in the number and length (from 30 μm in *Fangensis spelaeus* to 95 μm for the larger solenidia of *F. insulanus*), they can be easily recognized among sensilla chaetica and trichomes. Studying an additional number of micrographs, we found solenidia on legs I and II of species of all families. We provide the first SEM micrograph that clearly shows wall pores in the shaft of a solenidium in Opiliones (Fig. 2d).

Spines

Stylocellus globosus and the four species of *Fangensis* studied herein have a previously undescribed longitudinal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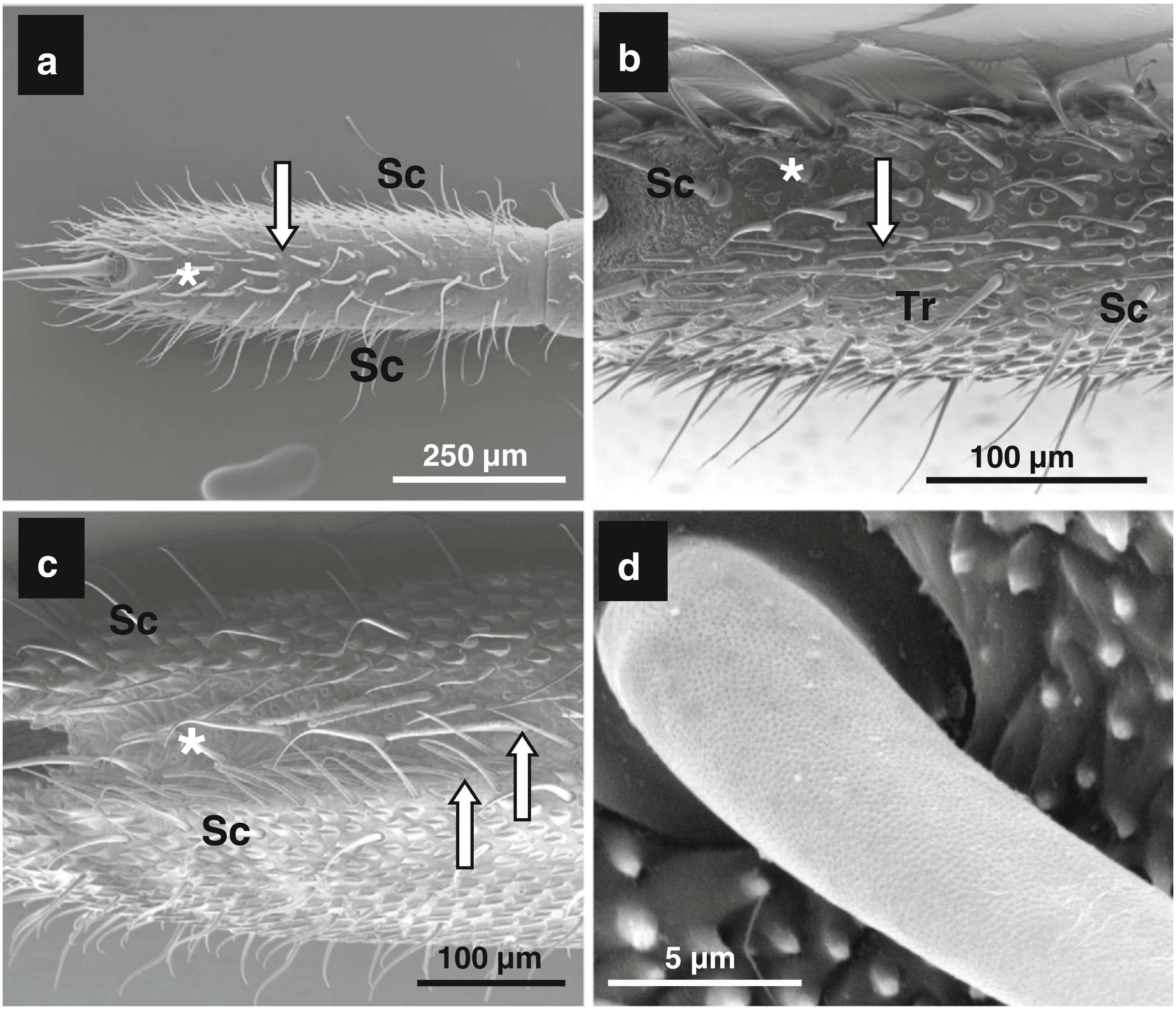

Fig. 2 Solenidia in Cyphophthalmi. **a** adult female *Rakaia magna australis*, dorsal region of tarsus of right leg II; solenidia marked by *white arrow*; (*asterisk* shows the subapical process). **b** Adult male *Fangensis leclerci*, dorsal region of tarsus of right leg II; (*arrow* marks solenidia; *asterisk* shows the subapical process). **c** Adult female *Fangensis insulanus*, dorsal region of tarsus of leg I. Two types of solenidia are present here, short (*left arrow*) and long (*right arrow*) (*asterisk* shows the subapical process). **d** *Leptopsalis* sp. from Bantimurung Bulusaraung N.P., Sulawesi Selatan, Indonesia (specimen voucher MCZ DNA101938), adult. Shaft of a solenidium showing its multi-pored nature. *Sc* sensillum chaeticum, *Tr* trichome

row of spines, pointing forward, on the ventral region of legs I and II (Fig. 4a, b). These are heavily built and do not have sockets, and their shafts are striated and do not bear visible pores on the wall (Fig. 4c). Though they are present in both sexes, there is sexual dimorphism in *S. globosus*, the males bearing more spines which are also closer together. The size of the spines is between 30 and 40 μm.

Subapical process

We present for the first time SEM micrographs of such a structure (Figs. 1e, 2a–c, 3a–d) in a number of species, in adult males, adult females, and immatures. It occurs on the distal third of the dorsal region of legs I and II, among solenidia. Though there is variation between species, their morphology within a species does not differ between stages and sexes. The shaft is always larger at the basal region and tapers toward the distal portion, but the degree of tapering as well as the length ratio between the thick and thin portions vary among species (*Fangensis leclerci* vs. *Rakaia magna australis*). Also, some species have a smooth subapical process (e.g., *F. leclerci*), whereas in others it has a rough texture (*F. spelaeus*). The distal portion can be more (Figs. 3b, d) or less curved (Figs. 3a, c), and the length varies from ~50 to 100 μm. Finally, in *Ogovea cameroonensis*, the subapical process emerges from a depression in the cuticle.

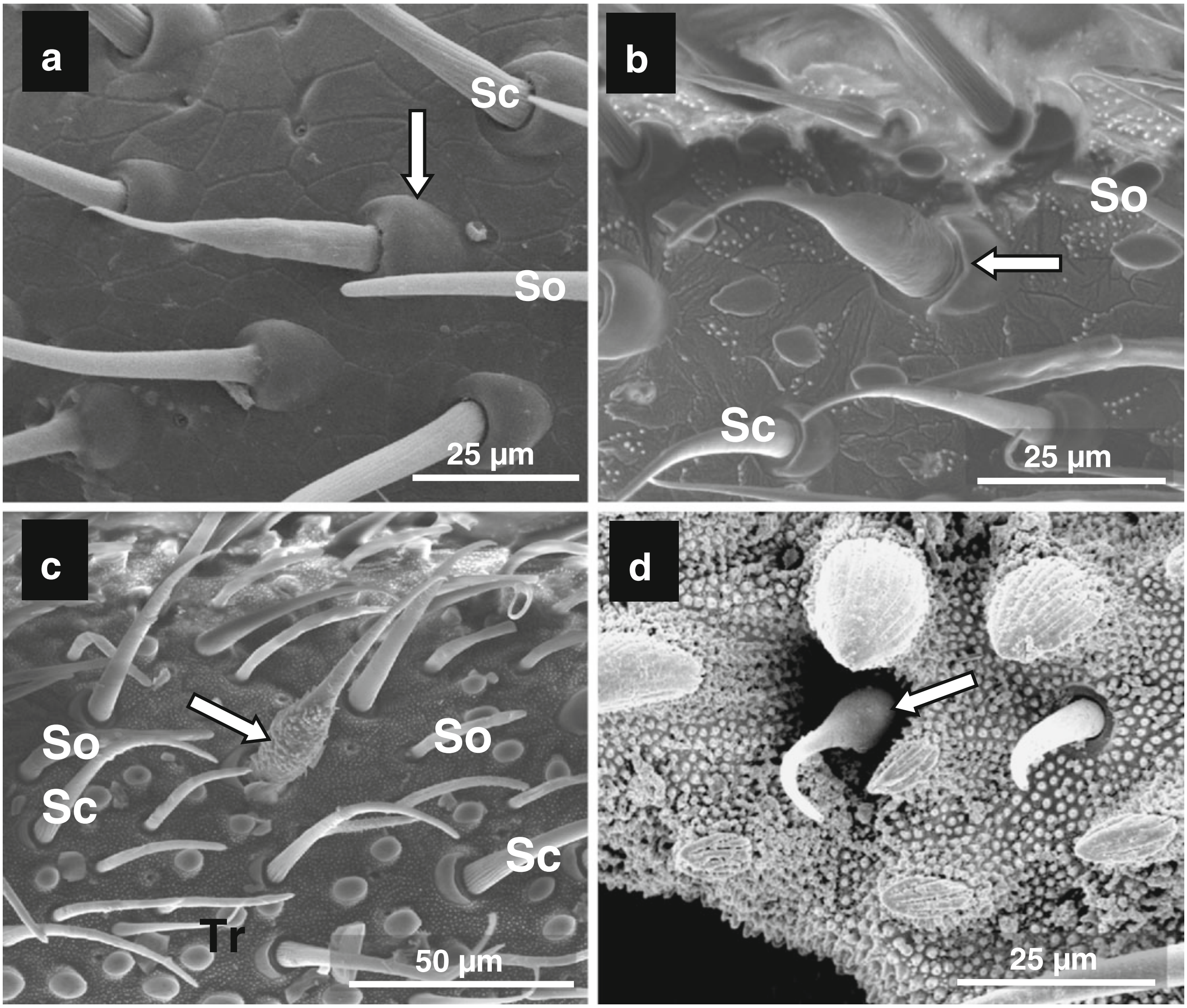

Fig. 3 Subapical process (*arrows*) in Cyphophthami. **a** Adult female *Rakaia magna australis*, dorsal region of tarsus of right leg I. **b** Adult male *Fangensis leclerci*, dorsal region of tarsus of right leg I. **c** Adult female *Fangensis spelaeus*, dorsal region of tarsus of right leg I. **d** Adult female *Ogovea cameroonensis*, dorsal region of tarsus of leg II *Sc* sensillum chaeticum, *So* solenidium, *Tr* trichome

Trichomes

The shaft of a trichome inserts directly in the cuticle (no basal membrane) forming an angle of ~15°–30°. The shaft is between 20 and 80 μm in length, and they are found only in the distal regions of the legs and pedipalp of all cyphophthalmid species (Figs. 1e, 2b, 3c, 4a). They have no terminal or wall pores and do not seem to deflect. Their arrangement is not patterned, and their density varies among species.

Glandular openings

We found previously undescribed glandular openings on the ventral region of legs I of *Fangensis cavernarum*, present only in males (Fig. 4a, d). The group of pores measures ~36 × 12 μm.

Discussion

Hansen's organs are present both in males and females of the Afrotropical genus *Ogovea*. They occur in all four coxae, near the socket where the trochanter's condyle inserts. In addition, coxae IV bear a larger one close to the gonostome opening (Giribet and Prieto 2003). They also occur on the femur, tibia and tarsus (two organs each), patella and metatarsus (one organ each) and abdominal sternites (Hansen 1921). The function of Hansen's organ is unknown. It is currently interpreted as an autapomorphy for

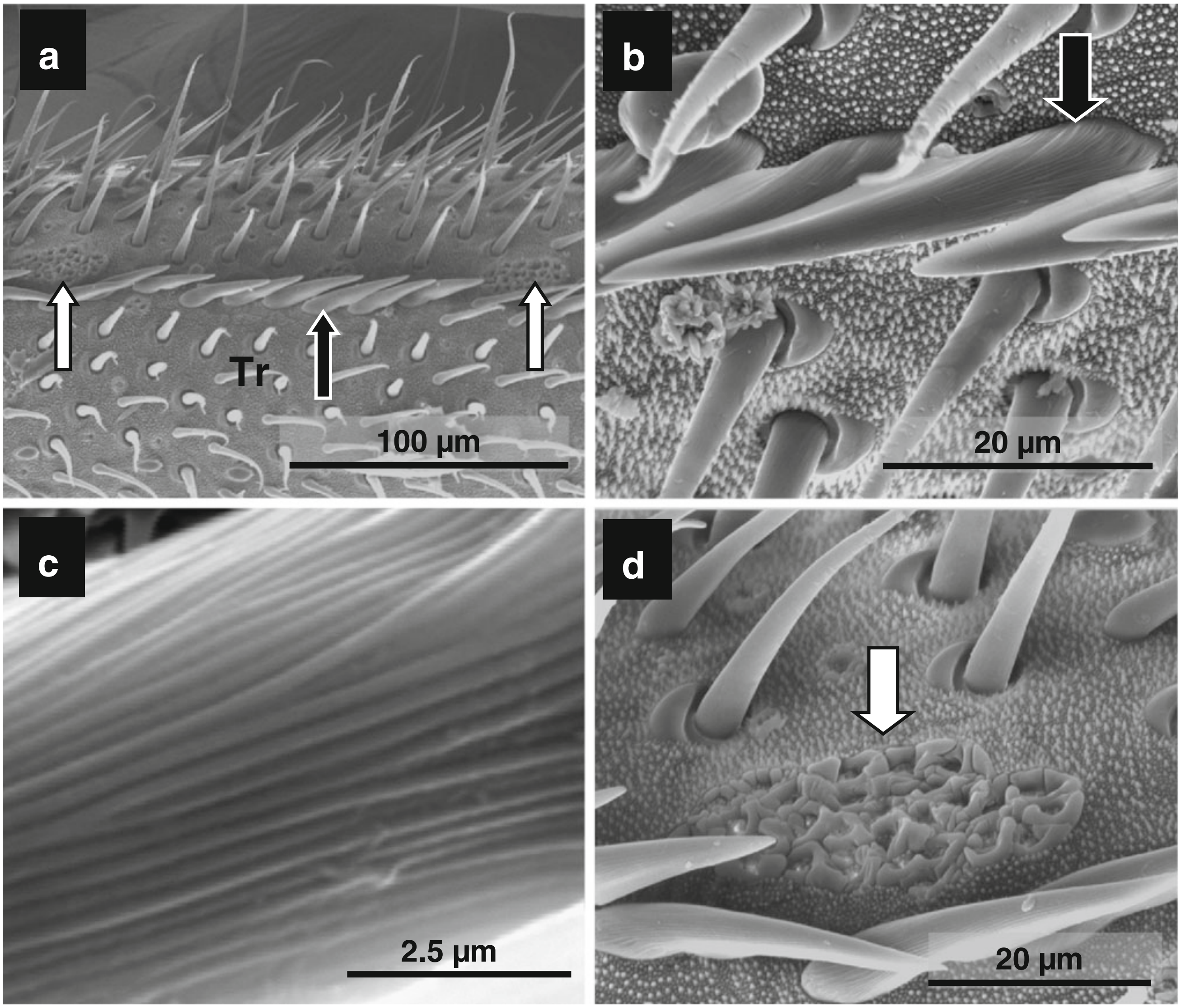

Fig. 4 Row of spines and glandular openings in Cyphophthalmi. **a** Adult male *Fangensis cavernarum*, ventral region of leg I. Row of spines (*black arrow* shows one spine) and glandular openings (*white arrows*). **b** Adult female *Fangensis cavernarum*, ventral region of leg I. Spine (*black arrow*). **c** Female of *Fangensis cavernarum*. Shaft of a spine showing its striated nature and the absence of wall pores. **d**. Adult male *Fangensis cavernarum*, ventral region of tarsus of leg I. Glandular openings (*white arrow*). *Tr* trichome

Ogovea (Giribet and Prieto 2003), although Juberthie (1970; pages 1378 and 1382) found them in males of the monotypic genus in *Metasiro*.

The prosomal paired hairs had never been previously illustrated with SEM, but Hansen and Sørensen (1904) already described them. Interestingly, they found setae different from the ones we report herein in *Rakaia magna australis*, for being "abruptly pointed at the apex (the most typical form, as in most species of *Purcellia*)". *Rakaia magna australis* have them tapering gradually, as in *Cyphophthalmus duricorius* Joseph, 1868 according to Hansen and Sørensen (1904). Rafalski (1958: Figs. 2, 3, 4) drew these hairs in *Cyphophthalmus duricorius* but did not mention them in the text. Their function remains unknown.

What we refer to as "*sensilla chaetica*" has been called "proper hairs" or "bristles" by Rafalski (1958). Juberthie (1979) used the term *sensilla chaetica,* and this term has been used for such sensilla since then (see references in Willemart et al. 2009a). They measure up to 200 µm in the leg II of *Troglosiro aelleni* (Juberthie 1979) and are found throughout the body of all species of Opiliones. S*ensilla chaetica* are thought to be contact mechano-chemoreceptors (Willemart et al. 2009a).

Hansen and Sørensen (1904) described "lines… (in which) the minute expanded point where the nerve terminates is always near the middle of the line". This is the description of a slit sense organ. According to Hansen and Sørensen (1904: 42), *Purcellia ilustrans* Hansen and

Sørensen 1904 males bear “lines” on the prosoma, abdominal tergites, on the first and second segments of chelicerae, femur, patella and trochanter of the pedipalp, coxae of leg I, and trochanter, femur, patella, tibia, metatarsus and tarsus of all leg-pairs. However, they did not mention the orientation relative to the body axis. On the ovipositor, they also found two “transverse lines”. Van der Hammen (1985) did not find slits in *Siro rubens* Latreille, 1804 and suggested that this absence may be related to the granulated micro sculpture of the tegument. No studies have been conducted on topography, histology or sensitivity of these sensilla in cyphophthalmids, and they have not been used as a taxonomic character. It is known, from studies conducted mainly on spiders, that slit sensilla are detectors of minute deformations in the cuticle, the latter being caused by muscular activity, hemolymph pressure, and by substrate-borne vibrations (Barth 2002).

Solenidia were first described in Opiliones, by Hansen and Sørensen (1904), in *Purcellia* and *Pettalus* (Pettalidae), *Ogovea* (Ogoveidae), *Siro* and *Parasiro* (Sironidae), and *Stylocellus* (Stylocellidae). They also reported their occurrence on the dorsal region of legs I and II, forming a row, in both sexes. Rafalski (1958: Fig. 14) illustrated such hairs in *Siro carpaticus* Rafalski, 1956. Juberthie (1979) called them “solénidions baculiformes” and “solénidions olfactifs”. Van der Hammen (1985: Fig. 22) also described and illustrated solenidia in the most distal segment of the pedipalps, appendages that bear solenidia also in more recently studied species (e.g., Giribet and Prieto 2003: Fig. 20). Outside Cyphophthalmi, these sensory setae have also been reported in Eupnoi and Dyspnoi (see Willemart et al. 2009a). Some setae present in Acari have also been called solenidia (see Ochoa et al. 2005), but the homology between these and those of Opiliones is doubtful. Foelix (1976) mentioned the occurrence of thin-walled hairs with wall pores, which correspond to olfactory setae in insects and arachnids (e.g., Altner and Prillinger 1980; Zacharuk 1985; Talarico et al. 2006), but he failed to mention the species or the body region where they were found. Most probably, he was referring to solenidia. Interestingly, these sensilla are found on the legs that have a sensory function in species outside Cyphophthalmi (Willemart et al. 2009a).

Juberthie (1979, 1988) described, in males and females of *Troglosiro aelleni* and *Austropurcellia scoparia* Juberthie 1988, a hair that occurs on the distal third of the dorsal region of legs I and II, among solenidia. The shaft of what he called “processus sensitive” tapers in the distal region, measuring ca. 50 μm in the former species. Van der Hammen (1985: Fig. 28) drew it on the leg I of *Siro rubens* but did not mention it in the text. Juberthie (2000) then described it in *Austropurcellia forsteri* (Juberthie 2000) and used the name we adopt here, “subapical process”. Like solenidia, these sensilla are found on the legs known to have a sensory function in species outside Cyphophthalmi (Willemart et al. 2009a). However, their function is unknown,

Finally, trichomes are probably non-sensory hairs that are found in all four groups of Opiliones. Willemart et al. (2009a) discussed the many names these structures have received in the recent literature. Trichomes probably help protecting the integument when in high densities. In Eupnoi, it has been shown that they help prevent the attachment of mites (McAloon and Durden 2000).

New characters for studying the evolution of cyphophthalmids

Cyphophthalmids are a great model for biogeographic studies due to their low vagility (e.g., Boyer et al. 2007a) and ancient age (e.g., Boyer et al. 2007b; Boyer and Giribet 2009; Murienne et al. 2010; Giribet et al. 2010). Many studies rely on morphological characteristics to reconstruct the phylogeny of the group (e.g., Shear 1980; Giribet and Boyer 2002; Giribet 2003; de Bivort and Giribet 2004; Boyer and Giribet 2009), and we now provide new characters that can easily be observed with the use of SEM.

The prosomal paired hairs, as noted by Hansen and Sørensen (1904), are absent in harvestmen belonging to Eupnoi, Dyspnoi, and Laniatores. They may therefore constitute an autapomorphy of Cyphophthalmi. Sensilla chaetica and trichomes are found in all species of Opiliones (Willemart et al. 2009a). Slit sensilla are found in all arachnids except palpigrades (Millot 1949; Pittard and Mitchell 1972; Weygoldt and Paulus 1979). Solenidia have been described in Cyphophthalmi, Eupnoi, and Dyspnoi but not in Laniatores (Hansen and Sørensen 1904; Willemart et al. 2009a). The glandular openings described herein are absent in most of the cyphophthalmids studied and deserve future study in more species. The subapical process may be another autapomorphy of Cyphophthalmi, since it has never been observed in harvestmen that do not belong to Cyphophthalmi. Its variation in shape could make a useful character for phylogenetic analysis. Finally, the previously undescribed row of spines found in a few species of cyphophthalmids is another potential character worth exploring further, whether the number of spines or the absence/presence. We hope to have provided additional structures that can be of value for taxonomic purposes and help understanding the evolution of this group of Opiliones.

Sensory ecology

Behavioral data on species of Cyphophthalmi is scarce, nothing is known about their sensory capabilities or how they communicate. Because they have tiny eyes in lateral position, when they have eyes at all, no trichobothria or metatarsal organs, they are probably non-visual and non-acoustical like most harvestmen (Willemart et al. 2009a). Herein, we provided evidence that they may communicate chemically, be it by contact chemoreception (using sensilla chaetica) or by olfaction (using solenidia). We therefore predict that chemicals are widely used by these animals in distinct behavioral contexts including sexual, since several sexually dimorphic glands are known in the group.

Sexually dimorphic structures

Sexually dimorphic structures are usually an indicative of a sexual role and the result of sexual selection (Andersson 1994). The occurrence of structures present only in male harvestmen has been known for centuries, being even observed by Aristotle (Savory 1962), but only recently their behavioral roles have been described (Martens 1975; Willemart et al. 2006, 2009b). Several sexually dimorphic structures have been discussed in cyphophthalmids: the adenostyle associated to the tarsus IV of males in all species of Cyphophthalmi; the anal and the sternal pore glands found in males of all families—now thought to be homologous structures (Giribet and Prieto 2003; Sharma and Giribet 2005, 2009)—and the cuticular structures associated to them, such as depressions (e.g., Troglosironidae), protuberances (Neogoveidae, Ogoveidae), tails (*Pettalus*), bilobed sternites (many Pettalidae), or trichomes (“scopulae” of Pettalidae); the modifications observed in the anal plates of males; the protruding anal plates of some female European *Siro*; or the Rambla’s organ observed in the retrolateral side of the male tarsus IV in several stylocellid species (Schwendinger and Giribet 2005; Giribet et al. 2007; Clouse et al. 2009). We now add two more, the ventral spines in *Stylocellus globosus* and the glandular openings on legs I of *Fangensis cavernarum*. The row of spines most probably does not have a sensory function, since they are strongly built, are not inserted in sockets, and are therefore not movable, and no pores could be detected on the shaft. They may have some mechanical function. The ventral glandular openings are structurally very similar to structures described in Laniatores (Willemart et al. 2010) and are also present in the tarsus of the leg but it is still premature to speculate about their function. Future behavioral studies may help understanding the exact role of these sexually dimorphic structures in cyphophthalmids.

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