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The antennal sensory array of the nocturnal bull ant *Myrmecia pyriformis*

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ABSTRACT

Insects use antennal sensilla to not only detect chemical and mechanical cues but also to sense changes in temperature, humidity and CO_2 levels. Very little is known about the variation in numbers, size and structure of sensilla in ants. Here we describe in detail the array of sensilla on the apical segment of the antennae of the nocturnal Australian bull ant *Myrmecia pyriformis*. Using scanning electron microscopy techniques we identified eight types of sensilla: trichodea curvata, basiconica, trichodea, coelocapitular, chaetica, trichoid II, ampullacea and coeloconica. Mapping the spatial location of each sensillum revealed distinct distribution patterns for different types of sensilla which were consistent across different individuals. We found, in most cases, the number of sensilla increases with the size of the apical antennomere, which in turn increases with body size. Conversely, the size of sensilla did not appreciably increase with the size of the apical antennomere. We discuss the size, numbers and distribution of sensilla of *M. pyriformis* compared to other ant species. Lastly, given the inconsistent use of sensillum nomenclature and difficulties associated in reliable identification we have attempted to consolidate the ant sensilla literature to make possible interspecific comparisons.

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1. Introduction

The antennae and the compound eyes represent the main sensory organs which provide information about an ant's surroundings. While compound eyes are theoretically well understood, this is not the case for many aspects of insect antennae. This is hardly surprising as antennae are complex sensory arrays studded with different types of sensilla which process a range of inputs in different modalities. They also vary markedly in appearance, despite a common underlying architecture.

The gross external morphology of sensory sensilla is given by the outer cuticular element and generally follows the same basic structure (Frazier, 1985). An outer hair, peg or other stimulus conducting structure is attached to a socket or protrudes through an opening (or more correctly an invagination) in the cuticular surface (Altner and Prillinger, 1980). Some sensilla are found sunken within the antennal lumen but these still follow a similar general structure. The morphology of the external cuticular elements is, at least in part, dictated by the function of the particular sensillum. For instance, chemoreceptors must have pores, slits or other inlets to allow molecules to penetrate into the lumen of the sensillum. This permits different types of sensilla to be identified, to a certain degree, based on external morphology alone (Nakanishi et al., 2009).

Apart from chemoreception, ant sensilla provide information about mechanical cues, humidity, temperature and CO_2 levels in the surrounding area (Fresneau, 1979; Ozaki et al., 2005; Roces and Kleineidam, 2000; Soroker et al., 1995; Wilson, 1972). Sensing these environmental conditions is important for most insects but it takes on additional importance in social insects where coordinating activities among individuals, living in an enclosed space and caring for young adds an extra layer of complexity to sensory requirements. Despite the heavy reliance of ants on their antennae, we know relatively little about sensilla, especially regarding their distribution and abundance. Some studies have addressed this in trail-following species, such as *Solenopsis invicta* (Renthal et al., 2003) and *Lasius fuliginosus* (Dumpert, 1972b), and also in tandem running and individually foraging ants, such as *Camponotus compressus* (Barsagade et al., 2013; Mysore et al., 2010) and *Dinoponera lucida* (Marques-Silva et al., 2006), respectively. Furthermore, an initial attempt towards comparing the morphology of sensilla across the ant phylogeny was made (Hashimoto, 1990a,b). However, the qualitative comparisons carried out in this case were made with different purposes in mind and, therefore, are of limited value without access to all of the raw data. Unfortunately, what is

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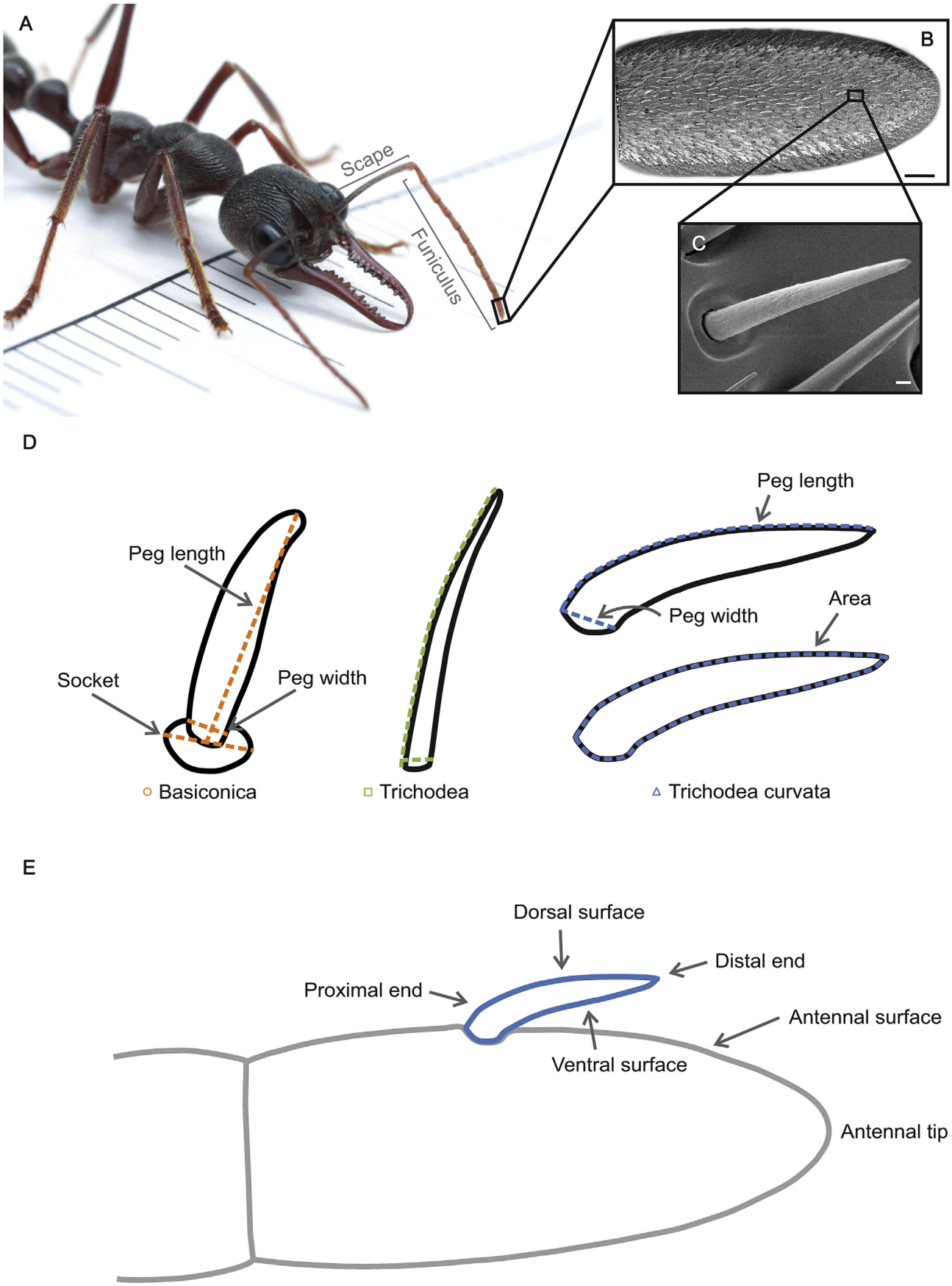

Fig. 1. The study species, *Myrmecia pyriformis*. (A) Profile view of the worker ant indicating the apical segment, the region of the antenna studied. Photo credit: Ajay Narendra. Scanning electron micrographs of the (B) apical segment of the flagellum and (C) a single sensillum. Scale bar = (A) 1 mm; (B) 50 μm; (C) 1 μm. (D) Schematics of sensilla basiconica, trichodea and trichodea curvata showing how different measurements were taken. (E) Schematic of sensilla trichodea curvata explaining dorsal and ventral surface of a sensillum as well as proximal and distal ends in relation with the rest of the antenna (drawing is not to scale).

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largely missing are comprehensive datasets containing basic information on the numbers, size and distribution of different sensillum types. These are necessary for thorough comparisons of the antennal arrays of different species.

Here, we studied the ant *Myrmecia pyriformis* (Fig. 1), which belongs to the Australian ant genus *Myrmecia* (Hymenoptera: Formicidae: Myrmeciinae). This genus is unusual among ants in having large eyes, a potent sting and workers that forage solitarily (Narendra et al., 2013; Reid et al., 2013). In addition, their morphology and behaviour are relatively unspecialised in comparison to other ants, which perhaps hints at the conditions under which eusociality in ants arose (Ward and Brady, 2003). This genus is speciose and ecologically diverse with different species being diurnal, crepuscular, or nocturnal (Greiner et al., 2007; Narendra et al., 2011). Our particular study species *M. pyriformis* emerges from the nest during the evening twilight, spends the night foraging on a single food tree, and returns to the nest in the morning twilight (Narendra et al., 2010). Workers of this species are polymorphic with a continuous gradient of body sizes and ants of all sizes appear to engage in foraging activities. Given their large size (12–26 mm (Narendra et al., 2011)), solitary foraging habits, and visually driven navigation, this species has been the subject of a number of studies on night vision and navigation (Jayatilaka et al., 2011; Narendra et al., 2011, 2010, 2013; Reid et al., 2011, 2013). The present study is part of a larger comparative project investigating the sensory costs of miniaturisation. We are particularly interested in the types of sensilla, their size, their shape variation and their distribution in the polymorphic nocturnal ant *M. pyriformis* and how these features compare across different species. Such comparisons are, however, difficult to make given the inconsistent use of sensillum nomenclature and the difficulties associated with reliably identifying different sensillum types. Hence, here we attempt to consolidate the known ant sensilla literature to make possible interspecific comparisons.

2. Methods

2.1. Study species

Worker ants were collected from a single colony located at the Campus Field Station at The Australian National University, Canberra (35°16′50.14″S, 149°6′42.13″E). Individuals used for scanning electron microscopy (SEM) analysis were killed by immersion in 50% ethanol and stored in vials until further processing. We studied the dorsal side of the apical antennomere in nine workers of varying size (1–9 in Table 1) and in addition compared the dorsal and ventral surfaces of the apical segment in a very small and a fairly large worker (1 and 7 in Table 1). A total of 78 workers were additionally photographed to determine the relation between body length and head width (Fig. 2).

2.2. SEM specimen preparation

Ants were photographed, and body length and head width were measured. Antennae were separated from the head capsule and mounted on aluminium stubs with adhesive, conductive carbon tape. The antennae were positioned with either the ventral or the dorsal side facing upwards and allowed to air dry. Samples were then coated with Au/Pd (60:40) for 2–4 min at 20 mA and observed using one of two instruments, either a Hitachi S-4300 SE/N scanning electron microscope or a Zeiss UltraPlus FESEM, under an accelerating voltage of 3 kV. To obtain images of the internal aspect of the apical segment, it was split with a scalpel blade. Soft tissue was removed by placing the resulting halves in 10% KOH solution for 12 h. The cleaned cuticle was then prepared for SEM observation as described above.

2.3. Analysis

We focussed mainly on the dorsal surface of the apical antennomere as this segment bears the largest number of chemo-, hygro- and CO_2- receptors in ants (Dumpert, 1972b; Jaisson, 1969; Mysore et al., 2010; Nakanishi et al., 2009; Renthal et al., 2003). Studying the dorsal region provided us the best opportunity to study all sensillum types in detail. Images were stitched, cropped and adjusted for contrast using CorelDRAW® Graphics Suite X5 (2010 Corel). No other modifications were made. The abundance of each type of sensillum was determined from the stitched images of the apical segment, with each image taken at $\times 1.5k$ magnification. Maps of the antennal tip showing the location of each individual sensillum were created using a Matlab (2007a Matworks Natick, Massachusetts) based custom-written program Digilite (Jan Hemmi and Robert Parker, The Australian National University). In most analyses we have used the apical segment length rather than area

Table 1
Numbers of each type of sensillum on the dorsal surface of the apical segment of *Myrmecia pyriformis*. The split level rows show the absolute number of sensilla (top) and the number of sensilla relative to the apical segment area (bottom, in italics). Each row represents a different worker ant labelled from 1 to 9. BL = Body Length (mm), HW = Head Width (mm), ASL = Apical Segment Length (μm), ASA = Apical Segment Area (μm^2).

	BL	HW	ASL	ASA	Basiconica	Trichodea	Trichodea curvata	Coelocapitular	Ampullacea	Coeloconica	Trichoid-II	Chaetica	∑
1	14.9	2.2	426	630	26	38	115	0	17	14	40	412	662
					0.04	*0.06*	*0.18*	*0.00*	*0.03*	*0.02*	*0.06*	*0.65*	*1.05*
2	14.1	2.4	456	670	36	64	135	1	24	13	36	484	792
					0.05	*0.10*	*0.20*	*0.00*	*0.04*	*0.02*	*0.05*	*0.72*	*1.18*
3	13.8	2.2	479	710	34	49	143	2	21	12	51	443	753
					0.05	*0.07*	*0.20*	*0.00*	*0.03*	*0.02*	*0.07*	*0.62*	*1.06*
4	16.9	2.8	521	890	57	63	147	1	24	24	81	633	1029
					0.06	*0.07*	*0.17*	*0.00*	*0.03*	*0.03*	*0.09*	*0.71*	*1.16*
5	20.5	3.8	612	1150	66	70	144	1	22	15	90	547	954
					0.06	*0.06*	*0.13*	*0.00*	*0.02*	*0.01*	*0.08*	*0.48*	*0.83*
6	19.2	3.6	618	1290	60	69	202	0	24	17	107	690	1169
					0.05	*0.05*	*0.16*	*0.00*	*0.02*	*0.01*	*0.08*	*0.53*	*0.91*
7	22.2	3.9	625	1090	61	64	176	4	26	21	92	705	1149
					0.06	*0.06*	*0.16*	*0.00*	*0.02*	*0.02*	*0.08*	*0.65*	*1.05*
8	22.4	3.9	689	1090	74	66	212	1	24	15	91	706	1188
					0.07	*0.06*	*0.19*	*0.00*	*0.02*	*0.01*	*0.08*	*0.65*	*1.09*
9	21.0	3.9	697	1290	85	81	216	0	21	26	105	697	1231
					0.07	*0.06*	*0.17*	*0.00*	*0.02*	*0.02*	*0.08*	*0.54*	*0.95*

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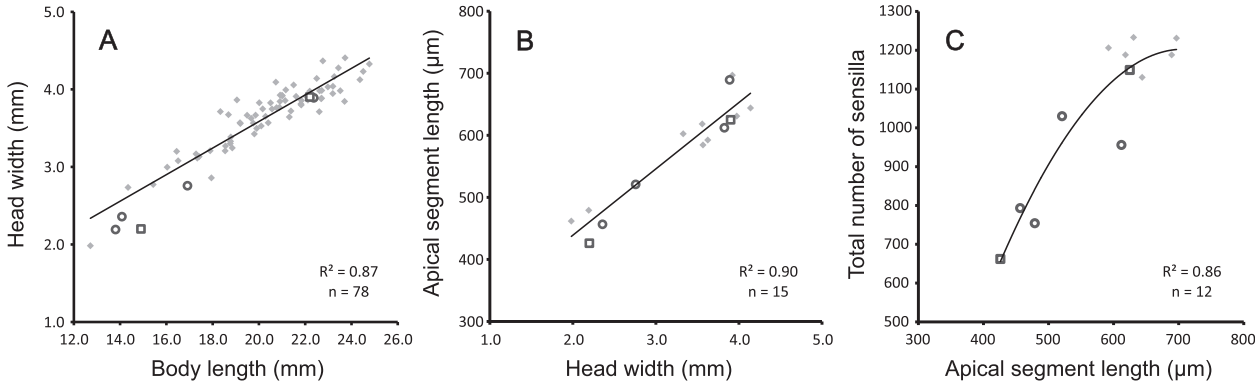

Fig. 2. Morphometric measurements in *Myrmecia pyriformis*. Relationship between (A) head width and body length, (B) apical segment length and head width and (C) total number of sensilla and apical segment length. Black open circles: represent the four individuals in Fig. 10; black open squares: represent the two individuals in Fig. 11; grey markers: represent other sampled individuals. A line of best fit is shown in black.

to represent size of antennomere. We provide information on both the apical segment length (ASL) and apical segment area (ASA), which in *M. pyriformis* are highly correlated ($R^2 = 0.986$). ASA has inherent errors acquired from measuring a curved surface, but is a good measure for representing sensillum density. In contrast, ASL is a more reliable measurement as it is does not take curvature into account. However, ASA may be more appropriate for inter-species comparison as it provides an accurate representation of apical segment shape. Hence, for most analyses we have used ASL to represent size of antennomere and used ASA only to represent sensillum density.

Eight distinct sensillum types were identified using previous descriptions of the external morphology in other ant species (Dumpert, 1972a,b; Hashimoto, 1990b; Kleineidam et al., 2000; Kleineidam and Tautz, 1996; Marques-Silva et al., 2006; Nakanishi et al., 2009; Ozaki et al., 2005; Renthal et al., 2003; Rutchy et al., 2009). In the past, different studies have used different nomenclatures to name sensillum types hampering comparisons. Here we

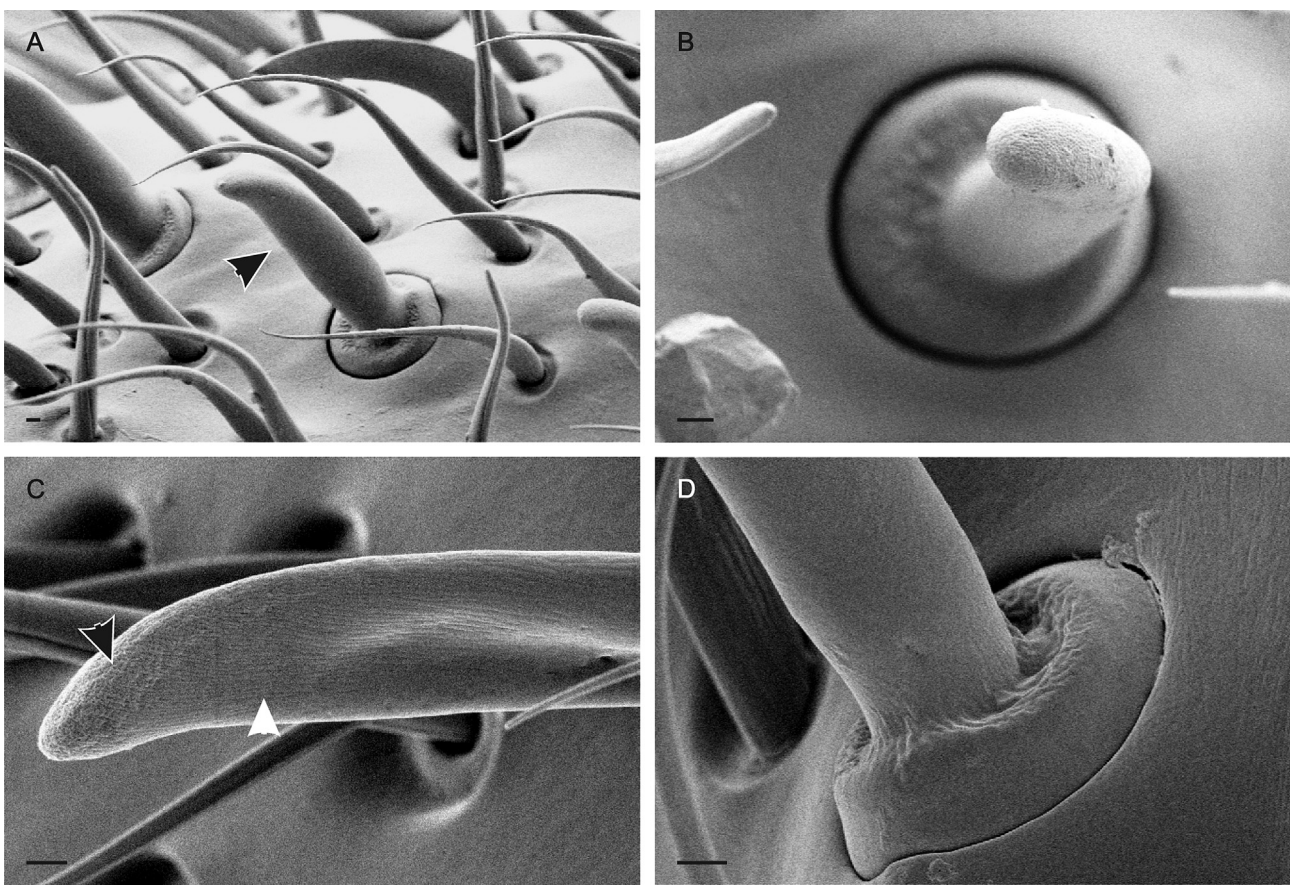

Fig. 3. Scanning electron micrographs of sensilla basiconica. (A) Overview of a sensillum basiconicum (black arrow) amongst other sensilla. (B) Top view of the sensillum shows a circular socket surrounding the base of the peg. (C) Pores cover the dorsal, distal surface of the peg (black arrow) and striations cover the proximal ventral surface (white arrow). (D) Structure of the socket and the base of the peg. All scale bars = 1 µm.

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Table 2
Dimensions of each type of sensillum on the dorsal surface of the apical segment of *Myrmecia pyriformis* (mean ± standard deviation). Peg l.: Peg length; Peg w.: Peg width. Measurements taken from all 9 individuals from Table 1. In the case of sensilla basiconica 'opening' refers to the maximum width of the socket, in sensilla ampullacea and coeloconica to the maximal width of the external opening of the sensilla and in trichoid-II sensilla to the maximum width of the opening in the cuticular surface around the base of the peg.

	Basiconica	Trichodea	Trichodea curvata	Coelocapitular	Ampullacea	Coeloconica	Trichoid-II	Chaetica
Peg l. (μm)	25.2 ± 2.1	25.8 ± 3.0	25.7 ± 3.1	N/A	N/A	N/A	32.8 ± 3.5	34.9 ± 7.1
Peg w. (μm)	3.9 ± 0.4	2.0 ± 0.2	5.1 ± 0.5	N/A	N/A	N/A	2.6 ± 0.3	2.0 ± 0.4
'Opening' (μm)	7.9 ± 0.7	N/A	N/A	1.4 ± 0.1	0.8 ± 0.1	2.5 ± 0.3	4.7 ± 0.4	N/A
Area (μm^2)	97.5 ± 15.2	35.5 ± 6.5	83.5 ± 12.2	1.4 ± 0.1	0.5 ± 0.1	4.1 ± 1.0	49.6 ± 7.7	38.0 ± 15.6
n (sensilla)	65	53	77	5	63	56	60	97

follow the nomenclature of Dumpert (1972b) as this has been most widely used and provides names for most of the sensilla we identified. For the only two sensilla not covered by Dumpert's nomenclature (1972b) we have used "trichoid-II sensillum" and "coelocapitular sensillum" as per Nakanishi et al. (2009). Additionally, for ease of comparison between studies the homologies in terminology have been listed in Appendix 1.

Measurements of individual sensilla were carried out using ImageJ 1.45 s (Rusband, National Institutes of Health, USA). For each sensillum type the length, diameter, and 2D area (see Fig. 1D for examples) were measured from at least five sensilla for each specimen. In the case of sensilla trichodea, trichodea curvata and trichoid-II sensilla a curved line was traced on the outer edge of the sensillum to measure the length (see Fig. 1D). In the case of other sensilla the longest straight line between the tip and the base was measured. Only 'above ground' structures were measured to determine the length of sensilla. For the width of sensilla and the diameter of sockets or openings we always measured the widest possible diameter. Measurements were only carried out on sensilla that were clearly imaged in full profile (Fig. 1E). Sensilla that were at an angle, pointing away or towards the observer, were ignored. This ensured that the measurements taken were representative of the

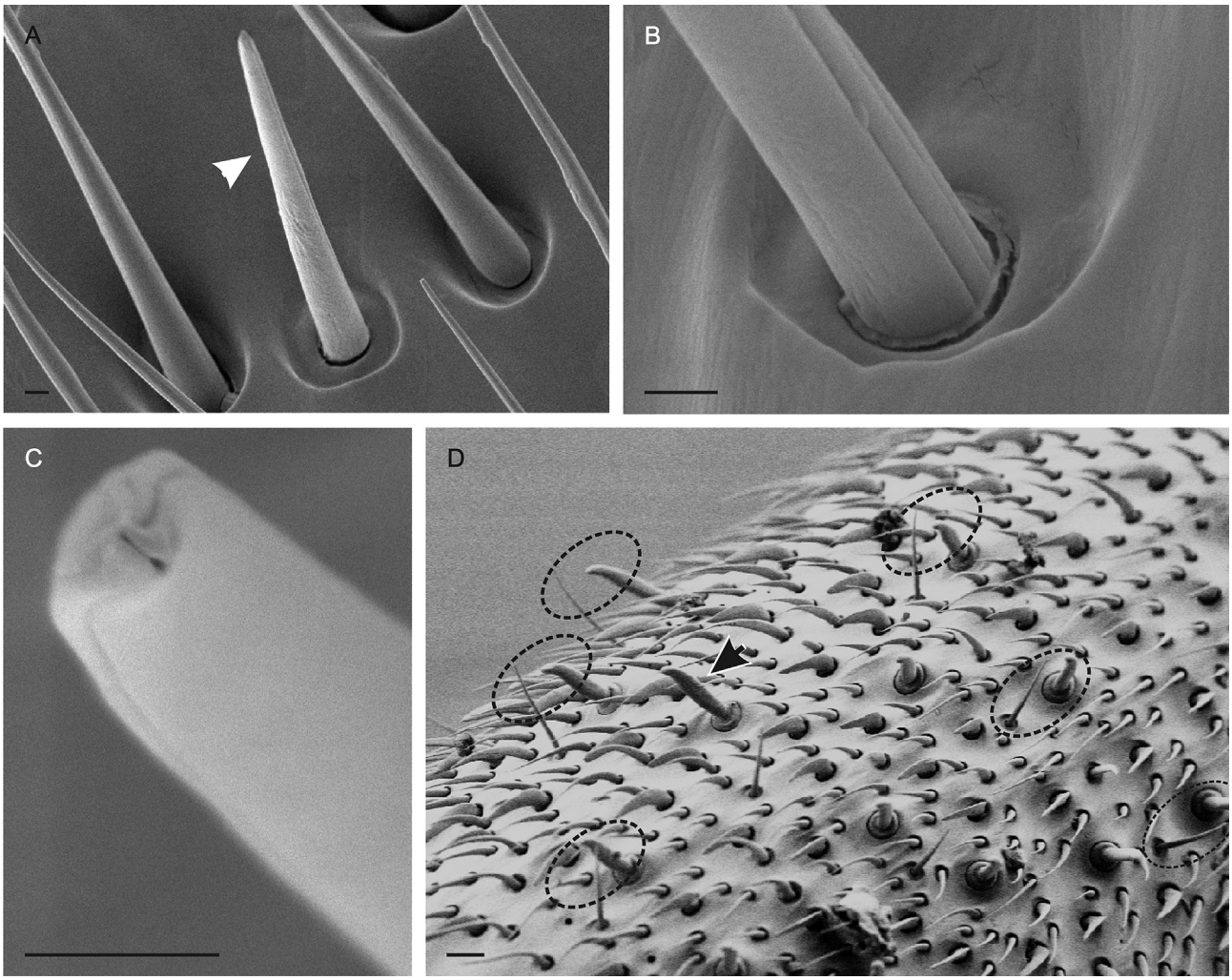

Fig. 4. Scanning electron micrographs of sensilla trichodea. (A) Overview of sensilla trichodea (white arrow) amongst other sensilla. (B) Base of the peg. (C) Peg tip shows a closed terminal pore and lateral grooves. (D) Paired basiconica and sensilla trichodea (dashed ovals) and unpaired sensilla basiconica (black arrow). Scale bars for (A), (B), (C) = 1 μm, (D) = 10 μm.

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true dimensions of sensilla but limited the sample size. When describing the anatomy of sensilla we use the terms ventral, dorsal, proximal and distal as indicated in Fig. 1E.

3. Results and discussion

3.1. Overview

Sensory hairs in *M. pyriformis* are located throughout most of the body but are most abundant and diverse on the 12-segmented antennae, particularly in the apical segment (Fig. 1A and B). Despite the minute size of the sensilla (Fig. 1C), their sheer density (Fig. 1B) sometimes makes them visible to the naked eye as fine pilosity. The body length of the workers studied ranged from 12.7 to 24.8 mm (Fig. 2A) with larger animals generally having larger heads (Fig. 2A) and larger apical antennomeres (Fig. 2B). The number of sensilla also increased with the size of apical segment (Fig. 2C, Table 1). We identified eight different types of sensilla on the apical segment of *M. pyriformis* with one, the coelocapitular sensillum, found mostly on the ventral region.

3.2. Morphology and function

This section outlines the external morphology of each type of sensillum and gives some indication of its function based on its anatomy and on evidence from previous studies. Some of the terminology used here, such as the 'dorsal' and 'ventral' sides of sensilla, and length of each sensillum are explained in the methods section above and in Fig. 1. We refer to the external apertures of pit sensilla as 'openings' as that is how they appear externally. However, they are not true openings into the underlying haemolymph, but depressions or invaginations of the cuticle.

3.2.1. Sensilla basiconica

These sensilla are one of the shortest (25.2 μm ± 2.1; $n = 65$) and have thickened pegs (3.9 μm ± 0.4; $n = 65$) with a rounded tip (Fig. 3A and B, Table 2). Pores are visible along the dorsal surface, particularly around the tip (Fig. 3C, black arrow), while striations cover the distal, ventral portion (Fig. 3C, white arrow). A thick, circular socket surrounds the base of the sensilla (Fig. 3B and D). This socket is elevated above the level of the antennal surface, similar to that of *Myrmecia gulosa* (Hashimoto, 1990b). These sensilla have not been observed in male ants (e.g., *Camponotus compressus*, Mysore et al., 2010). Anatomical, electrophysiological and behavioural evidence indicates that sensilla basiconica function as contact chemoreceptors (*Camponotus vagus*: Masson, 1974; *Camponotus japonicus*: Ozaki et al., 2005).

3.2.2. Sensilla trichodea

These sensilla have slender pegs (width = 2.0 μm ± 0.2; $n = 53$), which are comparable in length to sensilla basiconica (25.8 μm ± 3.0; $n = 53$). They have deep longitudinal grooves (Fig. 4A–C) and an apical pore which was always observed in an either closed or collapsed state as seen in Fig. 4C (this may be due to desiccation or to the high vacuum in the SEM column). The peg inserts into an opening surrounded by a region of smooth slightly

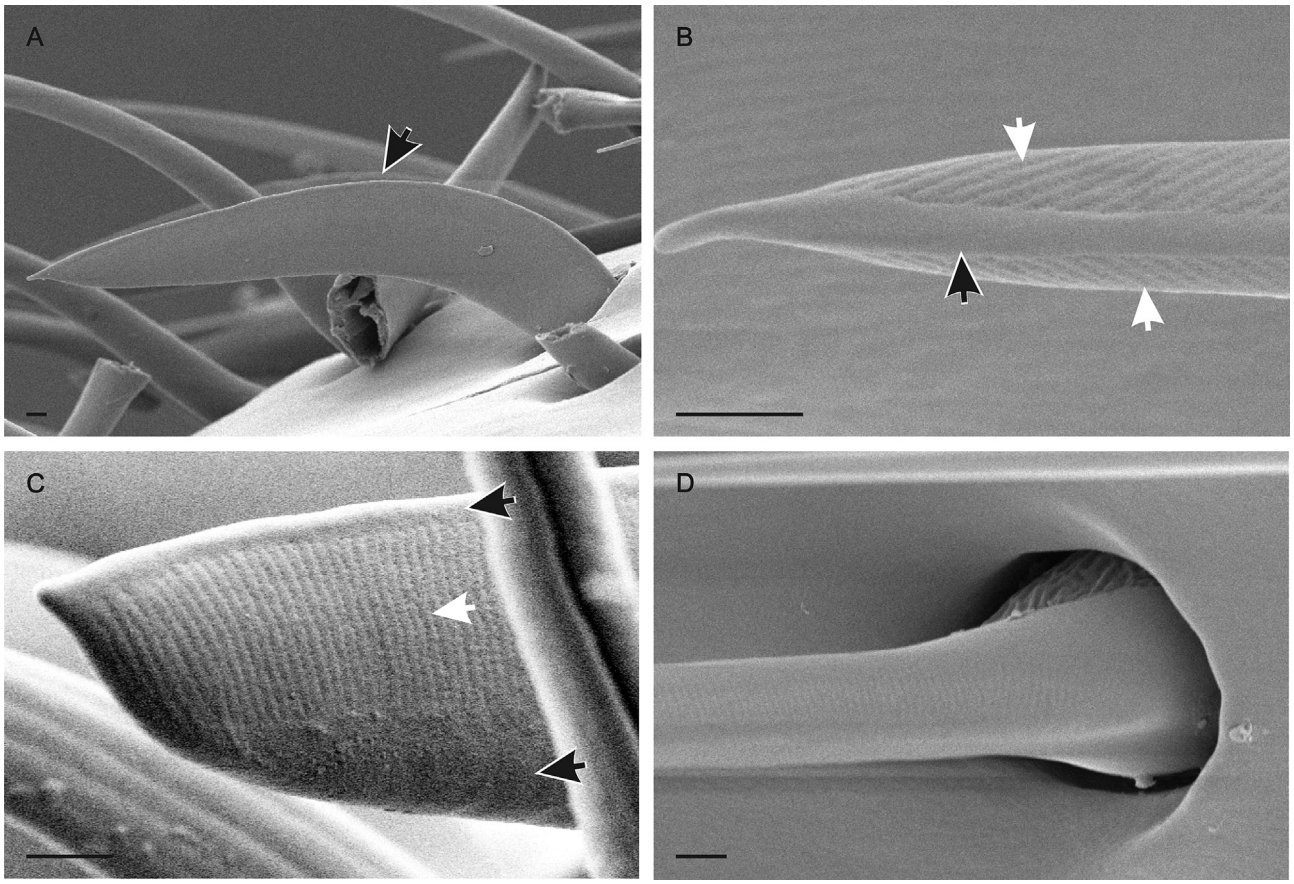

Fig. 5. Scanning electron micrographs of sensilla trichodea curvata. (A) Overview of a sensillum trichodeum curvatum (black arrow) amongst other sensilla. (B) Sensillum tip shows bands of pores on either side of the peg (white arrows) with an unperforated band at the top (black arrow). (C) Lateral aspect of the peg tip shows rows of pores (white arrow) and unperforated regions (black arrows). (D) Base of the peg and insertion. All scale bars = 1 μm.

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depressed cuticle of oval shape (Fig. 4B). In contrast to other sensilla that are angled towards the tip of the antenna, these sensilla project almost perpendicularly from the antennal surface, which makes them quite conspicuous. We are unaware of any studies that have identified the function of sensilla trichodea, but their close association with sensilla basiconica and the presence of a large terminal pore in many ant species suggest that they may function as contact chemoreceptors (see Hashimoto, 1990b).

3.2.3. *Sensilla trichodea curvata*

Unlike most other sensilla, the peg is not comprised of a tapering cylinder but is instead bilaterally flattened and strongly bent towards the antennal tip (Fig. 5A). As a result they are quite wide (5.1 μm ± 0.5; $n = 77$) for their length (25.7 μm ± 3.1; $n = 77$). These sensilla have pores arranged in a band of transverse rows that narrows proximally. The pores are extremely small (approximately 0.04 μm) and collectively appear as grooves at low magnification.

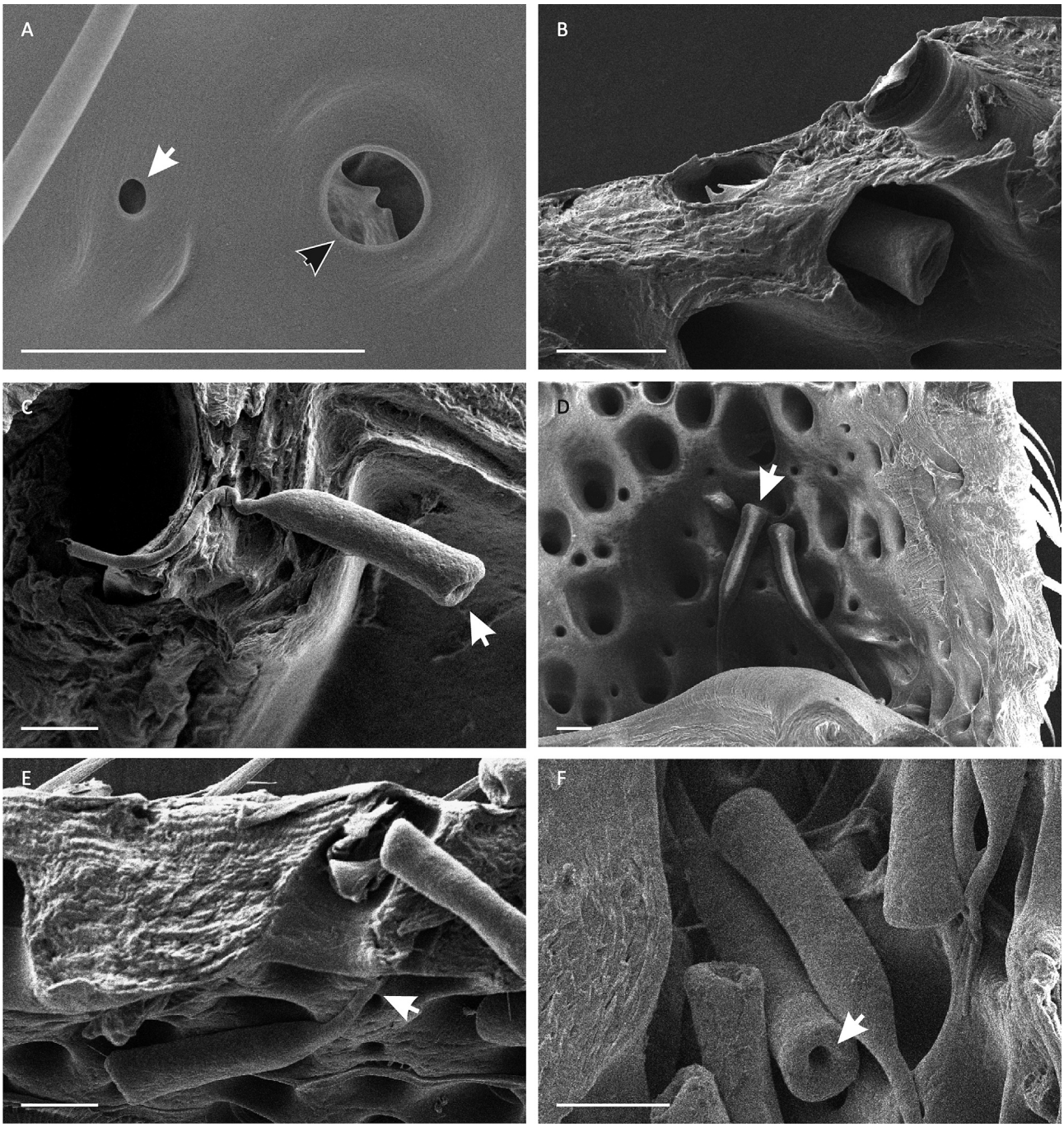

Fig. 6. Scanning electron micrographs of the internal and external structure of the apical segment of the antenna show sensilla ampullacea and coeloconica. (A) External structure of sensilla ampullacea (white arrows) and coeloconica (black arrow). (B) Cross-section through the antennal cuticle shows the peg of a sensillum coeloconicum within the chamber. (C) Detached ampoule of the sensillum ampullaceum reveals no porosity, but a single large opening (white arrow). (D) Micrograph of an uncoated specimen reveals the sensory peg within the enclosing ampoule of sensilla ampullacea (white arrow). (E) Cross-section through the cuticle shows a sensillum ampullaceum hanging within the antennal lumen by a slender tube (white arrow) connecting to the external opening. (F) Detached sensilla ampullacea showing opening for neural innervation (white arrow). All scale bars = 1 μm.

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Pores are absent from the base of the sensillum, from the dorsal ridge and also from the ventral surface (Fig. 5B and C). The peg inserts into an opening in the cuticular surface without a socket. Intricate corrugations were observed at the ventral base of the sensillum (Fig. 5D). The slender forms of this sensillum tapered to a sharp point, while the thicker forms had a bevelled tip (Fig. 5A and C). Electrophysiological evidence indicates that sensilla trichodea curvata are sensitive to various volatile compounds, including alarm pheromones (e.g., *Lasius fuliginosus* Dumpert, 1972a).

3.2.4. Sensilla ampullacea

Externally, sensilla ampullacea appear as small, round openings on the cuticular surface (diameter = 0.8 μm ± 0.1; $n = 63$) (Table 1, Fig. 6A, white arrow). Examination of the internal structure of the cuticle reveals a long, thin tube leading into a larger chamber or ampoule containing the sensory peg (Fig. 6C). In uncoated samples the peg seems to collect electrical charge making it visible through the wall of the ampoule (Fig. 6D, white arrow). The tube which connects the external opening to the ampoule traverses the entire thickness of the cuticle and allows the ampoule to hang inside the antennal lumen (Fig. 6E). A round opening at the base of the chamber allows innervation of the sensillum (Fig. 6F). Electrophysiological evidence from the leaf-cutter ants, *Atta cephalotes* and *Atta sexdens* indicates that sensilla ampullacea have a warm and a CO_2 receptor neuron (Kleineidam et al., 2000; Kleineidam and Tautz, 1996).

3.2.5. Sensilla coeloconica

In these sensilla the external opening is substantially larger than in sensilla ampullacea (diameter = 2.5 μm ± 0.3; $n = 56$) making the tip of the sensory peg occasionally visible just below the surface (Fig. 6A, black arrow). The peg of sensilla coeloconica is contained within a chamber embedded within the antennal cuticle and it possesses a bilaterally flattened end with a number of points (Fig. 6A and B). Rutchy et al. (2009) measured sensory neuron activity and established that sensilla coeloconica respond to changes in atmospheric temperature.

3.2.6. Trichoid-II sensilla

The peg is long and tapering (length = 32.8 μm ± 3.5; width = 2.6 μm ± 0.3; $n = 60$), it can be either straight or curved (Fig. 7A and B) ending in a 'pinched' tip (Fig. 7C). Pores are present along the length of the sensillum, but they are much sparser than in sensilla basiconica and sensilla trichodea curvata, with no visible apical pore. The peg inserts into an opening in the antennal surface where a cuticular half ring appears to surround the base of the peg where it inserts into the opening (Fig. 7D). To our knowledge the only other ant, in which this sensillum has been documented is *C. japonicus* and it is not clear what its function may be (Nakanishi et al., 2009). It has also been observed in other Hymenoptera including parasitoid wasps (Bethylidae) and in honeybees (Apidae), where it has been referred to as sensilla trichodea II and sensilla trichodea B, respectively (Li et al., 2011; Suwannapong et al., 2012). We believe that in the past this sensillum has been grouped with sensilla trichodea curvata as they can look very similar at low magnification or in information-poor images (e.g. low resolution, low contrast, blurry, etc.).

3.2.7. Sensilla chaetica

These are slender hair-like sensilla (width = 2.0 μm ± 0.4; $n = 97$) (Fig. 8A–C white arrows) which vary in length

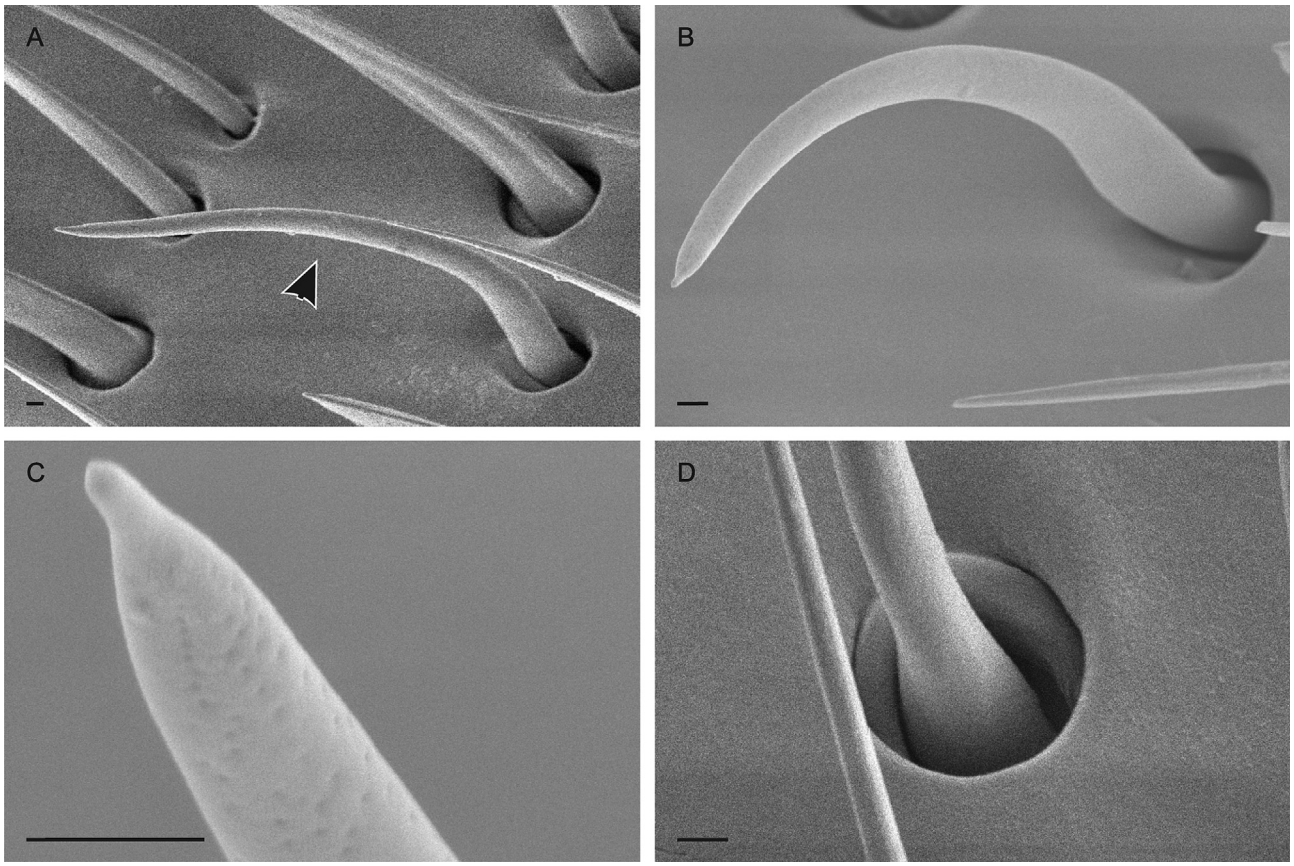

Fig. 7. Scanning electron micrographs of trichoid-II sensilla. (A) Overview of the trichoid-II sensillum (black arrow) amongst other sensilla. (B) Top view of the sensillum. (C) Tip of the sensillum and the sparse pores that cover the majority of the peg. (D) Socket and base of the peg. All scale bars = 1 μm.

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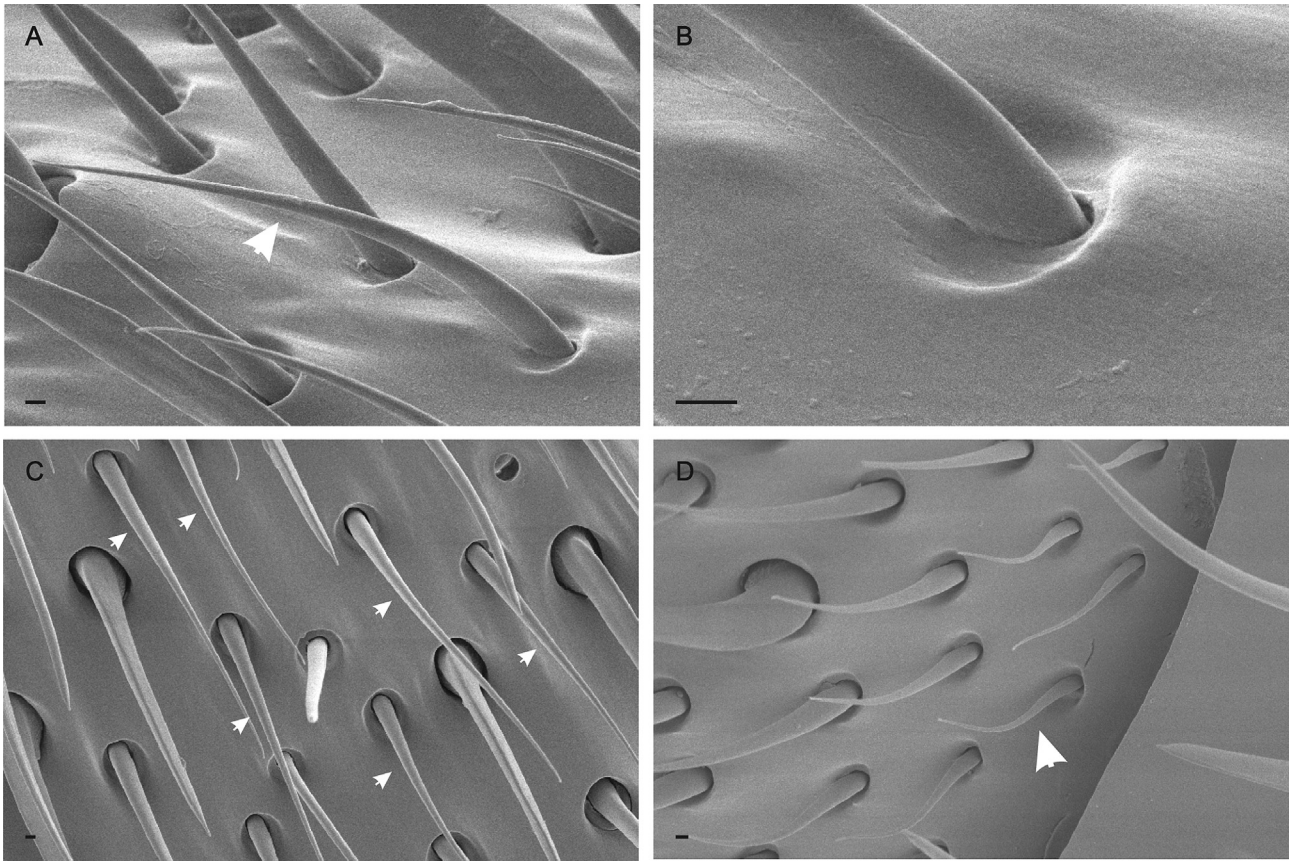

Fig. 8. Scanning electron micrographs of sensilla chaetica. (A) Overview of a sensillum chaeticum (white arrow) amongst other sensilla. (B) Base of the peg and insertion into the cuticular surface. (C) Top view of several sensilla chaetica (white arrows) amongst other sensilla. (D) Small sensilla chaetica (white arrow) near the articulation between the apical and the preceding segment. All scale bars = 1 μm.

(34.9 μm ± 7.1; $n = 97$), with the shortest found in the area just ahead of the joint with the next segment (Fig. 8D, white arrows) and the longest found just below, projecting over the joint. They have smooth surfaces, appear not to have any pores and lack a socket (Fig. 8B). Such filliform sensilla that have no pores, striations or openings are usually considered to be mechanoreceptors (Dumpert, 1972b; Marques-Silva et al., 2006; McIver, 1975).

3.2.8. Coelocapitular sensilla

These sensilla are quite small and inconspicuous. They appear as small, nub-like projections (diameter = 1.4 μm ± 0.1; $n = 5$) around which there is a circular depression of the surrounding cuticle (Fig. 9A and B). At higher magnification the external surface of the 'nub' or peg appears highly convoluted with spongy looking, globular irregularities with no visible pores (see Fig. 9B). At low magnification this inconspicuous sensillum (Fig. 9C, black arrows) resembles the stumps left behind by broken sensilla (Fig. 9D, white arrow). It is also present in *C. japonicus* (Nakanishi et al., 2009), in honeybees (Yokohari et al., 1982), and in other insect orders such as Coleoptera and Mantophasmatodea (Drilling and Klass, 2010; Giglio et al., 2008). This type of sensillum has been thoroughly studied in the honeybee, where its anatomy has been described, its function tested electrophysiologically and its neural connections to the glomeruli mapped (Nishino et al., 2009; Yokohari, 1983; Yokohari et al., 1982). This sensillum acts as both a hygro- and a thermoreceptor.

3.3. Distribution of sensilla in the apical segment

3.3.1. Dorsal surface

Each of the eight types of sensillum identified in *M. pyriformis* has a specific distribution and occupies distinct regions of the dorsal side of the apical segment. Among the chemoreceptors, sensilla trichodea curvata (Fig. 5) were the most abundant sensilla present throughout the dorsal surface of the apical segment, except at the extreme tip (Fig. 10A, blue triangles). Sensilla basiconica (Fig. 3) were the least common chemoreceptors but were fairly evenly distributed along the surface of the apical segment (Fig. 10A, orange circles). However, they were missing from a small area around the tip and were sometimes more prominent towards one of the sides. Sensilla basiconica were often found paired with sensilla trichodea (Fig. 4) with the latter always being the more distal of the two. This is similar to what has been observed in *S. invicta* (Renthal et al., 2003) and various other ant species (Hashimoto, 1990b). Sensilla trichodea also occur unpaired and this is particularly evident at the tip of the apical segment where they are present in unusually high numbers (Fig. 10A, green squares). Apart from this area of high density, sensilla trichodea occur evenly throughout the apical segment but are absent at its base. The rarest sensillum overall was the coelocapitular sensillum (Fig. 9) which only occurred between one to four times per dorsal apical segment and was altogether missing in some individuals; when present this sensillum was found close to the tip (Figs. 10A and 11A, purple

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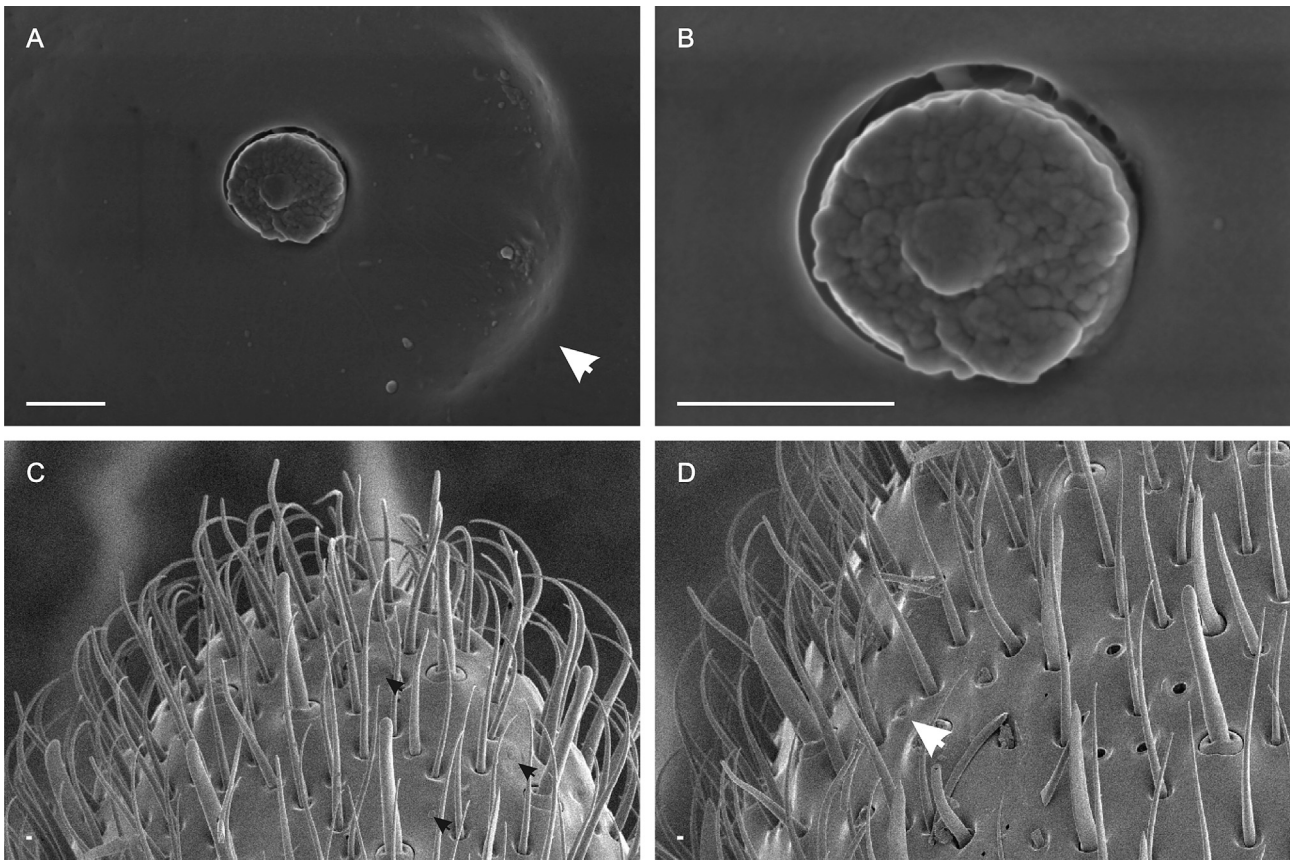

Fig. 9. Scanning electron micrographs of coelocapitular sensilla. (A) Overview of a coelocapitular sensillum with surrounding depression of the cuticle (white arrow). (B) High magnification image of the peg with surface sculpturing. (C) Overview image of the tip of the apical segment of the antenna (ventral surface) showing inconspicuous coelocapitular sensilla (black arrows). (D) Overview image of a section of the apical segment of the antenna (ventral surface) showing broken sensillum (white arrow) resembling a coelocapitular sensillum. All scale bars = 1 μm.

pointers). Conversely, the most common and abundant sensilla are sensilla chaetica (Fig. 8), which are found throughout the apical segment (Fig. 10B, blue crosses). Trichoid II sensilla (Fig. 7) are present in numbers similar to sensilla trichodea and basiconica, and are found in the middle portion of the apical antennomere (Fig. 10B, red triangles). Both sensilla ampullacea and coeloconica (Fig. 6) are typically found together and exhibit a clumped distribution in the sub-apical region of the segment (Fig. 3B, black closed and open circles).

3.3.2. *Ventral surface*

While the distribution of sensilla is very similar in the dorsal and ventral surfaces, the abundance of certain types of sensillum drops very noticeably on the ventral surface. The main differences are that there are far fewer sensilla basiconica, trichodea and trichoid-II sensilla on the ventral surface (Fig. 11). Sensilla ampullacea and coeloconica are extremely rare and sometimes absent from the ventral surface but the abundance of sensilla trichodea curvata and chaetica does not change much (Fig. 11). Lastly, and in contrast to all other sensillum types, coelocapitular sensilla are most abundant on the ventral surface (Fig. 11). Interestingly, there are ten coelocapitular sensilla in the small worker (D1) and nine in the large worker (D2) which suggests that individuals, regardless of size, may have a very similar total number of coelocapitular sensilla on the ventral surface of the apical segment. Similarly, in *C. japonicus* six coelocapitular sensilla are present on the ventro-lateral side of the apical segment of the workers of *C. japonicus* (Nakanishi et al., 2009).

3.3.3. *Sensilla campaniformia*

We did not observe these sensilla on the ventral or dorsal surfaces of the apical segment of *M. pyriformis*. However, sensilla campaniformia have been described in a number of ants including *Lasius fuliginosus*, *Dinoponera lucida* and *S. invicta* (Dumpert, 1972b; Marques-Silva et al., 2006; Renthal et al., 2003). These sensilla are rare and their location on the antennae seems to vary between species. About 3–4 of these sensilla occur on the apical segment in *L. fuliginosus* (Dumpert, 1972b), about 3–4 on the most proximal funicular segment (see Fig. 1A) but not elsewhere on the funiculus in *S. invicta* (Renthal et al., 2003) and about 2–3 on the apical segment of *D. lucida* (Marques-Silva et al., 2006). It is worth noting that there have been instances of coelocapitular sensilla being mistakenly named sensilla campaniformia (see Yokohari, 1983).

3.4. *Number and size of sensilla*

3.4.1. *Numbers*

Among *M. pyriformis* individuals, the number of sensilla on the apical antennomere tends to increase with the size of the antennomere (Table 1). This is true across all types of sensilla except in the case of the three types of intracuticular sensilla (sensilla ampullacea, coeloconica and coelocapitular) which all seem to have relatively stable numbers across different sized workers. This is particularly evident in the case of sensilla ampullacea where, irrespective of size, there are 21–24 sensilla present on the dorsal surface. In other species, however, this number is not conserved.

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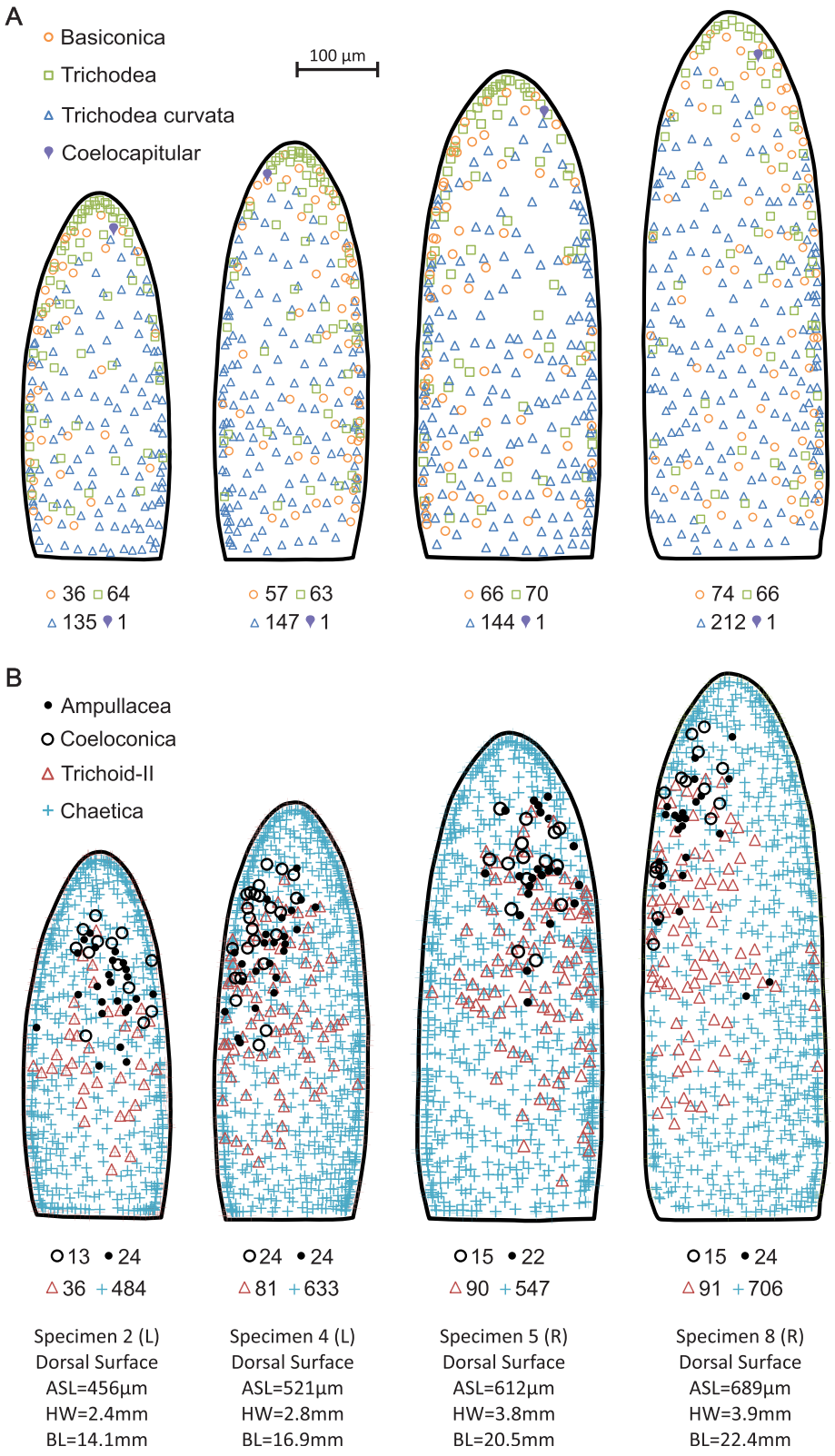

Fig. 10. Distribution maps of different sensilla on the dorsal surface of the apical antennal segment in *Myrmecia pyriformis* workers. (A) Distribution of sensilla basiconica, sensilla trichodea, sensilla trichodea curvata, and coelocapitular sensilla. (B) Distribution of sensilla ampullacea, coeloconica, trichoid-II and chaetica. Numbers of each type of sensillum are shown together with the corresponding symbol. Each column corresponds to a single individual, various measures of size are given as apical segment length (ASL), head width (HW) and body length (BL). Data from right (R) and left (L) antennae (all right antennae have been mirror-imaged for ease of comparison with left antennae). It must be noted that although the density of sensilla appears to increase towards the margins of the segment this is due to the curvature of the antenna.

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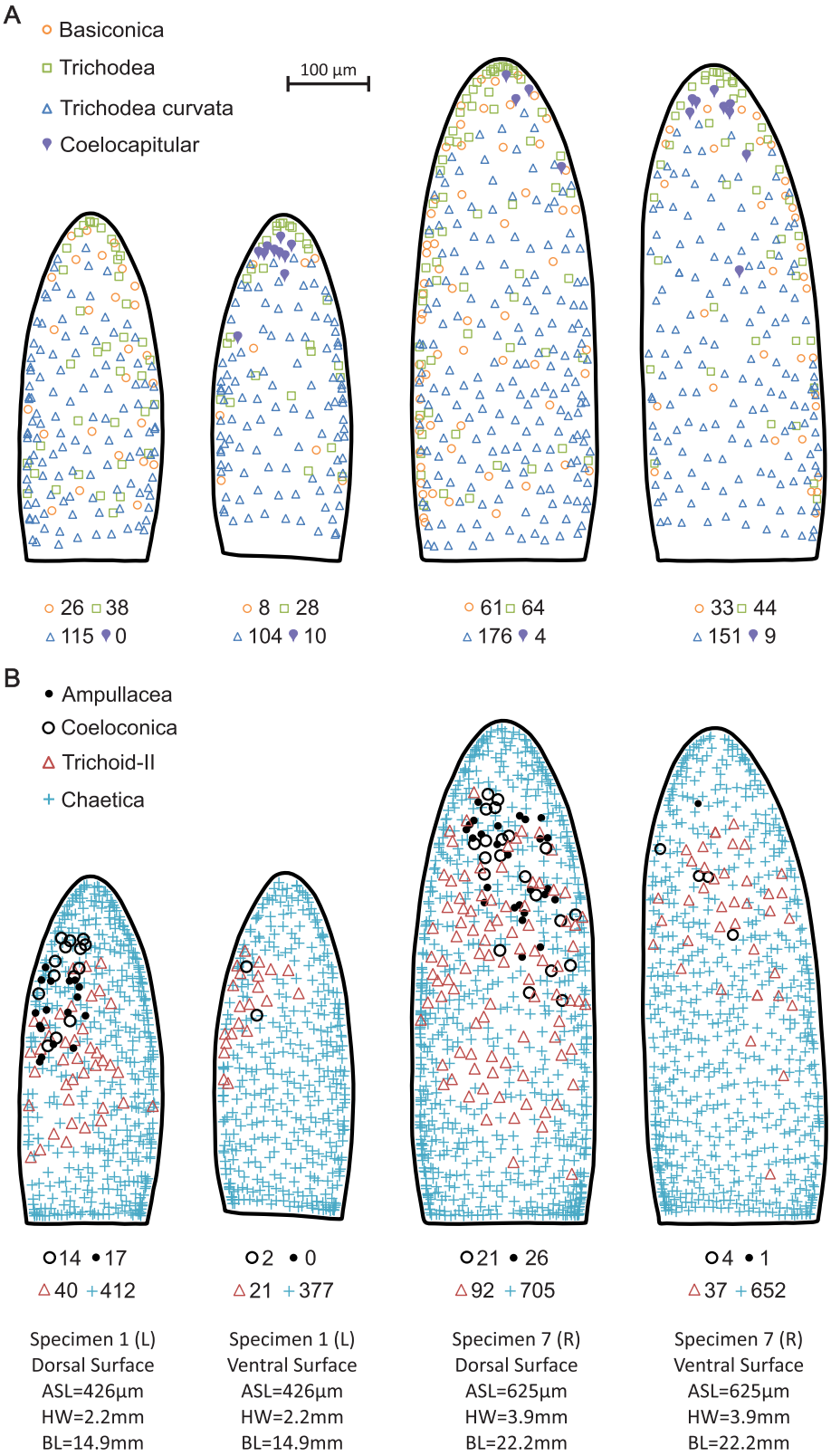

Fig. 11. Distribution maps of different sensilla on the dorsal and ventral surface of the apical antennal segment in *Myrmecia pyriformis* workers. (A) Distribution of sensilla basiconica, sensilla trichodea, sensilla trichodea curvata, and coelocapitular sensilla. (B) Distribution of sensilla ampullacea, coeloconica, trichoid-II and chaetica. Numbers of each type of sensillum are shown together with the corresponding symbol. The first two columns correspond to a small individual (column 1 = dorsal, column 2 = ventral, as indicated) and the last two columns to a large individual. Various measures of size are given as apical segment length (ASL), head width (HW) and body length (BL). Data from right (R) and left (L) antennae (all right antennae have been mirror-imaged for ease of comparison with left antennae). It must be noted that although the density of sensilla appears to increase towards the margins of the segment this is due to the curvature of the antenna.

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Table 3
Abundances of each type of sensillum in different species of ants as reported in available publications. The body size of each species is given as head width (HW) based on information from the relevant publication (labelled by number) or, when size is not reported, from measurements taken from photographed collection specimens found at www.antweb.org (largest size always reported unless data are given for multiple castes; labelled*). Area of the antenna studied and source publication as follows: [1]Dorsal surface of apical segment (present publication); [2]Not specified (Jaisson, 1969); [3]Entire surface of apical segment (Kleineidam et al., 2000); [4]Entire surface of apical segment (Mysore et al., 2010); [5]Entire surface of apical segment (Nakanishi et al., 2009); [6]Not specified (Marques-Silva et al., 2006); [7]Estimates of the entire surface of the apical segment reported here (Fresneau, 1979); [8]Entire surface of apical segment, examined by splitting the antennomere in two halves (Dumpert, 1972b); [9]Mysore et al. (2009).

	HW (mm)	Basiconica	Trichodea	Trichodea curvata	Coelocapitular	Ampullacea	Coeloconica	Trichoid-II	Chaetica
Myrmecia pyriformis (minor)[1]	2.4[1]	36	64	135	1	24	13	36	484
Myrmecia pyriformis (major)[1]	3.9[1]	85	81	216	0	21	26	105	697
Aphaenogaster gibbosa[2]	0.9*					8	4		
Atta sexdens[3]	4.9*					10			
Camponotus compressus (minor)[4]	2.3[9]	204	61	181					
Camponotus compressus (medium)[4]	4.0[9]	188	57	167					
Camponotus compressus (major)[4]	5.6[9]	157	43	139					
Camponotus japonicus[5]	2.5*	54	60	168	6	10	10	60	823
Dinoponera lucida[6]	5.1*						8		
Formica polyctena[7]	2.4*	43		62		9	6		
Lasius fuliginosus[8]	1.6*	36	69	152		9	8		440
Myrmica laevinodis[2]	1.0*					9	8		

There are about half as many sensilla ampullacea in the extremely large *Atta sexdens*, and all other species, regardless of size, have similar numbers as *A. sexdens* (see Table 3). A similar trend is also observed in sensilla coeloconica but there is not much information on coelocapitular sensilla. Meanwhile, the extracuticular sensilla (all other types studied here) seem to increase proportionally with increasing apical segment area (see Table 1, in italics). In sensilla basiconica the number of sensilla per unit area seems to consistently increase with increasing apical segment size but the increase is very small and similar consistent changes are not observed in the other sensillum types. Therefore, based on this small sample, it seems most likely that the numbers of extracuticular sensilla in *M. pyriformis* scale proportionally. This increase in sensillum numbers with size, however, does not hold true in other studied species. For instance, in the polymorphic ant *C. compressus*, minor workers have the highest numbers of sensilla basiconica, trichodea and trichodea curvata despite having shorter apical segments (345 μm) relative to the majors (407 μm) (Mysore et al., 2010).

Unfortunately direct comparisons of the absolute numbers of sensilla between species are difficult to make, because either different areas of the antenna were studied or abundance was estimated in different ways (see Table 3). However, we can still make some rough comparisons. For instance, Table 3 shows that minor workers of *M. pyriformis* and *C. japonicus* have similar head widths and similar numbers of sensilla basiconica, trichodea, and trichodea curvata. But, because the numbers available for *M. pyriformis* represent the abundance of sensilla on the dorsal surface alone, while in *C. japonicus* the whole apical segment is represented, we can conclude that *M. pyriformis* must have nearly twice as many sensilla. This may be because the apical segment of *M. pyriformis* is longer (456 μm) than in major workers of *C. japonicus* (290 μm). However, the similarly sized minor workers of *C. compressus* also have shorter apical segments (354 μm) than *M. pyriformis* but seem to have many more sensilla. It is interesting to note that even within the *Camponotus* genus, ants of comparable sizes (minor worker of *C. compressus* and worker of *C. japonicus*) exhibit large variation in the number of sensilla basiconica (204 and 54), but very little variation in sensilla trichodea (61 and 60) and trichodea curvata (181 and 168). These differences point to the fact that size alone does not dictate the number of sensilla that are present across different species.

It is likely that the lifestyle of a species plays a significant role in the ratios of sensilla found on the antennae. For instance, workers of *M. pyriformis* are nocturnal (Narendra et al., 2010) and are exclusively solitary foraging animals, whereas workers of *C. compressus* are strictly diurnal, forage individually, but also engage in tandem running (Narendra and Kumar, 2006). Another example may be the similarly sized *C. compressus* and *M. pyriformis* minors. The lower numbers of sensilla basiconica in *M. pyriformis* (Table 3) may reflect the simple social structure of their colonies. Behavioural and immunohistochemical assays have shown that this sensillum is involved in the recognition of nest-mates' cuticular hydrocarbons (Ozaki et al., 2005). When foraging, *M. pyriformis* workers of the same colony do not seem to interact with each other and are often aggressive (AN, personal observation). Perhaps the relatively small number of sensilla basiconica may be correlated with this lack of recognition. From this perspective it would be interesting to know more about the function of sensilla, particularly which olfactory sensilla respond to what olfactory cues, and to see if it is possible to map differences in lifestyle onto changes in the antennal topography.

Finally, while it can be difficult to draw comparisons between different ant species due to differences in methodology, it seems that in general, in the apical antennomere, sensilla chaetica are the most abundant, while coelocapitular sensilla, coeloconica and ampullacea are the least abundant sensilla (Table 3).

3.4.2. Size

The size of some sensilla varies not only between species, but also within a single species and surprisingly even within individuals (see Fig. 12, Tables 2 and 4). In *M. pyriformis*, the peg length was most variable, particularly in sensilla chaetica and trichodea, while the peg diameter in each sensillum type did not vary much. Some individuals displayed a larger range of sensillum size than others (Fig. 12). However, this is probably due to the small number of sensilla that were sampled. For each individual we measured a minimum of 5 sensilla of each type. This is a substantial proportion of the total sensillum population for certain types such as sensilla coeloconica and ampullacea but a tiny fraction for others. Therefore, at the individual level, this may not capture a complete picture of the size variation. Despite this, the overlapping ranges of small and large individuals indicate that there is no clear trend of increase in the size of sensilla with increase in the size of the apical segment. It is possible that individuals with larger apical segments may have a sensillum population that is biased towards larger sensilla but, if present, this bias must be relatively subtle as it is not apparent in our data. A comparison across different species

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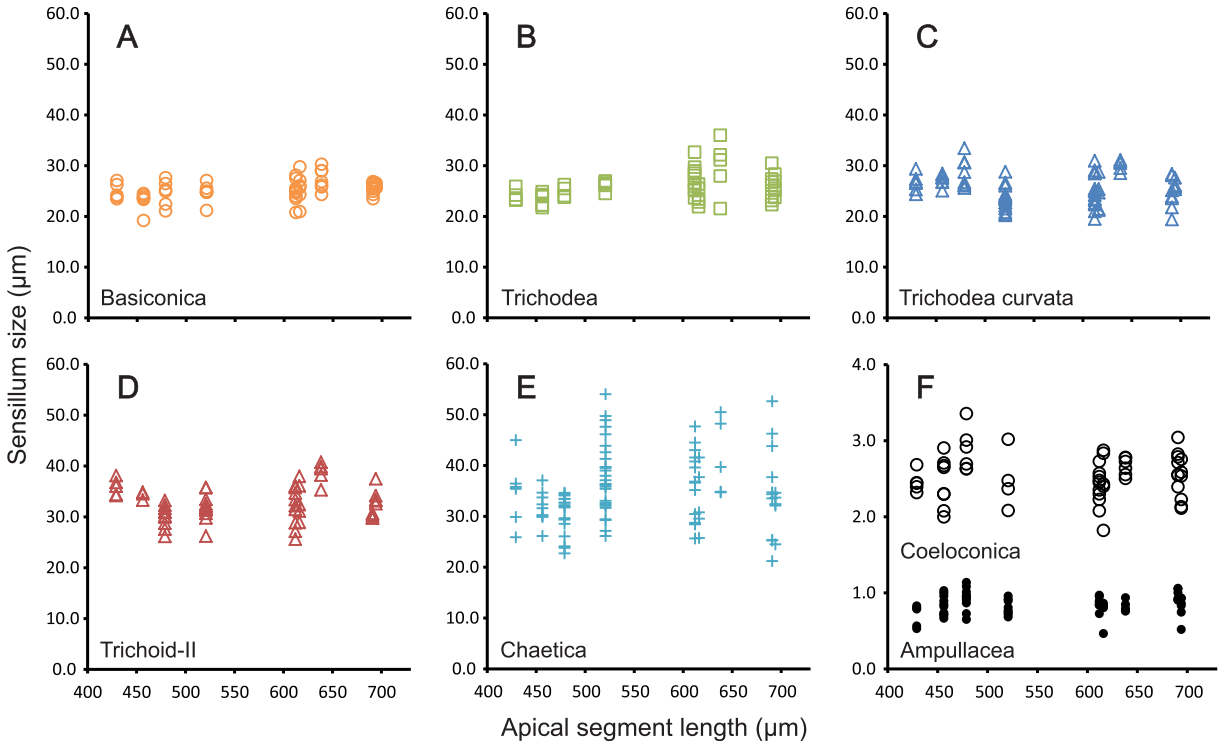

Fig. 12. Size variation of sensilla in nine differently sized *Myrmecia pyriformis* workers. Sensillum size is shown for (A) sensilla basiconica, (B) trichodea, (C) trichodea curvata, (D) trichoid-II, (E) chaetica and (F) sensilla coeloconica (open circles) and ampullacea (closed circles). Sensillum size refers to sensillum length in panels A–E (extracuticular sensilla) and diameter of the opening for panel F (intracuticular sensilla). The data of individual scatterplots are arranged in columns, which represent individuals of different sizes corresponding to specimens 1–9 from left to right.

Table 4
Size of sensilla across different species. Peg l.: Peg length; Peg w.: Peg width. Source publications: for [1–9] see Table 3; [10](Barsagade et al., 2013); [11](Renthal et al., 2003); All measurements are given in µm.

	Basiconica	Trichodea	Trichodea curvata	Ampullacea	Coeloconica	Trichoid-II	Chaetica
Myrmecia pyriformis[1]	Peg l. 24.4 Peg w. 3.8	Peg l. 24.9 Peg w. 2.8	Peg l. 25.5 Peg w. 5.1	Opening 0.9	Opening 2.5	Peg l. 31.1 Peg w. 2.7	Peg l. 34.3 Peg w. 1.9
Atta sexdens[3]				Opening 1–2			
Camponotus compressus[10]	Peg l. 5.7 Peg w. 1.2						
Camponotus japonicus[5]	Peg l. 20.0 Peg w. 6.0	Peg l. 20.0 Peg w. 2.0	Peg l. 30.0 Peg w. 6.0	Opening <1	Opening 1.2	Peg l. 70.0 Peg w. 3.0	
Dinoponera lucida[6]							Peg l. 20–30; 140–160
Solenopsis invicta[11]	Peg l. 13.0 Peg w. 3.0		Peg l. 15–25 Peg w. 1.0–2.5				

indicates that the dimensions of sensilla trichodea, trichodea curvata, ampullacea and coeloconica observed in *M. pyriformis* were consistent with those found in other species, while other sensilla varied in size across species. This indicates that the large apical segment of *M. pyriformis* does not lead to a consistent increase in the size of sensilla.

The variability in sensillum length and other parameters, which was observed in individuals of *M. pyriformis* may be related to the local architecture of the apical segment. The array of sensilla on this antennomere is the most complex in the antenna and because of the limited amount of space there must be trade-offs at play. In the case of chemoreceptors, at least, it is beneficial to increase the surface area of the sensillum (Wicher, 2012), but in order to maximise the total receptivity of the apical antennomere to different types of information it may be worthwhile to sacrifice the size of some sensilla in order to be able to fit larger numbers of them. Thus it may be that any given sensillum may vary in size depending on what other sensilla are around it and how much space they take up, both above and below 'ground'. If this is the case it would be expected that on more proximal antennomeres where space is not at such a prime, and sensilla are not so closely packed, the size of sensilla of a particular type would be much less variable.

4. Conclusions

Workers of *M. pyriformis* have an antennal array comparable to that of other species in terms of the sensillum type, size and

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numbers. This seems to indicate that their heavy reliance on vision does not have detrimental effects on the antennal sensilla. Perhaps this should not come as a surprise as both sensory systems provide very different types of information and are not really in competition with one another, at least on the external surface.

Of the eight sensilla we identified in *M. pyriformis* six have been concurrently described in a variety of other ants (Dumpert, 1972b; Hashimoto, 1990b; Renthal et al., 2003), other studies have identified subsets of these six sensilla (Marques-Silva et al., 2006; Mysore et al., 2010; Ozaki et al., 2005), while Nakanishi et al. (2009) found all eight types. While we observed coelocapitular sensilla on the antennae of *M. pyriformis*, many studies on other ant species do not report their presence. Conversely, we did not observe sensilla campaniformia, while studies on other species have. However, it is not entirely clear whether both of these are present in ants or if both names have been used to refer to the same type of sensillum (see Yokohari, 1983). Furthermore, these sensilla tend to occur in very low numbers and are very small and inconspicuous, often resembling the stumps of broken sensilla (see Fig. 9C, D). This would make them easy to miss and hard to identify, particularly when high quality, high magnification images are not available. Similarly the trichoid-II sensillum has only been described in *M. pyriformis* and *C. japonicus*. However, this receptor can be extraordinarily hard to distinguish from sensilla trichodea curvata or sensilla chaetica at low magnifications and has most likely been identified as one of these two types in the past; it is not until the eye has been trained to identify specific diagnostic features that it becomes apparent at all. Therefore, it is probable that most differences in the types of sensilla described for different species are not due to actual differences in the array but due to differences in classification, the difficulty in distinguishing between similar sensilla and, on occasion, misidentification of sensilla.

With respect to the size and numbers of sensilla it is hard to draw firm conclusions about differences across different species from the information that is currently available (see Table 4). The main change observed was a reduction in the number of sensilla basiconica in *M. pyriformis* relative to other species; as discussed above, this may tie in with the simple social structure of *M. pyriformis* colonies. This observation along with other factors, such as the variability among species in the ratios at which different types of sensilla are found, lead us to speculate that, while certain aspects of the antennal array, such as the total number of sensilla, may be explained to some degree by the size of the animal and the size of the apical segment, it appears that lifestyle may play an important role in shaping the antennal array. However, three types of sensilla seem to be less prone to variability. Numbers of sensilla ampullacea, coeloconica and coelocapitula across species seem to be very similar indicating that these sensilla have very little to do with lifestyle specialisations and that they must provide essential information for life in an ant colony. This is consistent with their function as monitors of ambient temperature and CO_2 levels, factors that would appear to be important environmental conditions in ant colonies with limited ventilation.

Within *M. pyriformis* it seems that the size of sensilla does not increase with the size of the worker while the numbers do (see Fig. 12 and Table 1 respectively). Furthermore, the number of sensilla seemed to increase proportionally with worker size. While this seems intuitive, the scenario is exactly the opposite in *C. compressus* (Mysore et al., 2010), where the number of sensilla decreased with increasing worker size (see Table 3). It remains to be tested whether: (a) large workers of *M. pyriformis* need better chemoreceptive abilities or (b) the major workers of *C. compressus* have fewer sensilla since they typically do not engage in foraging, unlike in *M. pyriformis* where animals of all sizes engage in foraging. We suspect the latter to be the most likely scenario.

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Appendix 1

Nomenclatures used by referenced studies in chronological order. When denominations are used that do not seem to correlate to an established type of sensillum these data are ignored. The terms which compose the nomenclature used herein are given in bold.

Jaisson (1969)	Basiconica				Organes en forme de bouteille	Organes en “bouchon de champagne”		
Dumpert (1972a,b)	**Basiconica**	**Trichodea**	**Trichodea curvata**		**Ampullacea**	**Coeloconica**		**Chaetica**
Fresneau (1979)	Basiconica		Trichodea curvata					
Hashimoto (1990a,b)	Basiconica	Chaetica	Trichodea curvata		Ampullacea	Coeloconica		Bristle
Renthal et al. (2003)	Basiconica	Trichodea	Trichodea curvata		Ampullacea	Coeloconica		Trichodea
Marques-Silva et al. (2006)	Basiconica					Coeloconica		Trichodea
Nakanishi et al. (2009)	Basiconic	Chaetic-A	Trichoid-I	**Coelocapitular**	Ampullaceal	Coeloconic	**Trichoid-II**	Chaetic
Mysore et al. (2010)	Basiconica	Trichodea	Trichodea curvata					
Barsagade et al. (2013)	Basiconica							Trichodea/trichodea curvata?

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