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Ultrastructural characterization of antennal sensory architecture in three species of Himalayan *Myrmica* (Hymenoptera: Formicidae)

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Abstract

Ants rely on antennal sensilla for chemical communication and for perceiving environmental cues, which are essential for colony organization and survival. However, information on sensillar organization in high- altitude Himalayan ants remains limited. The present study provides the first detailed comparative analysis of the types, morphology, and distribution of antennal sensilla in three Himalayan *Myrmica* species: *Myrmica aimonissabaudiae* Menozzi, 1939*, Myrmica cachmiriensis* Forel, 1904, and *Myrmica inezae* Forel, 1902, occupying distinct ecological niches. Differences in sensillar organization were observed among the three species. A novel sensilla chaetica branched has been observed in ants for the first time. This study establishes a baseline for understanding sensory morphology and ecological adaptation in the Himalayan genus *Myrmica* Latreille*,* 1804.

Introduction

Ants are among the most ecologically dominant and evolutionarily successful insect groups, occupying nearly every terrestrial habitat on Earth. With more than 14,000 described species, ants play crucial roles in ecosystem functioning, including soil turnover, seed dispersal, nutrient cycling, and arthropod population regulation. Their ecological success is largely attributed to their advanced social organization and highly efficient communication systems, which allow colonies to coordinate complex behaviors such as foraging, nest defense, brood care, and division of labor (Hölldobler & Wilson, 1990).

Environmental conditions often shape the structural organization of antennal sensilla. For instance, *Bombyx mori* exhibits thermosensitive and hygrosensitive sensilla that undergo structural changes under dry and moist conditions, which help in efficient environmental sensing and adaptation (Steinbrecht & Müller, 1991); similarly, bees and wasps inhabiting urban environments exhibit subtle morphological modifications in their antennal sensory systems, including changes in antennal size, flagellomere dimensions, and the abundance of thermo- and olfactory- related sensilla, suggesting that sensory structures can respond to environmental factors such as temperature and habitat fragmentation (Ferrari et al., 2024). *Scolia hirta* exhibits pronounced sexual dimorphism in antennal sensilla, with males and females possessing different sensillar types and distributions adapted for mate detection and ecological roles (Ferrari & Polidori, 2026); studies in desert ant such as, *Cataglyphis bicolor* exhibits antennal sensilla with a longitudinally aligned ampulla-duct system that reduces water loss and enhances desiccation resistance in arid habitats (Kleineidam et al., 2000), *Atta vollenweideri* possesses apical peg-in-pit sensilla coeloconica that function as thermoreceptors enabling temperature detection during foraging and nest ventilation (Ruchty et al., 2009; Kleineidam et al., 2007), *Solenopsis invicta* shows caste and sex-based variation in antennal sensilla with males having fewer types of sensilla and lacking sensilla basiconica (Renthal et al., 2003).

Within the family Formicidae, the subfamily Myrmicinae represents one of the largest and most diverse ant lineages, containing thousands of species distributed across diverse

ecological habitats worldwide. Members of Myrmicinae exhibit considerable diversity in nesting behavior, diet, and colony organization, ranging from seed-harvesting ants to fungus-growing species. Many myrmicine ants inhabit structurally complex environments where chemical communication and sensory perception are crucial for colony functioning, making the antennal sensory system particularly important in this group (Ward et al., 2015).

The genus *Myrmica*, belonging to the subfamily Myrmicinae, is widely distributed across temperate and montane regions of the Northern Hemisphere and is especially diverse in mountainous ecosystems. Species of this genus exhibit several ecological and life-history traits that enable survival in cold climates, including overwintering behavior, heterodynamous life cycles, and relatively small colony sizes (Bharti et al., 2016; Bharti et al., 2023). In the Himalayan region, *Myrmica aimonissabaudiae* Menozzi, 1939 occurs across open meadows and coniferous forests at elevations of 1300-3500 m, whereas *Myrmica cachmiriensis* Forel, 1904 forms small colonies in shaded habitats between 1829-3500 m. In contrast, *Myrmica inezae* Forel, 1902 is typically associated with decaying wood and stone-covered substrates in coniferous forests at elevations of 1900-3000 m (Bharti et al., 2016).

Despite the ecological diversity of Himalayan *Myrmica* species, the morphology and distribution of their antennal sensilla remain poorly understood. Thus, the present study provides the first detailed investigation of the types, morphology, diversity, and distribution of antennal sensilla in three Himalayan *Myrmica* species. By documenting sensillar structures in these ants, this work contributes to a better understanding of sensory adaptations in ants inhabiting high-altitude environments.

Material and methods

Specimen Collection

Worker ants of three *Myrmica* species were collected from different localities in the Manali region of Himachal Pradesh, India during June. Workers of *M. aimonissabaudiae* were collected from nests beneath stones at the Atal Bihari Vajpayee Institute of Mountaineering and Allied Sports (32° 13′48″N, 77°11′29″E; 1815 m). Workers of *M. cachmiriensis* were collected from the Gulaba region (32°14′58″N, 77°11′22″E; 1871 m), while *M. inezae* were collected from Kothi (32°20′21″N, 77°12′43″E; 2531 m) (Fig 1A-C; Table 1). Approximately 50 workers per species were collected and preserved in absolute ethanol in 15 ml glass vials at room temperature. A subset of individuals was used for taxonomic identification (n = 20).

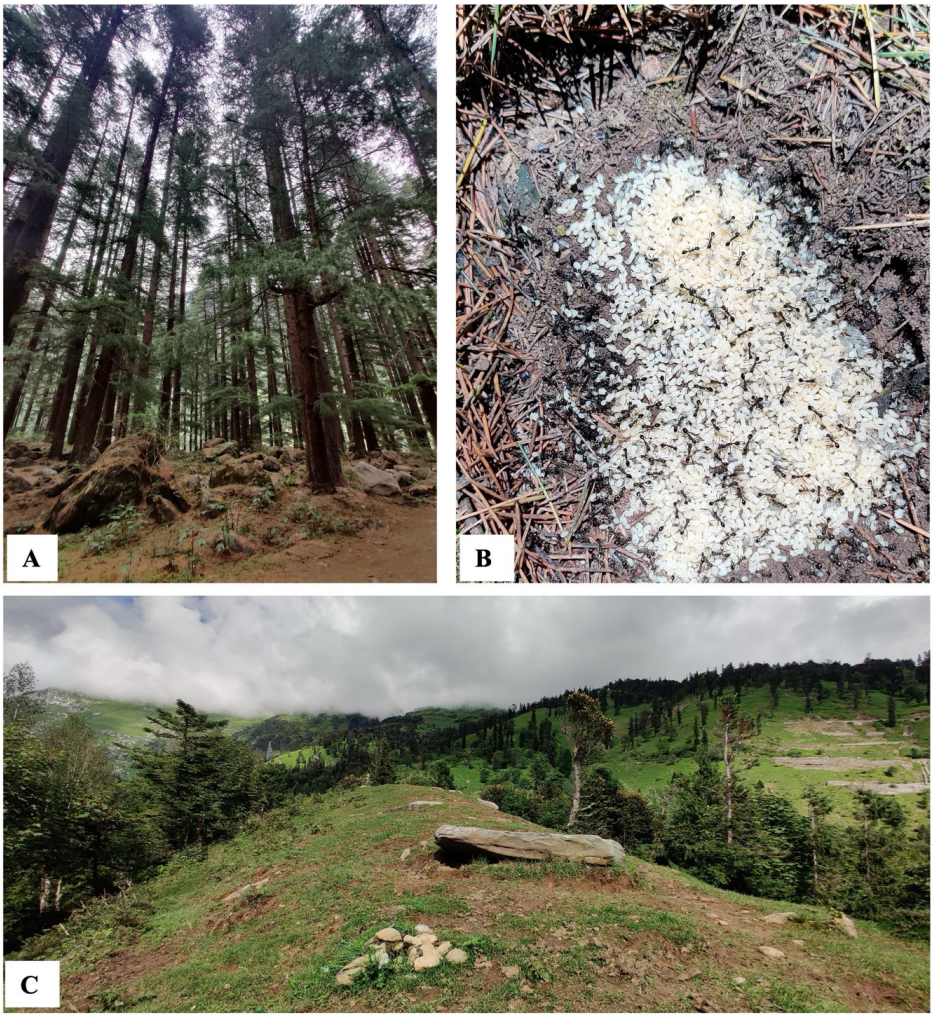

Fig 1. (A) Habitat of *Myrmica aimonissabaudiae* Menozzi, 1939 covered with *Cedrus* trees in Atal Bihari Vajpayee Institute of Mountaineering & Allied Sports (ABVI) (32°13’48”N, 77°11’29”E) at 1815m (B) Under stone nest of *Myrmica aimonissabaudiae* Menozzi, 1939 (C) Gulaba region (32°14’58”N, 77°11’22”E) at 1871m from where *M. cachmiriensis* Forel, 1904 were collected.

Table 1. Collection sites of the three species of *Myrmica* Latreille, 1804.

Species	Location	Habitat	Altitude	Temperature	Humidity
Myrmica aimonissabaudiae Menozzi, 1939	Atal Bihari Vajpayee Institute of Mountaineering & Allied Sports (ABVI), Manali	Nests were close to trees under stones, forest area with parks, trees around houses, anthropogenic activities	1815m	16 °C	22%
Myrmica cachmiriensis Forel, 1904	Gulaba, Manali	Shady region with trees; secluded area	1871m	13 °C	22%
Myrmica inezae Forel, 1902	Kothi, Manali	Under stones nest, grassland with trees and shrubs on sides; untouched area, undisturbed areas	2531m	11 °C	21%

Scanning Electron Microscopy (SEM)

For SEM analysis, 5 workers per species were selected. Head capsules with intact antennae were excised; antennae were carefully detached from the antennal socket under a stereomicroscope. Specimens were then transferred directly from ethanol into phosphate-buffered saline (PBS) (pH 7.2). The samples were subsequently rinsed sequentially in pure hexane to remove non-polar surface contaminants, pure acetone to eliminate polar residues and effectively displace any remaining hexane from the sample surface, and 95% ethanol to remove polar impurities and facilitate rapid evaporation, following the protocol described (Gellert et al., 2022). Each solvent treatment was performed only after the complete evaporation of the preceding solvent.

Prepared head capsules (oriented with the dorsal side upward) were mounted on aluminum stubs using conductive carbon tape. The samples were then sputter-coated with a gold-palladium alloy for 2-4 min at 20 mA using a Quorum Q150 ES Plus sputter coater. Imaging was carried out using a Zeiss Gemini 1 Sigma 500 field-emission scanning electron microscope (SEM) operated at an accelerating voltage of 5 kV to obtain high-resolution surface micrographs.

Morphometric Analysis and Sensilla Quantification

Sensillar distribution was examined across all antennal segments, from the scape to the apical flagellomere, with emphasis on the apical segment due to its higher sensillar density. Measurements and analysis of sensillar abundance and distribution were conducted using ImageJ software (64-bit, bundled with Java 8). Peg length was measured as the longest straight-line distance from base to tip; however, for sensilla possessing a coelom or cavity, the diameter of the sensilla opening was measured (Ramirez-Esquivel et al., 2014) (Fig 2A-C). The two-dimensional projected area of sensilla was calculated using the polygon selection tool in ImageJ and calibrated with the SEM internal scale bar. Sensillar distribution patterns were mapped using the Cell Counter plugin in ImageJ and were examined for SEM imaging and morphometric analyses. Sensilla abundance was assessed from multiple micrographs (n = 5 per surface), and density was

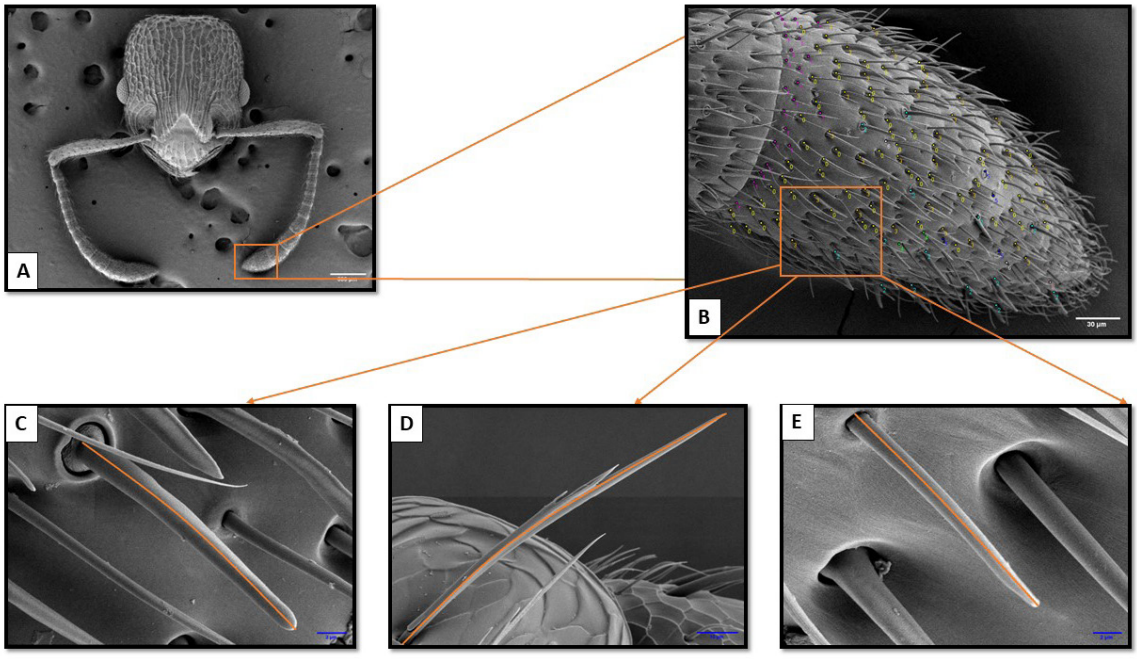

Fig 2. (A) Scanning electron micrograph of head of *Myrmica aimonissabaudiae* Menozzi, 1939 (B) Apical segment of antenna of *Myrmica aimonissabaudiae* Menozzi, 1939 (C) High magnification image of Sensilla Basiconica (D) High magnification image of Sensilla chaetica branched (E) High magnification image of Sensilla Trichoidea.

expressed as the number of sensilla per unit area (sensilla/µm²). All data are reported as mean ± standard deviation.

Sensilla classification and statistical analysis

Sensillar types were identified and classified based on external morphology, orientation, and surface ornamentation following established classification schemes for Hymenoptera (Dumpert, 1972; Yokohari, 1983; Nakanishi et al., 2009; Ramirez-Esquivel et al., 2014). Differences in sensillar type frequencies among *M. aimonissabaudiae*, *M. cachmiriensis*, and *M. inezae* were tested using a chi-square test of independence (PAST v4.03).

Results

On the basis of morphological characteristics such as shape, size, length, basal attachment to the socket, and presence of a coelom, eight distinct types of sensilla along with their respective subtypes were identified, namely, böhm bristles; sensilla ampullacea; sensilla basiconica; sensilla chaetica; sensilla coelocapitular; sensilla coeloconica; sensilla trichoidea; and sensilla trichoidea curvata (Table 3; Fig 3; Fig 4).

A chi-square test of independence was conducted using PAST4.03 software to examine the association between sensilla type and species across *M. aimonissabaudiae*, *M. cachmiriensis*, and *M. inezae*. The analysis revealed a statistically significant relationship between sensilla type and species ($\chi^2 = 46.711$, df = 18, $p < 0.001$). Monte Carlo simulation confirmed this significance ($p = 0.0002$). The effect size, measured by Cramér's V (0.104) and contingency coefficient (0.145), indicated a modest but statistically robust association, demonstrating that the distribution pattern of sensilla types differs significantly among the three *Myrmica* species.

The relative abundance of each sensilla type on the apical segment is illustrated in the clustered bar graph, and the apical segment of each species is also shown (Fig 5-6). A Venn diagram depicting the presence and absence of sensillar types among the three species is presented (Fig 7). For clarity, the morphological characteristics and distribution of the sensilla are discussed in two separate sections: sensilla common to three species and sensilla exclusive to one species.

Common to all three species

Böhm bristles (BB): Böhm bristles are located on the scape ball and exhibit a flexible (articulated) basal attachment. BB are short, non-porous, straight hairs with smooth surfaces, pointed tips, and a broad, flexibly articulated base. These sensilla occur in clusters of 5-6 distributed over the scape ball (Fig 3A). They are longest in *M. aimonissabaudiae* (11.028 µm ± 4.332 µm; n = 6) and shortest in *M. inezae* (9.74 µm ± 2.78 µm; n = 8) (Table 2).

Sensilla basiconica (SB I): Sensilla basiconica has two subtypes (SB I and SB II), and SB I is common to all three species (Fig 4B, 4G). Both exhibit a rigid, non-articulated basal insertion into the cuticle. SB I arise from a well-defined socket, are slender, elongated, and thinner than SB II. In contrast, SB II are shorter, stouter, and thicker with a less tapered profile and comparatively smoother surface. They originate from relatively shallow sockets, appear less prominent, and are sparsely distributed, primarily on the apical segment (Fig 4C; Fig 6)

SB I is longer in *M. cachmiriensis*, measuring 37.29 µm ± 2.3 µm, and shorter in *M. inezae,* measuring 29.715 µm ± 2.5 µm (Table 2). SB I is present in XIth and XIIth segments.

Table 2. Length of different types of sensilla among the three species of *Myrmica* Latreille, 1804 where n = number of sensilla measured.

Type of sensilla	*Myrmica aimonissabaudiae* Menozzi, 1939	*Myrmica cachmiriensis* Forel, 1904	*Myrmica inezae* Forel, 1902	Function
Ampullacea	Absent	0.425 µm ± 0.1 (n = 2)	Absent	Thermoreceptive and CO_2 receptive
Böhm Bristles	11.028 µm ± 4.332 µm (n = 6)	9.74 µm ± 2.78 µm (n = 8)	10.081 µm ± 1.014 µm (n = 7)	Mechanoreceptive
Basiconica I	30.07 µm ± 2.37 µm (n = 10)	37.29 µm ± 2.3 µm (n = 7)	29.715 µm ± 2.5 µm (n = 13)	Olfactory/ Chemoreceptive
Basiconica II	Absent	31.69 µm ± 2.1 µm (n = 6)	21.715 µm ± 2.4 µm (n = 8)	Olfactory/ Chemoreceptive
Branched Chaetica	94.9 µm ± 10.15µm (n = 11)	85.95 µm ± 6.36 µm (n = 8)	86.36 µm ± 7.32 µm (n = 6)	Mechanoreceptive
Chaetica I	63.7 µm ± 8.9 µm (n = 9)	52.7 µm ± 12.54 µm (n = 9)	20.57 µm ± 4.35µm (n = 10)	Mechanoreceptive
Chaetica II	11.7 µm ± 1.407 µm (n = 4)	17.36 µm ± 2.36 µm (n = 6)	19.45 µm ± 2.78 µm (n = 7)	Mechanoreceptive
Coelocapitulum	Absent	Absent	2.6 µm ± 0.1 µm (n = 2)	Thermo and hygroreceptive
Coeloconica	1.67 µm ± 0.019 µm (n = 4)	1.65 µm ± 0.306 µm (n = 3)	1.64 µm ± 0.06 µm (n = 2)	Chemoreceptive
Trichoidea	20.708 µm ± 4.05 µm (n = 6)	11.45 µm ± 2.24µm (n = 5)	15.08 µm ± 4.812 µm (n = 6)	Chemo and mechanoreceptive
Trichoidea Curvata	33.33 µm ± 1.9 µm (n = 8)	36.128 µm ± 1.6 µm (n = 7)	30.538 µm ± 1.38 µm (n = 5)	Mechanoreceptive

Table 3. Distribution of sensilla among the three species; BB: Böhm bristles; SA: Sensilla ampullacea; SB I: Sensilla basiconica I; SB II: Sensilla basiconica II; SCh I: Sensilla chaetica I; SCh II: Sensilla chaetica II; SChB: Sensilla chaetica branched; SCo: Sensilla coeloconica; SCp: Sensilla Coelocapitulum; ST: Sensilla trichoidea; STC: Sensilla trichoidea curvata.

S. No.	Type of sensilla	*Myrmica aimonissabaudiae* Menozzi, 1939	*Myrmica cachmiriensis* Forel, 1904	*Myrmica inezae* Forel, 1902
1	BB	+	+	+
2	SA	-	+	-
3	SB I	+	+	+
4	SB II	-	+	+
5	SCh I	+	+	+
6	SCh II	+	+	+
7	SChB	+	+	+
8	SCo	+	+	+
9	SCp	-	-	+
10	ST	+	+	+
11	STC	+	+	+

Sensilla chaetica (SCh): Sensilla chaetica is the most abundant sensilla type, with three subtypes: SCh I, SCh II, and SChB. SCh I is fine bristle-like, tapers towards the tip, and has a flexible socket; it is present in all segments in *M. aimonissabaudiae* (Fig 3B, 3F). SCh I is longer than SCh II. Among the three species, SCh I is longer in *M. aimonissabaudiae*, measuring 63.7 µm ± 8.9 µm, and shorter in *M. inezae*, measuring 20.57 µm ± 4.35 µm (Table 2). SCh II is a little curved at the tip and shorter in length as compared to SCh I. SCh II is located at the intersegmental joints (Fig 3G), where its insertion into a distinct, flexible socket suggests a high degree of articulation, likely facilitating sensitivity to antennal movement. SCh I and SCh II are present in all antennal segments.

Sensilla chaetica branched (SChB) display a markedly distinct morphology not previously reported for sensilla chaetica in ants. They have a branched architecture that substantially increases surface area (Fig 3C). Unlike SCh I and SCh II, SChB arise from a relatively shallow and less flexible socket, indicating reduced basal articulation. This structural modification, together with increased surface complexity, may accommodate more dendritic processes and thereby increase chemoreceptive efficiency. Length of SChB is longer in *M. aimonissabaudiae*, measuring 94.9 µm ± 10.15µm, whereas it is shorter in the case of *M. cachmiriensis*, measuring 85.95 µm ± 6.36 µm (Table 2).

Sensilla coeloconica (SCo): Sensilla coeloconica is a round aperture, i.e., a coelom or pit embedded in the cuticle with dendrites in it (Fig 3H). It is distributed from the IXth antennal segment up to the apex. SCo has been observed in pairs, and the pattern remains uniform from the IXth to apical segment (Fig 6). The diameter of its aperture is narrower in the case of *M. inezae,* with a width of 1.64 µm ± 0.06 µm, and wider in *M. aimonissabaudiae*, with a width of 1.67 µm ± 0.019 µm (Table 2).

Sensilla trichoidea (ST): Sensilla trichoidea (ST) are slender hair- like structures inserted into well- defined cuticular sockets, with the shaft articulated via a flexible membranous joint that allows limited mobility. In *M. cachmiriensis* Forel, 1904, the shaft exhibits distinct longitudinal striations and terminates in a porous tip. In contrast, ST in *M. aimonissabaudiae* and *M. inezae* lacks striations, with porosity extending along the entire shaft (Fig 3D, 3E). In *M. inezae*, ST occurs along the entire antenna, while in the other two species it is restricted to the IXth segment to the apex. ST reached its maximum length in *M. aimonissabaudiae* (20.71 µm ± 4.05 µm) and the minimum in *M. cachmiriensis* (11.45 µm ± 2.24 µm) (Table 2).

Sensilla trichoidea curvata (STC): Sensilla trichoidea curvata are sword-shaped sensilla with a flattened tip, and their length varies among the studied species (Fig 4A, 4E; Table 2). In *M. aimonissabaudiae* and *M. cachmiriensis*, pore plates were observed, suggesting a chemoreceptive role. STC attained maximum length in *M. cachmiriensis* (36.128 µm ± 1.6), while the minimum length was recorded in *M. inezae* (30.538 µm ± 1.38).

Common to *M. cachmiriensis* and *M. inezae*

Sensilla basiconica II (SB II): SB II is longer than SBI. It is longer in *M. cachmiriensis* with 31.69 µm ± 2.1 µm length, and shortest in *M. inezae,* i.e., 21.715 µm ± 2.4 µm (XII^{II} segment) (Table 2). SB II has been seen in the apical segment only (Fig 6). The porosity of SB II gradually increases from base towards the tip (Fig 4C).

Sensilla exclusive to *M. cachmiriensis*

Sensilla ampullacea (SA): Typically, it has been referred to as 'peg in pit' and observed on the IXth and Xth antennal segments of *M. cachmiriensis* (Fig 4F) (Table 2). The diameter of its aperture is 0.425 µm ± 0.1 µm.

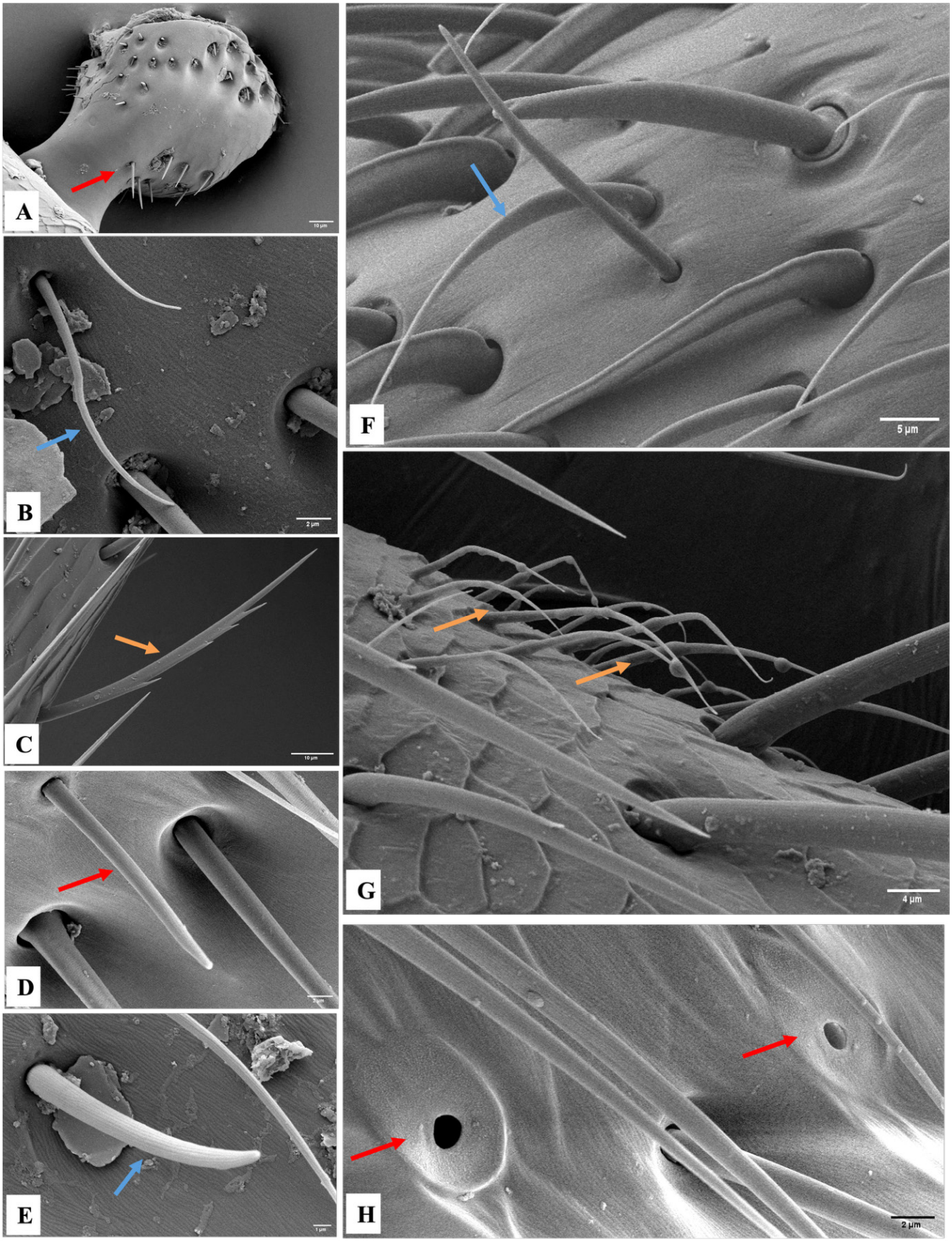

Fig 3. Scanning electron micrographs of different types of sensilla in *Myrmica aimonissabaudiae* Menozzi, 1939 (red arrow); *Myrmica cachmiriensis* Forel, 1904 (blue arrow); *Myrmica inezae* Forel, 1902 (orange arrow): (A) Böhm Bristles (BB) present on scape ball; (B), (F) Sensilla chaetica I (SCh I); (C) Sensilla chaetica branched (SChB); (D), (E) Sensilla trichoidea (ST); (G) Sensilla chaetica II (SCh II); (H) Sensilla coeloconica (SCo). Scale bars for (A), (C) = 10 µm; (B), (D), (H) = 2 µm; (E) = 1 µm; (F) = 5 µm; (G) = 4 µm.

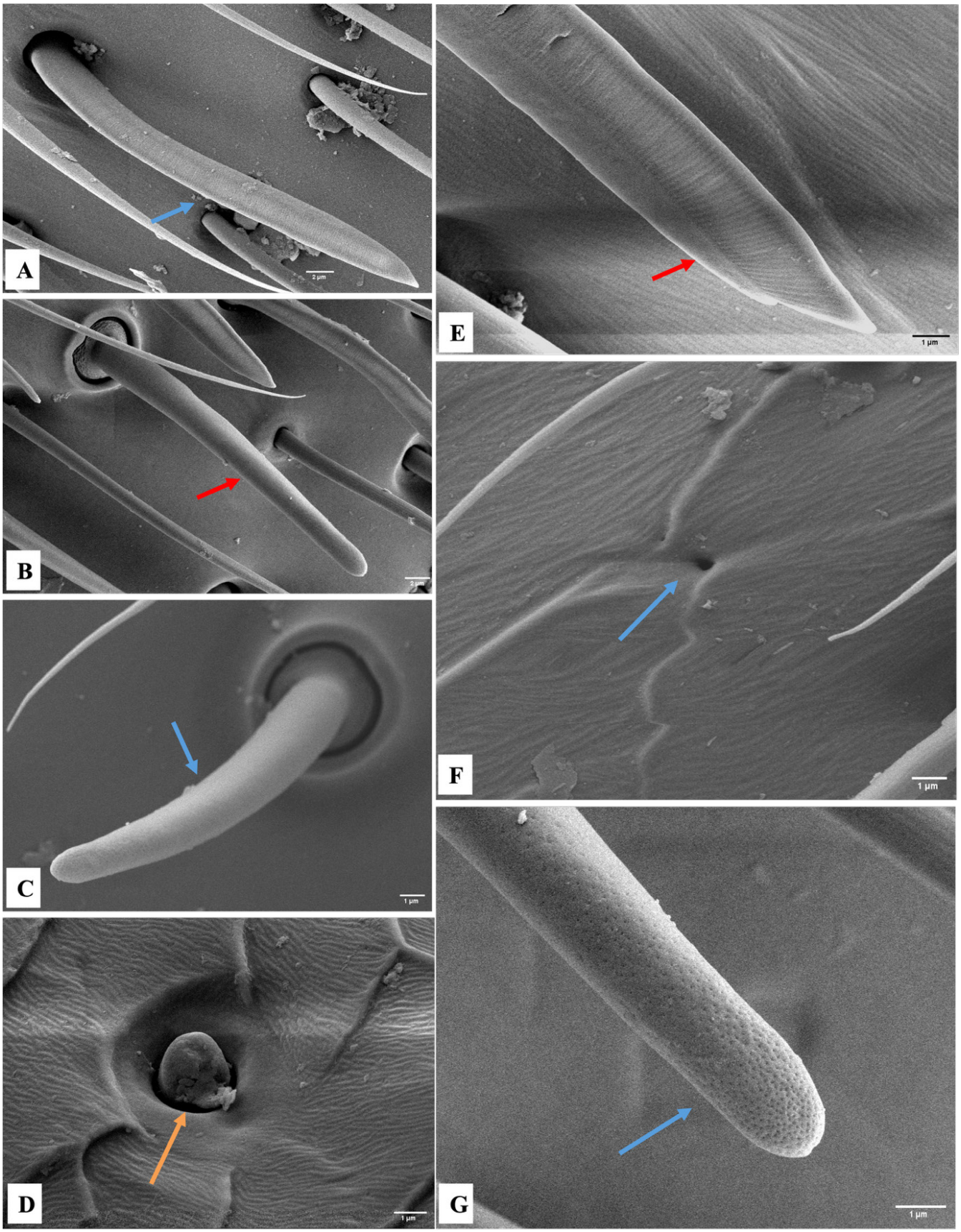

Fig 4. Scanning electron micrographs of different types of sensilla in *Myrmica aimonissabaudiae* Menozzi, 1939 (red arrow); *Myrmica cachmiriensis* Forel, 1904 (blue arrow); *Myrmica inezae* Forel, 1902 (orange arrow): (A), (E) Sensilla trichoidea curvata; (B), (G) Sensilla Basiconica I (SB I); (C) Sensilla Basiconica II (SB II); (D) Sensilla coelocapitulum (SCp) (F) Sensilla Ampullacea (SA). Scale bars for (A), (B) = 2 µm; (C), (D), (E), (F), (G) = 1 µm.

Sensilla Exclusive to *M. inezae* Forel, 1902

Sensilla coelocapitulum (SCp): It is a small nub-like projection that comes out of a small aperture. It has been observed only in *M. inezae* (Fig 4D, Table 2).

Discussion

The present study reveals interspecific variation in antennal sensilla among the three species, indicating their functional and ecological importance. Böhm bristles are either long or short (BB, respectively), straight hairs, non-porous sensilla with a smooth surface and a wide socket. Böhm bristles function as mechanosensory structures that monitor antennal movement and orientation by encoding the antenna's position relative to the head (Sant & Sane, 2019; Krishnan et al., 2012). In the present investigation, they were observed on the scape ball in all three species. Early reports documented their presence across various species of Formicidae, including *Camponotus*, *Paratrechina longicornis*, *Dolichoderus moggridgei*, *D. thoracicus*, *Monomorium indicum,* and *Polyrhachis* species, supporting their fundamental role in proprioception and mechanosensory function, which is critical for exploration, foraging, and social communication (Hashimoto, 1990; Ehmer & Gronenberg, 1997; Hazarika & Khanikor, 2022).

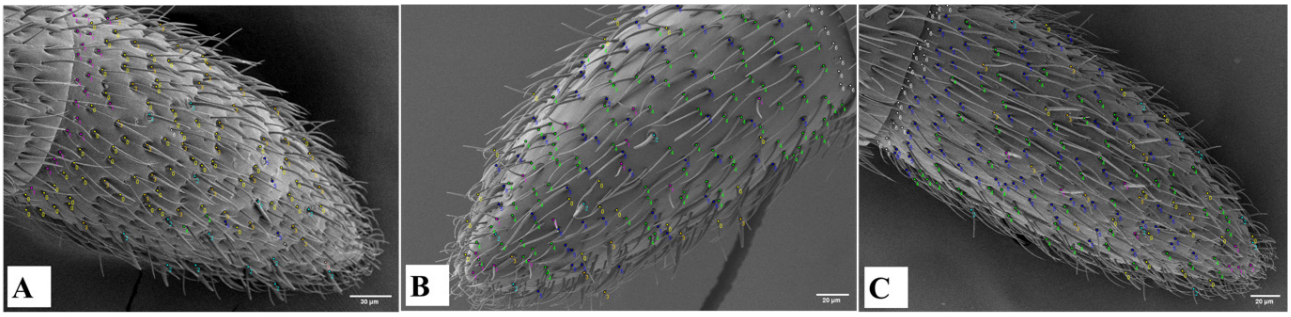

Fig 5. (A) *Myrmica aimonissabaudiae* Menozzi, 1939 apical segment abundance, 0: Sensilla Chaetica I; 1: Sensilla Chaetica II; 2: Sensilla Basiconica I; 3: Sensilla Trichoidea Curvata; 4, 6: Sensilla Trichoidea; 5: Sensilla Coeloconica; Fig 5 (B) *Myrmica cachmiriensis* Forel, 1904 apical segment abundance, 0,1: Sensilla Trichoidea; 2: Sensilla Basiconica II; 3: Sensilla Basiconica I; 4: Sensilla Chaetica I; 5: Sensilla Trichoidea Curvata; 6: Sensilla Chaetica II; Fig 5 (C) *Myrmica inezae* Forel, 1902 apical segment abundance, 0: Sensilla Basiconica I; 1: Sensilla Basiconica II; 2, 3: Sensilla Trichoidea; 4: Sensilla Trichoidea Curvata; 5: Sensilla Chaetica I; 6: Sensilla Chaetica II. Scale bars for 5 (A) = 30 µm; (B), (C) = 20 µm.

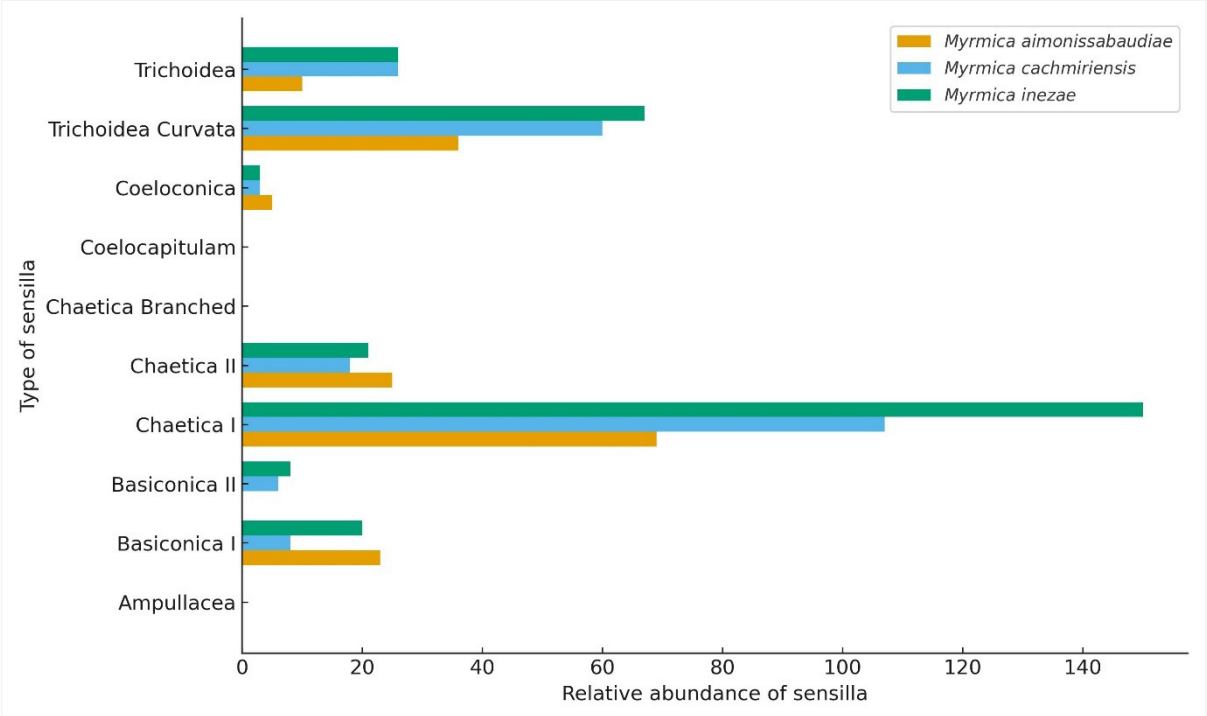

Fig 6. Comparative plot of a clustered bar graph of the type of sensilla and relative abundance of sensilla in the apical segment of three *Myrmica* species, where orange, blue, and green colors represent *Myrmica aimonissabaudiae* Menozzi, 1939, *Myrmica cachmiriensis* Forel, 1904, and *Myrmica inezae* Forel, 1902, respectively.

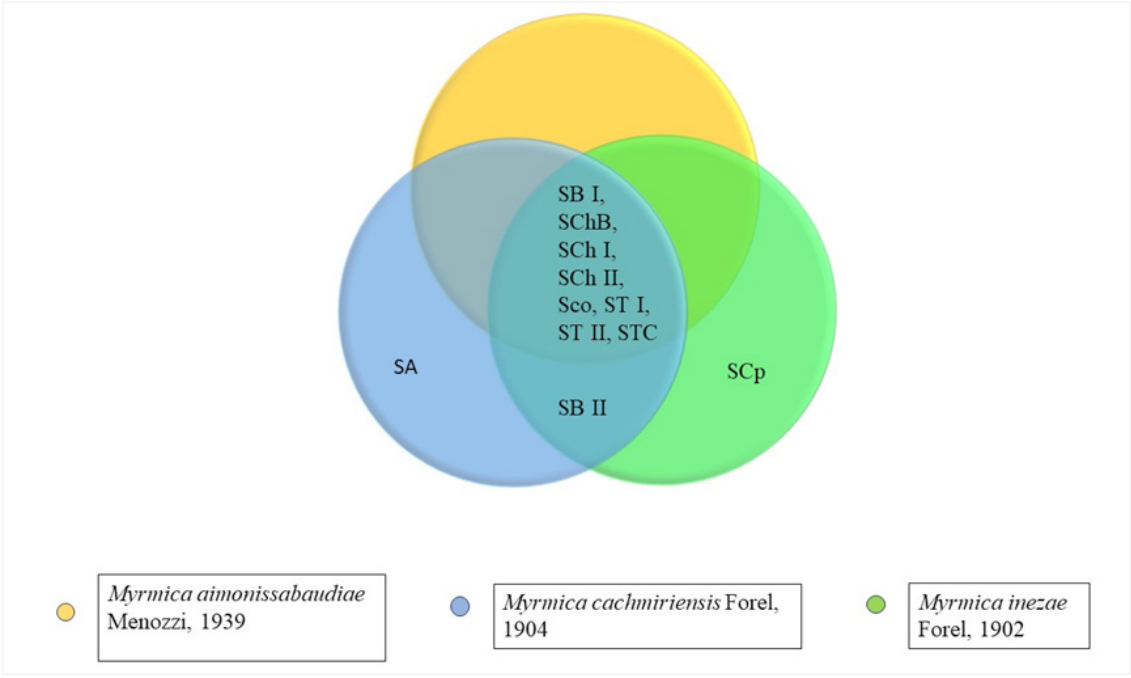

Fig 7. Venn Diagram of three *Myrmica* species depicting various sensilla types.

Sensilla basiconica (SB) have been consistently described as peg-like projections exhibiting conical or thumb-shaped morphology with rounded apices (Zacharuk, 1985; Nakanishi et al., 2009). Structurally, these sensilla comprise a cuticular peg articulated within a socket, with distal pores indicative of olfactory function (Hashimoto, 1990). For instance, in *Diacamma* species, SB are sex-specific, occurring exclusively in the female and worker castes, and functioning as contact chemoreceptors (Okada et al., 2006). In the present study, the multiporous, elongated, and slender subtype SB I is distinguished from SB II, which is comparatively shorter, more rounded, and less abundant. Both subtypes have porous apices, consistent with their established role in detecting volatile compounds. Notably, only SB I has been previously described in earlier studies (Kleineidam & Tautz, 1996; Renthal et al., 2003; Hosoishi & Ogata, 2009; Euzébio et al., 2013; Ramirez-Esquivel et al., 2014; Ramirez-Esquivel et al., 2017; Freelance et al., 2019).

Previous studies have characterized sensilla chaetica (SCh) as slender, socketed, hair- or bristle-like structures with smooth surfaces and without wall pores, a morphology strongly indicative of a mechanoreceptive function (Dumpert, 1972; McIver, 1975; Marques-Silva et al., 2006; Ramirez-Esquivel et al., 2014). These observations support their primary role in detecting tactile stimuli rather than chemical signals. The present study corroborates their aporous, bristle-like architecture while also providing novel insights by identifying two distinct subtypes. SCh I closely resembles previously described sensilla chaetica in *Crematogaster* and *Myrmecia pyriformis* (Hosoishi & Ogata, 2009; Ramirez-Esquivel et al., 2014). In contrast, SCh II is localized to the intersegmental regions of the antenna and has not been previously reported.

Sensilla chaetica branched (SChB) represent a previously undescribed subtype, thereby expanding the known morphological diversity and distribution of chaetic sensilla in ants. No comparable structures have been reported in other ant taxa, although they exhibit partial resemblance to the palmate sensilla described in *Temnothorax rugatulus* (Dumpert, 1972; Hashimoto, 1990; Kleineidam et al., 2000; Renthal et al., 2003; Marques-Silva et al., 2006; Nakanishi et al., 2009; Mysore et al., 2010; Barsagade et al., 2013; Ramirez-Esquivel et al., 2014; Yan et al., 2011). Palmate sensilla exhibit a scoop-like shape with longitudinal grooves and olfactory pores. In contrast, SChB lack the rounded, palm-like tip and instead show elongated, broader, and distinctly branched projections (Ramírez-Esquivel et al., 2017). In the present study, branching in SChB arises from the base, whereas in palmate sensilla it is limited to the distal tip, resulting in a more expanded surface structure in SChB. Such structural specialization may be an adaptation to low ambient temperatures, where detection of volatile chemical cues is reduced. In this context, the branched form of chaetic sensilla may improve sensory efficiency by increasing the receptive surface area. It is therefore suggested that the greater branching and elongation of SChB enhance the perception of volatile cues under extreme climatic conditions.

In *Myrmica aimonissabaudiae* Menozzi, 1939 and *M. inezae,* they occur from the scape to the VIIIth antennal segment, while in *M. cachmiriensis* Forel, 1904 they extend from the scape up to the IXth segment. Sensilla chaetica branched (SChB) are most abundant and longest in *M. aimonissabaudiae* Menozzi, 1939, which inhabits disturbed, anthropogenic environments.This pattern likely reflects ecological adaptation that may compensate for reduced sensillar diversity in this species (absence of SA, SB II, and SCp). In contrast, *M.*

cachmiriensis and *M. inezae,* which occupy more restricted and shaded habitats, exhibit sensilla types unique to these species. Further ultrastructural studies (e.g., Transmission electron microscopy) are needed to determine the relationship between branching and dendritic innervation in volatile cue detection.

Sensilla coeloconica (SCo) are pit-like structures with larger openings than sensilla ampullacea. They were first reported in *Solenopsis invicta* (Renthal et al., 2003) and later described in *Camponotus japonicus* (Nakanishi et al., 2009). Their role in temperature sensing using cold-sensitive neurons was observed in *Atta vollenweideri* (Ruchty et al., 2009). The present study supports these findings, as the observed sensilla show round cavities with relatively large openings, indicating their likely involvement in thermoreception.

Sensilla trichoidea (ST) were initially described as hair-like sensilla with surface porosity, indicating chemoreceptive function (Ramirez-Esquivel et al., 2014). Subsequent investigations emphasized their grooved and socketed morphology, which enhances surface area and facilitates detection of chemical cues (Barsagade et al., 2019). Previous studies have reported the presence of sensilla trichoidea on insect antennal segments in abundance, which function as contact chemoreceptors (Hashimoto, 1990; Ramirez-Esquivel et al., 2014; Barsagade et al., 2020). The present study demonstrates pronounced grooves and multiporosity, supporting their function as highly sensitive chemoreceptors.

Sensilla ampullacea (SA) are dome-shaped, aporous peg-in-pit sensilla known for their role in thermoreception, containing neurons sensitive to temperature changes (Ruchty et al., 2009; Kleineidam et al., 2007). They differ from sensilla coeloconica in having a smaller pit and a less exposed peg. SA have been reported in several ant species, including *Myrmecia pyriformis* and *Camponotus japonicus* (Ruchty et al., 2009; Nakanishi et al., 2009). In the present study, however, SA were observed only in *Myrmica cachmiriensis* Forel, 1904, suggesting a species-specific distribution that may reflect ecological adaptation. Similar thermosensory roles have been documented in *Atta vollenweideri*, where these sensilla detect temperature-related cues (Kleineidam et al., 2007). These findings indicate the functional importance of SA in thermosensory ecology.

Sensilla coelocapitulum (SCp) are peg-in-pit sensilla with a cap-like structure that function in thermoreception and hygroreception (Zacharuk, 1985; Ramírez-Esquivel et al., 2017; Ruchty et al., 2009). They enable detection of temperature and humidity, helping ants respond to microclimatic variations. *Myrmica inezae* inhabits shaded and sheltered environments, and the presence of SCp may represent an adaptation to such conditions.

In *Myrmica cachmiriensis* and *Myrmica inezae*, sensilla basiconica II (SB II) were observed paired with Sensilla Trichoidea (ST I), with the latter positioned more distally toward the apex (Fig 3F). A similar spatial arrangement has been reported previously in *Myrmecia pyriformis*, indicating a conserved pattern of sensillar organization across related ant species (Ramirez-Esquivel et al., 2014).

On the apical segments of the three examined ant species, both the density and diversity of antennal sensilla increase markedly (Fig 5A-C). The horizontal clustered plot of the apical segment shows the comparative abundance of these sensilla among the three species (Fig 6). Notably, sensilla basiconica II is entirely absent in *Myrmica aimonissabaudiae* across the entire antenna, including the apical segment. Among the other sensilla types, sensilla chaetica are particularly abundant in *M. inezae* and *M. cachmiriensis,* indicating species-specific variations in sensillar distribution and potentially reflecting ecological or behavioral adaptations.

Conclusion

The three *Myrmica* species studied here show clear differences in sensillar structure that reflect their morphology, ecology, and habitat. *M. aimonissabaudiae*, a weedy species found in disturbed areas, has a generalized antennal sensilla distribution, with sensilla chaetica branched being more abundant and longer than in the other two species (Table 2). *M. inezae*, and *M. cachmiriensis*, which are restricted to shaded, secluded habitats, show a more specialized sensillar arrangement. *M. inezae* possesses sensilla coelocapitulum, which are thermoreceptive and hygroreceptive, as reported in other Myrmicinae (Ramirez-Esquivel et al., 2014), while *M. cachmiriensis* has sensilla ampullacea, sensitive to temperature and CO_2, consistent with previous studies.

Sensillar diversity and abundance increase from the scape to the tip of the antenna in all species. The novel sensilla chaetica branched resemble palmate sensilla but differ in morphology, reflecting ecological differences from *Temnothorax*. These branched sensilla are most abundant and long in *M. aimonissabaudiae* and may help detect small volatile cues in challenging environments. Future studies using transmission electron microscopy could clarify their ultrastructure and functional significance in these ants.

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