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Ultrastructure of antennal sensilla of a prionine longhorn beetle, *Prionoplus reticularis* (White)

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ABSTRACT

Antennal sensilla are fundamental to an insects sensory perception of its environment. In species where one sex produces pheromones for attracting mates, we can predict antennal and sensilla morphology to be sexually dimorphic. *Prionoplus reticularis* White (Prioninae; Cerambycidae; Coleoptera) is a large longhorn beetle exhibiting a scramble competition polygyny mating system with sexual dimorphism present in antennae length, suggesting chemical cues are of importance in male mate searching. The present study aims to investigate the antennal ultrastructure morphology and sexual dimorphism in this species using scanning electron microscopy. Various sensilla were identified only in males: sensilla filiformia, sensilla auricillica, wall pore hairs, and distal sensilla chaetica. These sensilla are known to have chemosensory and mechanosensory functions in other insect groups, suggesting these sensory organs play an important role in male mating strategies.

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Introduction

An animal's perception of its surroundings is vital for its survival and reproduction, and for insects the antennae fulfil a key role in reception of sensory cues to inform behavioural decisions (Elgar et al. 2018). Antennae can be host to a variety of ultrastructures involved in mechanoreception, hygromoreception and thermoreception but are particularly associated with chemoreception (Schneider 1964). Chemoreception relates to the detection of chemical cues in the environment (Zacharuk 1980) and many insects are particularly influenced by such cues (Szyzka and Galizia 2015), using them to locate host plants or prey (Geier et al. 1999; Paschen et al. 2012), make decisions about food quality (Haverkamp et al. 2016), choose appropriate habitats and oviposition sites (Paschen et al. 2012), avoid predators (Kannan et al. 2022) and locate and select mates (Johansson and Jones 2007). Chemoreception can be further categorised into olfaction, analogous to smell and the perception of volatile molecules in the air, while gustation, analogous to

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taste, is the detection of non-volatile chemicals from surfaces (King and Gunathunga 2023). Whilst the antennae are comprised of just three units; the basal scape and pedicel, and a flagellum, these can be readily modified as reflected in the incredible diversity in antennal morphologies across insect taxa (Elgar et al. 2018).

The basic sensory unit of the antennae is a sensillum, which is an innervated ultra-structure comprised of sensory nerve cells, trichogen and tormogen cells, and sometimes auxiliary cells (Schneider 1964). Sensilla have been classified according to their structural morphology (e.g. peg and socket, hair, dome), wall thickness (e.g. thin-walled, thick-walled, single-walled, double-walled), presence and distribution of pores (e.g. terminal pore, wall pore, aporous, uniporous, multiporous, pitted, grooved) and innervation (e.g. number of sensory nerve cells, dendritic branching) (Altner and Prillinger 1980). Whilst it is problematic to label the function of a sensilla based on its morphology without supporting electrophysiological evidence, there are sometimes clues which can help us to provide a tentative role to a sensillum type; for instance many chemosensory sensilla will usually have pores visible in the cuticle, through which odour molecules pass (Altner and Prillinger 1980).

Darwin suggested that sexual selection, through female mate choice, could explain the seemingly bizarre array of traits that appear in some animal species (Darwin 1859). Sensory traits that improve the ability of males to discover females were also postulated by Darwin to be under the influence of sexual selection (Darwin 1871), but these have largely remained unstudied in the context of recent sexual selection research (Elgar et al. 2018). The reproductive benefit of finding a mate first can explain selection for longer antennae. For example, male gum-leaf skeletoniser moths, *Uraba lugens* (Walker), arriving at a trap containing a single female had, on average, longer antennae than males arriving at a trap containing two females, suggesting that longer antennae length improves the receptive ability of males to find a female pheromone plume at a lower concentration (Johnson et al. 2017).

In species of insects that rely on female sex pheromones to attract mates, we frequently observe sexual dimorphism in the antennae (Elgar et al. 2018). This may be obviously visible through an increase in antennal surface area through length of antennae and branching of the flagella, or, less visible to the human eye, through differences in the sensilla on the antenna (Elgar et al. 2018). Morphology, density, and distribution of sensilla have been shown to differ across a variety of insect orders. In the Mantodea, female sex pheromones are used by the false garden mantis, *Pseudomantis albofimbriata* (Stål), as sensory cues in mate finding, whilst the Eastern treerunner mantis, *Ciulfina biseriata* (Westwood), uses visual cues (Holwell et al. 2007). Sensilla basiconica, associated with olfaction, are only present on the antennae of males of *P. albofimbriata*. In contrast, *C. biseriata*, which used vision in mate searching, did not exhibit sensilla basiconica or dimorphism in the antennae (Holwell et al. 2007). Pheromones are well known in the Lepidoptera, and sexual dimorphism in antennal morphology is, unsurprisingly, common. Differences in the density and distribution of sensilla between sexes have been attributed to differences in importance of different sensory cues, e.g. female sex pheromones for males and host plant volatiles in females (Hansson et al. 1995; Castrejón-Gómez et al. 1999; Mark et al. 2018). Female produced sex pheromones in the smooth stick insect, *Clitarchus hookeri* (White), may explain the increased density of olfactory sensilla seen in males (Myers et al. 2015). In some cases, the driver of sexual

dimorphism of antennal ultrastructures can be less clear. This is the case with two species of closely related cave wētā (Orthoptera), *Pachyrhamma waitomoensis* (Richards) and *P. acanthoceras* (Milligan). Several sensilla subtypes associated with chemoreception are absent in males of *P. waitomoensis* that are not absent in males of *P. acanthoceras*, which may be due to differences in the structural complexity of the respective species' habitats (Fea et al. 2019).

Sexual dimorphism has also been found in the size, shape and distribution of antennal sensilla within the Coleoptera (Fukuda et al. 2016; Faucheux and Kundrata 2017; Faucheux et al. 2020; Pervez et al. 2020; Pervez et al. 2022). Sexual dimorphism is evidenced in the chrysomelid *Diabrotica virgifera virgifera* (LeConte) antennal sensilla, with males having pit fields containing both sensilla and glands producing esterase, an enzyme posited to break down female sex pheromone (Newman et al. 1993). In *Callosobruchus rhodesianus* (Pic) sensilla trichodea are more abundant in males than females (Fukuda et al. 2016). The differences between sexes suggest a functional role, correlating to ecological or behavioural differences between sexes. Understanding these variations can provide insights into the sensory ecology and evolutionary biology of beetles.

Distinctive long antennae are a characteristic feature of cerambycid beetles, giving rise to their common name – long horn beetles (Allison et al. 2004). Typically, the antennae are filiform, however, in some instances, these antennae may be strikingly modified, with comb-like flabellate flagellomeres, densely setose segments and, in one instance, a modified terminal flagellomere to form a venomous stinger (Berkov et al. 2008; Wang et al. 2017). Sexual dimorphism is common in the cerambycids, and this is often most pronounced in the antennae, with males having longer antennae than females (Zhang et al. 2011; Saikia et al. 2012; Rossi de Gasperis et al. 2018). This suggests that there may be sexual differences in the sensilla present on the antennae of cerambycids which allow for the detection of chemical cues of differing importance to each sex.

Within the cerambycids, there are seven major types of sensilla present on the antennae (recently standardised in Haddad et al. 2023) which are: Böhm sensilla, sensilla chaetica, chemosensory hairs (this term is used for any large, porous, hair-like sensilla, i.e. sensilla trichodea and porous sensilla chaetica which have been used interchangeably in the literature), sensilla basiconica, dome shaped organs (sensilla campaniforma), sensilla coeloconica and sensilla auricillica. Whilst only a few studies of sensilla in cerambycids have included electrophysiological data (Lopes et al. 2002; Wang et al. 2005; Álvarez et al. 2015; Wei et al. 2018), the likely function of a sensilla can be supported by evidence from studies in other groups.

The long horn beetle family, Prioninae, are particularly noted for sexually exaggerated antennae and the flagellomeres of the antennae can be serrate, pectinate, imbricate or flabellate (Linsley 1959). There is evidence to suggest that male and female prionines are both attracted to semiochemicals released by their host plant (Paschen et al. 2012), however only males respond to volatile female sex pheromones (Edwards 1961; Barbour et al. 2006; Rodstein et al. 2009; Paschen et al. 2012; Wickham et al. 2016). Mating systems with female produced sex pheromones, as found in the Prionine beetles, tend to fit the category of scramble competition polygyny, whereby males try to mate with as many females as quickly as possible (Dickinson 1992; Goldsmith and Alcock 1993; Goldsmith et al. 1996).

The huhu beetle, *Prionoplus reticularis* White (Cerambycidae: Prioninae), is the only member of the prionine family recorded across New Zealand (Sopow and Bain 2017).

The larvae feed on dead timber of native and exotic host plants (Edwards 1959; Sopow and Bain 2017). Adults are short-lived, non-feeding, large, and sexually dimorphic, with males having longer antennae than females (Edwards 1961). A male-attracting olfactory signal is produced by female *P. reticularis*, and it has been noted that females attract males whether they are visible or covered (Edwards 1961). *Prionopus reticularis* are also attracted to alpha – and beta – pinene lures suggesting that olfaction is important in the discovery of oviposition sites (note the sex of individuals arriving at the lure were not stated in this study; Pawson et al. 2020). Stimulation of the antennae of either males or females elicits a defensive response, where the head is raised and lowered, the antennae flail and the jaws are opened and will seize on anything they come into contact with (Edwards 1961). If this display occurs between two males, it can also lead to combat, with the pair grappling one another with fore legs to flip one another whilst the mandibles seize any object that they come into contact with (Edwards 1961).

There are a paucity of studies in the literature of antennal ultrastructures in prionines with only males from two species, *Titanus giganteus* Linnaeus, and *Prionus imbricornis* Linnaeus, imaged using scanning electron microscopy (SEM) (Dvořáček et al. 2020; Haddad et al. 2023). Both studies found the sensilla in prionines to be markedly different to other cerambycid sub-families, with an absence of sensilla chaetica and the presence of an unidentified sensilla resembling sensilla basiconica but unlike those found in other cerambycid groups. Dvořáček et al. (2020) suggested that sensilla chaetica are absent in Prioninae, however this requires further evidence.

In this study the ultrastructures of both male and female *P. reticularis* were investigated to assess whether there is evidence of sexual dimorphism present in antennal sensilla and to expand knowledge of prionine antennal sensory architecture.

Methods

Sample preparation

Specimens of *P. reticularis* were collected using a light trap at Riverhead Forest, Auckland, New Zealand in January 2021. The right-hand antennae were excised from male and female specimens (four of each sex). Following Haddad et al. (2023), the antennae were soaked in ethanol overnight, then rinsed in deionised water, and left to soak in dilute detergent overnight, before sonicating for 2–3 s at 60 Hz. This was repeated a second time before a final rinse in 70% ethanol and then soaking overnight in 95% ethanol. Antennae were mounted on stainless steel stubs with carbon adhesive tape then sputter coated with gold using a Leica EMACE200 (Leica Microsystems, Germany) for 60 s.

Scanning electron microscopy

Ultrastructural imaging was performed on a TESCAN CLARA field-emission gun scanning electron microscope (Tescan-Clara, Czech Republic) with the gun operated at 5 kV, a spot size of around 4 nm and a working distance between 11 and 12.5 mm. Images were taken of each segment of the antennae, from the scape to the ninth flagellomere. Figures were prepared using Adobe Photoshop 2020.

Terminology

Ultrastructures were classified based on their morphology, insertion, surface features, porosity (porous or aporous), and location of pores (wall or terminal pore). The naming convention used follows existing conventions (Dyer and Seabrook 1975; Altner and Prillinger 1980; Faucheux 2011; Ma et al. 2019; Abd El-Ghany and Abd El-Aziz 2021; Haddad et al. 2023), in particular the standardisation of cerambycid sensilla by Haddad et al. (2023).

Measurements

SEM Images were analysed in ImageJ v. 1.50i (Schneider et al. 2012). Following the methodology of Fea et al. (2019), we measured length of sensilla from the base to the apex for sensilla in both sexes. The mean and standard error are reported.

Results

The whole antennae of the adult male and female *P. reticularis* are shown in Figure 1A, B. Average (arithmetic mean) measurements for overall length of antennae and

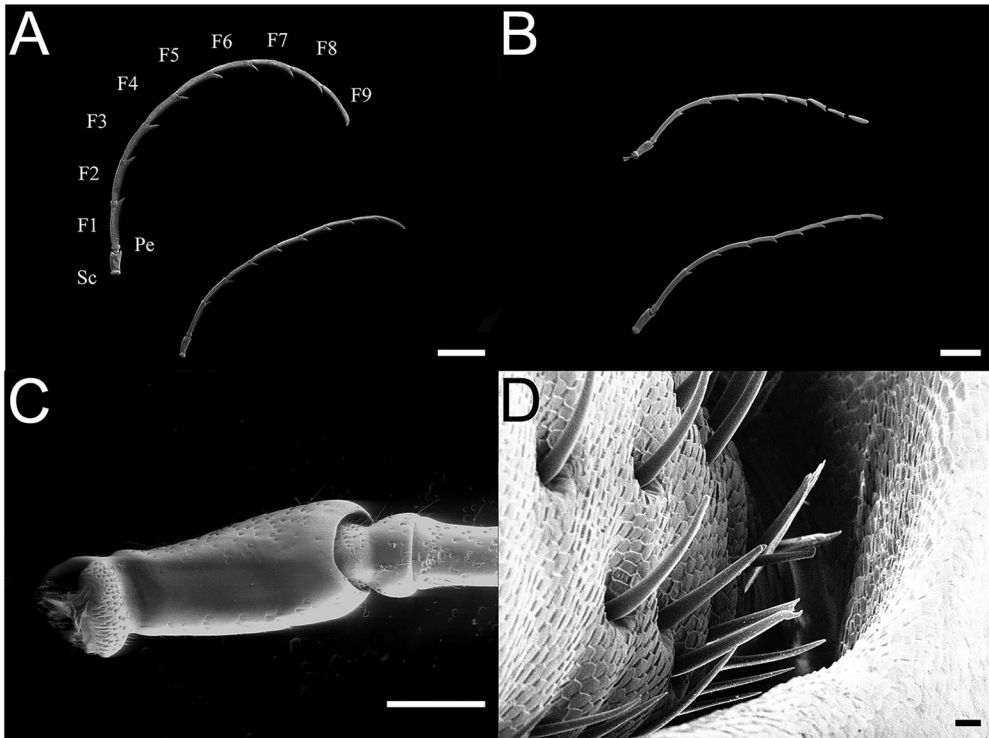


Figure 1. The ex-situ antennae of male (A) and female (B) *Prionoplus reticularis*. Individual antennomeres are labelled for one antennae, Sc = scape, Pe = pedicel, F1–9 = flagellomeres 1–9. Two individuals of each sex are presented to show variation between antennal size within the same sex. The scape and pedicel of a female are shown in greater detail (C) and a magnified view of the Böhm sensilla shown on a male pedicel (D). Scales: 5 mm (A), 5 mm (B), 1 mm (C), 20 μm (D).

antennomeres are presented in [Table 1](#). The antennae are serrate and comprised of the scape, pedicel, and the flagellum contains nine flagellomeres. The surface of the antennae is covered in cuticular scales that are roughly hexagonal in shape ([Figure 2A,D](#)) with the

Table 1. Average length of antennomeres in male and female *P. reticularis*.

Antennomere	Male			Female		
	<i>n</i>	Mean length (mm)	SD	<i>n</i>	Mean length (mm)	SD
Antenna Length	4	37.50	7.60	4.00	30.68	3.30
Pedicel	4	0.72	0.15	4.00	0.79	0.07
Scape	4	2.01	0.55	4.00	2.22	0.37
Flagellomere 1	4	4.25	0.88	4.00	4.79	0.70
Flagellomere 2	4	3.98	0.75	4.00	3.90	0.41
Flagellomere 3	4	3.97	0.70	4.00	3.46	0.39
Flagellomere 4	4	3.94	0.87	4.00	3.09	0.33
Flagellomere 5	4	3.87	0.80	4.00	2.97	0.27
Flagellomere 6	4	3.60	0.71	4.00	2.55	0.20
Flagellomere 7	4	3.54	0.74	4.00	2.35	0.11
Flagellomere 8	4	3.28	0.65	4.00	1.98	0.19
Flagellomere 9	4	4.35	0.80	4.00	2.59	0.28

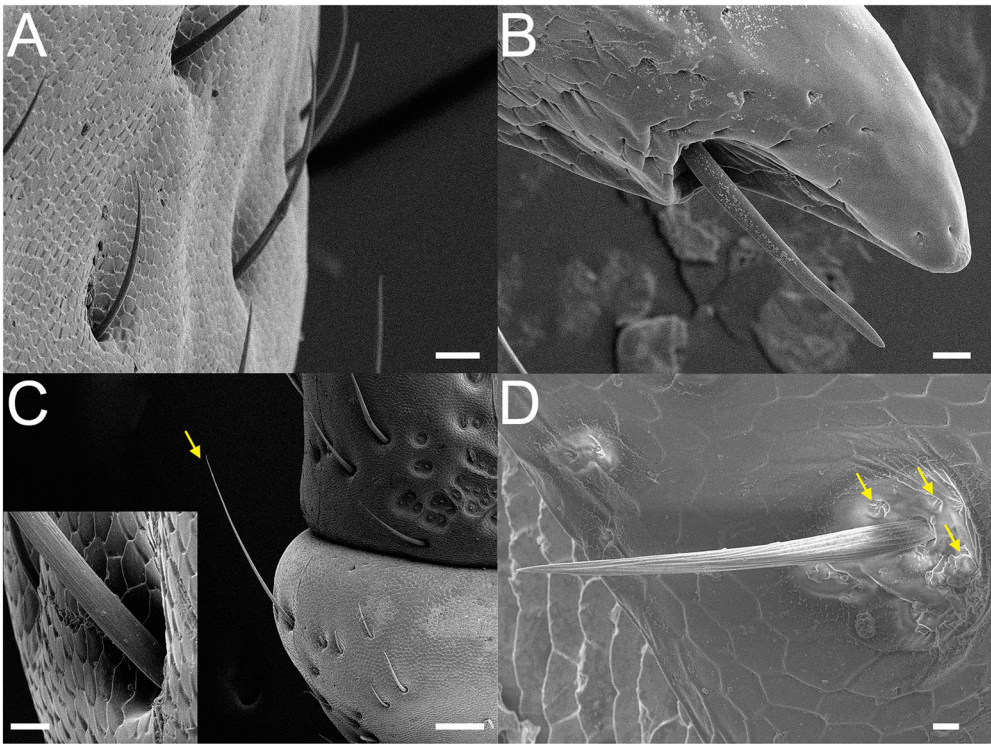


Figure 2. Aporous, stout sensilla chaetica present on the scape of a male, cuticular scales are visible (**A**). A single distal sensilla chaeticum with deep insertion on the distal protrusion of flagellomere 5 (**B**). A long sensilla chaeticum (yellow arrow), present on the pedicel of a male (**C**), longitudinal grooves on the surface of long SC (inset, **C**). A stout sensilla chaeticum on the flagellomere 5 of a female, showing characteristic glandular openings (yellow arrows) at the base with lower right hand gland exuding substance, hexagonal scales also visible on cuticular surface (**D**). Scales: 20 μm (**A**), 10 μm (**B**), 100 μm (**C**), 10 μm (inset, **C**), 5 μm (**D**).

exception of the base of the scape and the pedicel. The scape is cylindrical, with a slight kink on the lateral surface. The pedicel is pocillovovous (egg-cup) in shape, constricted at the mid-point before widening at the distal end (Figure 1C). Flagellomeres 1–8 are the same shape with a small sharp spur mirrored on both the lateral and medial faces and protruding on the distal, ventral edge, providing a serrated appearance to the antennae. The ventral surface of the antennae is densely pitted, with each pit containing several sensilla compared to the dorsal, medial surface which has fewer pits. The terminus of the ninth flagellomere is rounded and laterally compressed with well-defined pits. The male flagellomeres are densely covered in sensilla filiformia with flagellomeres 6–9 at least as long if not longer than flagellomeres 1–5. The female flagellomeres do not have the sensilla filiformia found in the males, however they are densely pitted and flagellomeres 6–9 are reduced, being smaller than flagellomeres 1–5. Average (arithmetic mean) measurements for individual sensilla length are presented in Table 2.

Böhm Sensilla

Böhm sensilla are present on the condyle, scape, and pedicel, particularly in the junction between these antennal sections (Figure 1C, D). The conical Böhm sensilla taper to a point and are set into a concave depression in the surface of the antennae. They are variable in length (Table 1) and have no visible pores on the surface for either sex.

Sensilla Chaetica (SC)

Distal, long and stout

Distal SC (Figure 2B) were observed on the serrate protrusions of the antennal flagellomeres, set within a deep socket. Distal SC were present on flagellomeres 1–8 and none observed on flagellomere 9. They are slightly striated, with blunt, pointed tips and aporous.

Long SC (Figure 2C) were rare and, if present, were found on the distal end of the scape and pedicel of both sexes. The surface of the long sensilla chaetica are aporous and striated with longitudinal grooves (Figure 2C, inset) with the apex terminating in a sharp point.

Table 2. Mean length of individual sensilla for both sexes (where present). n.b. one grooved peg sensilla was found on a female antennae, however the orientation was not conducive to measurement.

Sensilla Type	Male			Female		
	<i>n</i>	Mean Length (um)	SD	<i>n</i>	Mean Length (um)	SD
Bohm sensilla	11	67.12	24.4	7	72.19	24.37
Sensilla filiformia	70	327.23	42.5	–	–	–
Grooved peg sensilla	4	4.38	1.55	–	–	–
Sensilla auricillica	4	7.98	1.95	–	–	–
Sensilla basiconica broad	5	6.69	0.81	17	7.36	1.17
Sensilla basiconica thin	4	15.20	1.09	5	14.60	4.05
Sensilla chaetica distal	4	81.81	5.15	–	–	–
Sensilla chaetica long	1	385.77	–	3	429.50	68.59
Sensilla chaetica stout	20	78.58	19.7	5	83.55	45.29
Terminal pore hair	5	80.23	17.2	1	111.91	–
Wall pore hair	1	200.00	–	–	–	–

Of all the SC present, stout SC (Figure 2A, D) were the most numerous on both male and female antennae. They were present in greatest numbers on the scape and pedicel and the ninth flagellomere in females. They are shorter than other SC. In most cases they emerge from a narrow depression in the cuticle and lie flat along the surface of the antennae, their sharp tips pointing distally. The surface of the stout SC is aporous with a grooved wall and deeply striated with three corrugated openings present at the base, which occasionally exhibited exuded secretions (Figure 2D). The stout SC in females appear to be more deeply striated than the SC in males.

Sensilla filiformia

The flagellomeres on the male antennae are densely covered in long, aporous, ciliated sensilla filiformia that are not present on the female antennae (Figure 3A). These sensilla are characterised by their wavy, ciliated and flexible appearance, frequently entwining around one another which provide a slight pubescent appearance to the male antennae, distinguishable to the naked eye. Longitudinal striations run from the base of these sensilla up to around one third of the length of the structure (Figure 3D). Several sensilla filiformia were broken at the base or apex which revealed a hollow structure through

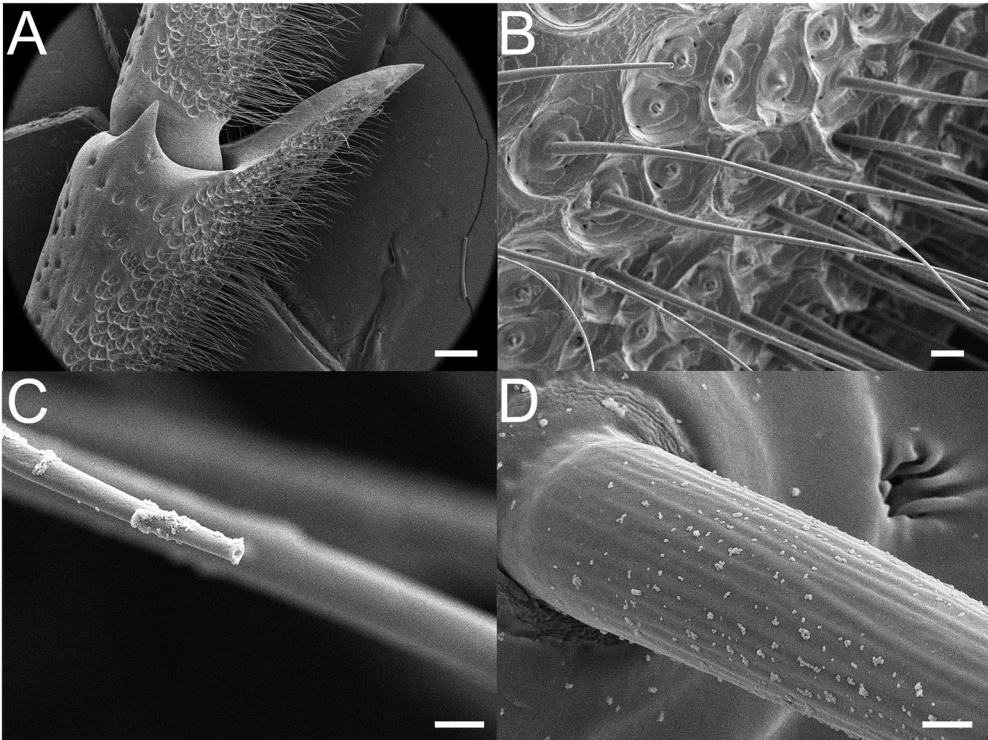


Figure 3. The ciliated appearance of the male antennae is derived from dense covering of sensilla filiformia shown here on flagellomere 2 (A). Sensilla filiformia emerge from a field of sensilla on the second flagellomere of a male. Glandular openings are visible surrounding the pits of various sensilla (B). The broken tip of a sensillum filiformium, exhibiting the hollow interior (C). The base of a sensillum filiformium showing the slight longitudinal striations (D). Scales: 200 μm (A), 20 μm (B), 2 μm (C), 5 μm (D).

its length (Figure 3B, C). The sensilla are situated in shallow insertions and surrounded by two to three corrugated openings (Figure 3B).

Sensilla basiconica (SB)

Stout (Type 1), thin (Type 2) and uniform (Type 3) sensilla basiconica

The ‘stout’ SB1 (Figure 4A, C) were present on all flagellomeres in both sexes, however they were more prevalent on females than males. They are shorter than ‘thin’ SB2 with a broader base and a blunt tip. The stout SB sits within a shallow socket on flagellomeres 1–8 and a much deeper socket on flagellomere 9. We found possible evidence of pores on the surface of the sensilla.

Thin SB2 (Figure 4A, B, D) were fewer than stout SB1 but present on all flagellomeres in both sexes. They are longer and narrower than stout SB1, have a sharper tip and are variable in size. They appear more frequently on the distal flagellomeres, particularly flagellomere 9.

On the ninth flagellomere of males, we found several SB that emerge from inside deep pits surrounded by cuticular collars (Figure 8). A stout SB1 was inset into a well-developed socket in the cuticle (Figure 8B). A thin SB2 showing the distinctive droplet shape at the tip is also present in a socket (Figure 8C). Finally, a smooth, uniform thickness SB3 with smooth walls and a uniporous, round tip was also present in deep sockets (Figure 8D) and only appeared on this terminal flagellomere.

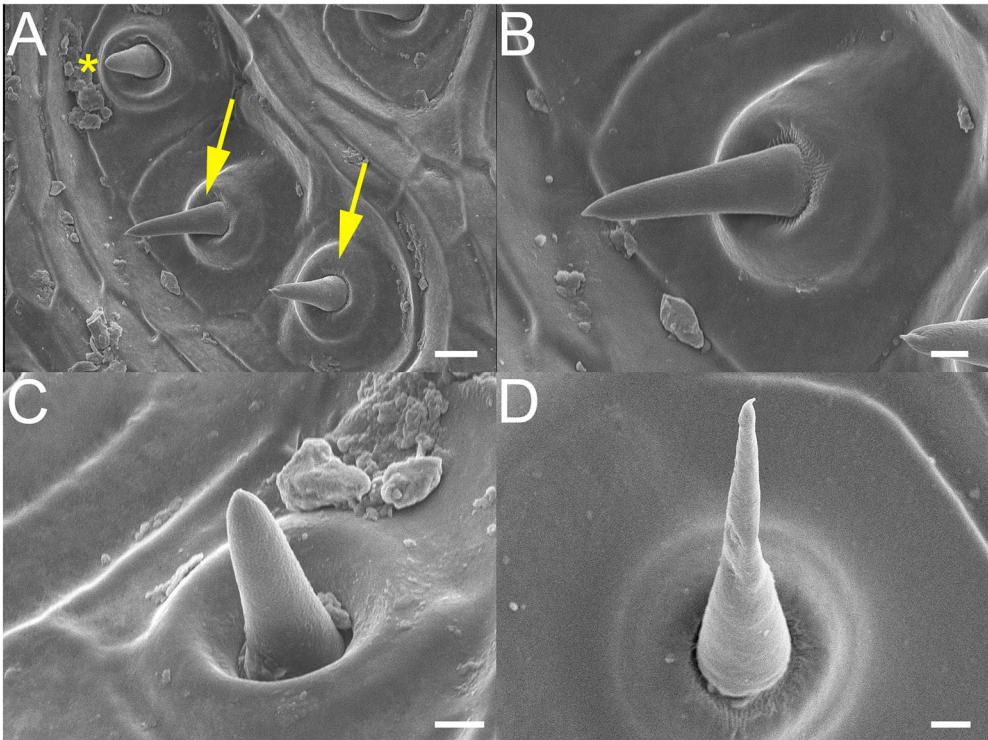


Figure 4. A single stout (asterisk) and two thin sensilla basiconica (arrows) within a depression on the pedicel of a female specimen (A). A thin sensillum basiconicum on the female pedicel (B). A stout sensillum basiconicum on the female pedicel (C). A thin sensillum basiconicum on the male fourth flagellomere (D). Scales: 5 μm (A), 2 μm (B), 2 μm (C), 2 μm (D).

Multi-porous grooved peg sensilla

Grooved peg sensilla (Figure 5) are a sub-type of sensilla basiconica that were infrequently found on flagellomeres 1–9 in both sexes but more prevalent in males. The sensilla are in broad, shallow, concave craters on the surface of the flagellomere. The base of the sensilla is broad, smooth, and circular in circumference, gradually tapering before narrowing distally to form deep, vertical grooves resembling digits.

Sensilla trichodea

Terminal pore hair and wall pore hair

We found one example of a possible wall pore hair sensilla (Figure 6A, B) on the ninth flagellomere of a male. The sensilla is long, straight and hair like (but shorter than the surrounding sensilla filiformia) with smooth walls. The surface appears to have rows of pores suggesting an olfactory role.

Terminal pore hair (Figure 6C,D) were typically found on the edges of flagellomeres, emerging from depressions in the cuticle and run parallel to the cuticle. The sensilla is

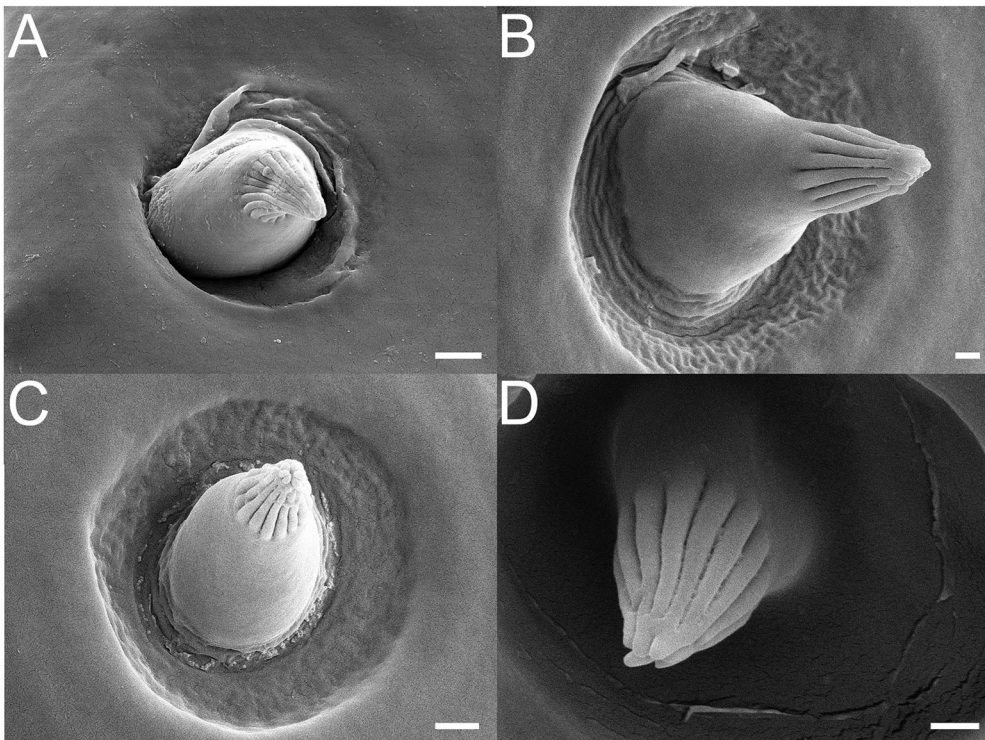


Figure 5. A multiporous grooved peg sensillum found on the pedicel of the female (A). A multiporous grooved peg sensillum found in a shallow depression on the second flagellomere of a male (B). A multiporous grooved peg sensillum found in a shallow depression on the second flagellomere of a male illustrating the variation in the base size of this sensillum (C). A multiporous grooved peg sensillum found in a moderate depression on the ninth flagellomere of a male illustrating the increase in depression depth on the terminal flagellum (D). Scales: 1 μm (A), 500 nm (B), 1 μm (C), 500 μm (D).

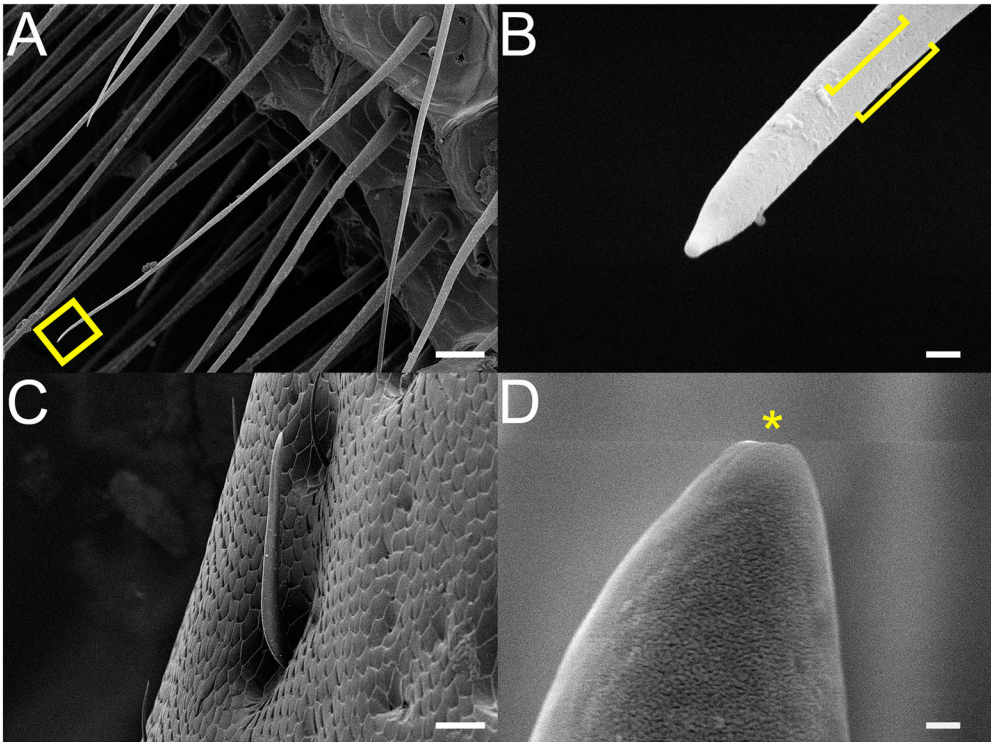


Figure 6. Proposed candidate for wall pore hair on the ninth flagellomere (box) (A), enlarged tip of wall pore hair, arrows showing lines of possible pores (B). A proposed candidate for a terminal pore hair (C) flagellomeres. A magnified view of the blunt tip of the sensillum in (C) showing pore at the apex (asterisk). Scales: 20 μm (A), 500 nm (B), 20 μm (C), 200 nm (D).

robust in appearance with a broad base rising to a blunt tip. There appears to be a furrow at the tip of the sensilla which may imply a terminal pore.

Sensilla auriculica

Sensilla auriculica (Figure 7) were irregularly present on flagellomeres 1–9 for males. They emerge from a broad socket with the antennal cuticle forming a collar around the base. The general appearance is similar to those found by Zhang et al. (2015), a conical sensillum that has been longitudinally compressed with a concave depression from the base to the apex giving the appearance of an ear with the apex terminating in a papilla. There was some variation in shape and torsion, with some having broader, rounder bases than others.

Glandular structures

Numerous rosette-like openings were present at the base of sensilla chaetica, sensilla filiformia, and sensilla basiconica (Figures 7B, D and 8C, D) which are epidermal glands with secretia observed.

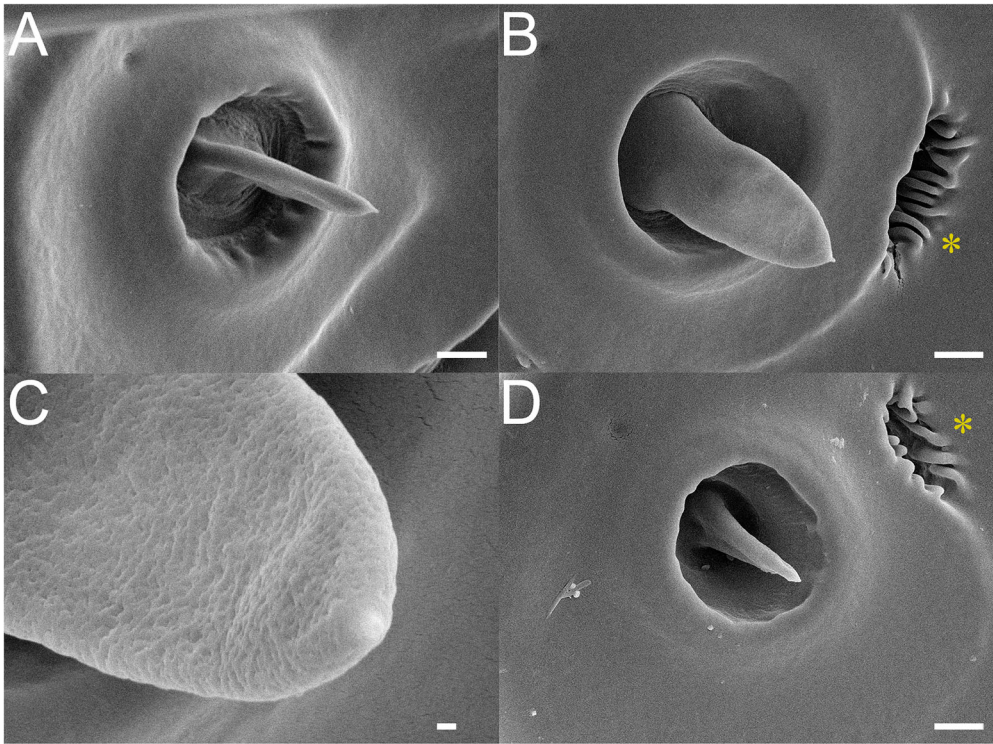


Figure 7. Sensillum auricullicum found on the first flagellomere (**A**), a sensillum auricullicum on the sixth flagellomere demonstrating a broader, flatter shape (**B**), rosette-like openings (**B**, yellow asterisk), an enlarged view of **B** showing the numerous pores on the surface (**C**), sensillum auricullicum on the sixth flagellomere with a shorter, narrower profile and torsion (**D**), rosette-like openings (**D**, yellow asterisk). Scales: 2 μm (**A**), 2 μm (**B**), 200 nm (**C**), 2 μm (**D**).

Discussion

We described the sensilla ultrastructures present on the antennae of male and female *P. reticularis* providing the first ultrastructure investigation of an endemic prionine and first investigation of a prionine in the Meroscelisini tribe. The most abundant antennal ultrastructures present on the antennae of both sexes, sensilla basiconica, are associated with chemoreception, further supporting the importance olfaction plays in this species perception of its environment (Edwards 1961; Pawson et al. 2020).

We found evidence of sexual dimorphism in the antennal sensilla, with several sensilla types only found on the male antennae. The most abundant ultrastructure, present only in males, were sensilla filiformia suggesting that these sensilla are important in male behaviour. Also present only in males, but in low numbers, were sensilla auricullica, wall pore hairs and distal sensilla chaetica. Grooved peg sensilla were common on male antennae but rarely seem on females. Sensilla auricullica showed a multiporous surface, suggesting a chemosensory function, and are proposed to be involved in the reception of female produced sex pheromones. The sensilla chaetica of the female antennae featured much deeper, more pronounced striae than male sensilla chaetica. Whilst the functional significance is unknown, the sensilla chaetica may be related to the

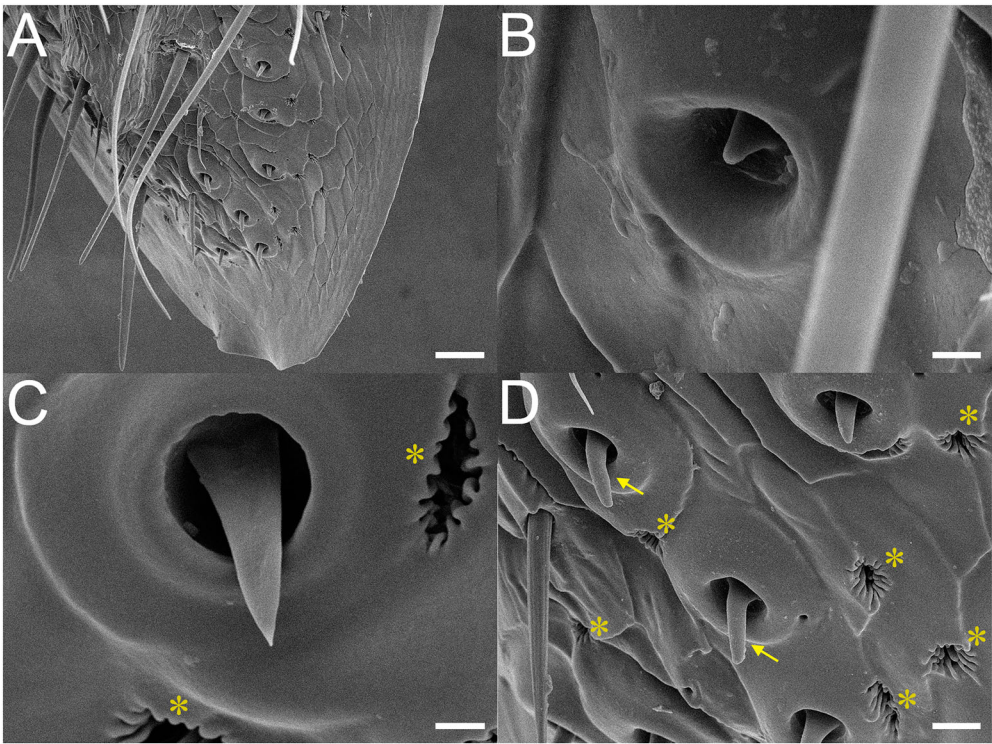


Figure 8. The tip of the ninth flagellomere of the male, showing the cuticular collars that enclose the sensilla (A), stout sensillum basiconicum (B), thin sensillum basiconicum with droplet shaped tip (C), rosette-like openings (C, yellow asterisk), smooth walled sensilla basiconica with uniform thickness and uniporous rounded tips (D, yellow arrow), rosette-like openings (D, yellow asterisk). Scales: 20 μm (A), 2 μm (B), 2 μm (C), 5 μm (D).

female assessing physical characteristics of suitable oviposition sites, as we have observed female *P. reticularis* using their antennae (and ovipositors) to interact with substrates prior to laying eggs (NWB, pers. obs.).

There are only two studies investigating the antennal ultrastructures of the Prioninae, both showing highly unusual antennal ultrastructures when compared to other cerambycid subfamilies (Dvořáček et al. 2020; Haddad et al. 2023). Similar to Haddad et al. (2023), we did not find dome-shaped organs (sensilla campaniforma) or peg-in-pits (sensilla coeloconica) present on the antennae of *P. reticularis*.

The antennae of both sexes of *P. reticularis* were covered in the sensory pits reported in the other two prionines in previous studies (Dvořáček et al. 2020; Haddad et al. 2023) and contained a sensillum similar in structure to the sensilla described variously as coeloconica (Dvořáček et al. 2020) and unidentified prionine sensilla (Haddad et al. 2023) which we suspect are both a type of sensilla basiconica. We agree that there are morphological differences to the sensilla basiconica found in other cerambycid subfamilies (Haddad et al. 2023) but suggest that these are likely still sensilla basiconica with three subtypes identified in *P. reticularis* – thin, broad and uniform. The sensilla in the sensory pits were typically surrounded by two to three corrugated, semi-circular glandular openings occasionally exhibiting a waxy like exudate that are seen in other

prionines, although the function of these is unknown (Dvořáček et al. 2020; Haddad et al. 2023).

Perhaps the most striking difference to other prionines is the dense pubescence of sensilla filiformia present on only the male antennae. This sexual dimorphism indicates that there is a role in reproductive behaviour, perhaps in mate searching or combat. Sensilla filiformia have been reported present in both sexes of the cerambycinine, *Phoracantha recurva* and are hypothesised to be mechanosensory receptors possibly related to wind detection (Faucheux 2011). In this species, both sexes scramble to reach an ephemeral resource, stressed *Eucalyptus* spp., which may indicate that whatever the cue these sensilla receive is equally important to both sexes.

Electrophysiological data in Orthoptera supports a mechanoreceptive role for sensilla filiformia, with detection of slight vibrations being of importance for predator avoidance (Gnatzy and Tautz 1980; Steinmann and Casas 2017). We can only speculate as to why sensilla filiformia are present in males. Whilst both males and females of *P. reticularis* are mobile, males likely spend more of their time in flight searching for females and could be perceived to need to process information relating to air movement (such as orientating to face the prevalent air current) or have an increased risk of encountering predators (such as the owl, *Ninox novaeseelandiae*, Edwards 1961). Other possible roles for mechanoreception in *P. reticularis* is in male–male combat and mate guarding. These sensilla may provide information relevant to fights, such as opponent size. Males engaged in mate guarding post-copulation outstretched their antennae and attempted to orientate themselves towards individuals that make contact with the antennae (NWB, pers. obs.). These sensilla would be excellent candidates for electroantennography and transmission electron microscopy work in the future combined with behavioural experiments.

Sensilla are fundamental to how insects perceive their surroundings and understanding the sensilla present on antennae can allow us to make inferences into the life history of a species and its sensory ecology. Sexual dimorphism in the types, distribution, and morphology of antennal sensilla suggest that sexual selection is acting on the antennae and, in the case of *P. reticularis*, provides evidence for the importance of chemical cues for males in mate-searching. We also suggest that future research should explore the role of sensilla filiformia in males, which may provide further insight into the mating system of *P. reticularis*.

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