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Flagellar sensillum patterns in Nyssoninae and Philanthinae wasps (Hymenoptera, Sphecidae)

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Morphology and distributional patterns of antennal sensilla were compared between four species in three genera of Sphecidae. Sensilla placodea have plates that are raised to resemble low domes in *Argogorytes mystaceus* and *A. fargei* or low pegs in *Bembix rostrata* and *Cerceris rybyensis*. Sensilla basiconica occur in both sexes of *Bembix* and *Cerceris*, but, similarly to Apidae (*s. lat.*), only in females of *Argogorytes*. The antennae of the two species of *Argogorytes* differ primarily in being larger in *A. mystaceus*, thus permitting space for more sensilla. In *Bembix rostrata*, the male antennae are adapted to function as 'gripping' organs.

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Introduction

The sensillar equipment of hymenopterans has attracted curiosity since the earliest students of microscopy (Hicks 1857; Leydig 1860). These studies addressed various aspects of the morphology, physiology and development of the sensilla. The value of the morphological and distributional patterns as taxonomic characters has been considered by Wacker (1925) and Walther (1979, 1981, 1983). To complement electrophysiological investigations by the author, the antennae of chosen Hymenoptera species have been surveyed by scanning electron microscopy (SEM). The results so far indicate that sensilla types appear similar among the bee 'families' (*s. str.*) Apidae, Colletidae, Halictidae and Andrenidae, but their distribution patterns vary between taxa and between sexes (Ågren 1975, 1977, 1978; Ågren & Svensson 1982).

The present paper compares material of four species of Sphecidae; *Bembix rostrata* (L., 1758) (also investigated by Walther 1983), *Argogorytes mystaceus* (L., 1761), *A. fargei* (Shuckard, 1837) (all Nyssoninae), and *Cerceris rybyensis* (L., 1771) (Philanthinae). The Sphecidae are considered to be the most closely related wasps to the Apidae (*s. lat.*) (Lomholt 1976).

Adult *Bembix* wasps have an interesting territorial behaviour (Schöne & Tengö 1981) and the two species of *Argogorytes* wasps investigated here are lured by deception to pollinate the orchid *Ophrys insectifera* (Kullenberg 1961). All four species are predators on other insects. *Bembix rostrata* feeds on brachyceran Diptera, both *Argogorytes* species feed on Jassidae (Homoptera) and *Cerceris rybyensis* preys on pollen-foraging bees returning to their nests (Lomholt 1976).

Material and methods

Scanning electron micrographs were taken of antennae from males and females of *Bembix rostrata, Argogorytes fargei, A. mystaceus* and *Cerceris rybyensis*. The wasp nomenclature follows that of Lomholt (1976).

All individuals were collected on the island of Öland, off the south-eastern coast of Sweden. Air-dried antennae were fastened to specimen stubs with conductive glue, gold-sputtered (200–400 Å) and examined in a JEOL JSM-35 scanning electron microscope (Ågren 1975).

Although the most recent nomenclature for sensilla, proposed by Altner (1977), is preferred and most objective, that of Esslen & Kaissling (1976), based on more subjective features, is more appropriate for the comparative morphological emphasis of this study (van Nieukerken & Dop 1987) since the internal structures of the investigated sensilla are still unknown. The s. trichodea C and D are not differentiated for the same reasons, but referred to as C/D. The flagellar annuli are designated fl^1, fl^2, . . . in a proximal to distal direction. The terminology of the surface sculpturing follows Harris (1979).

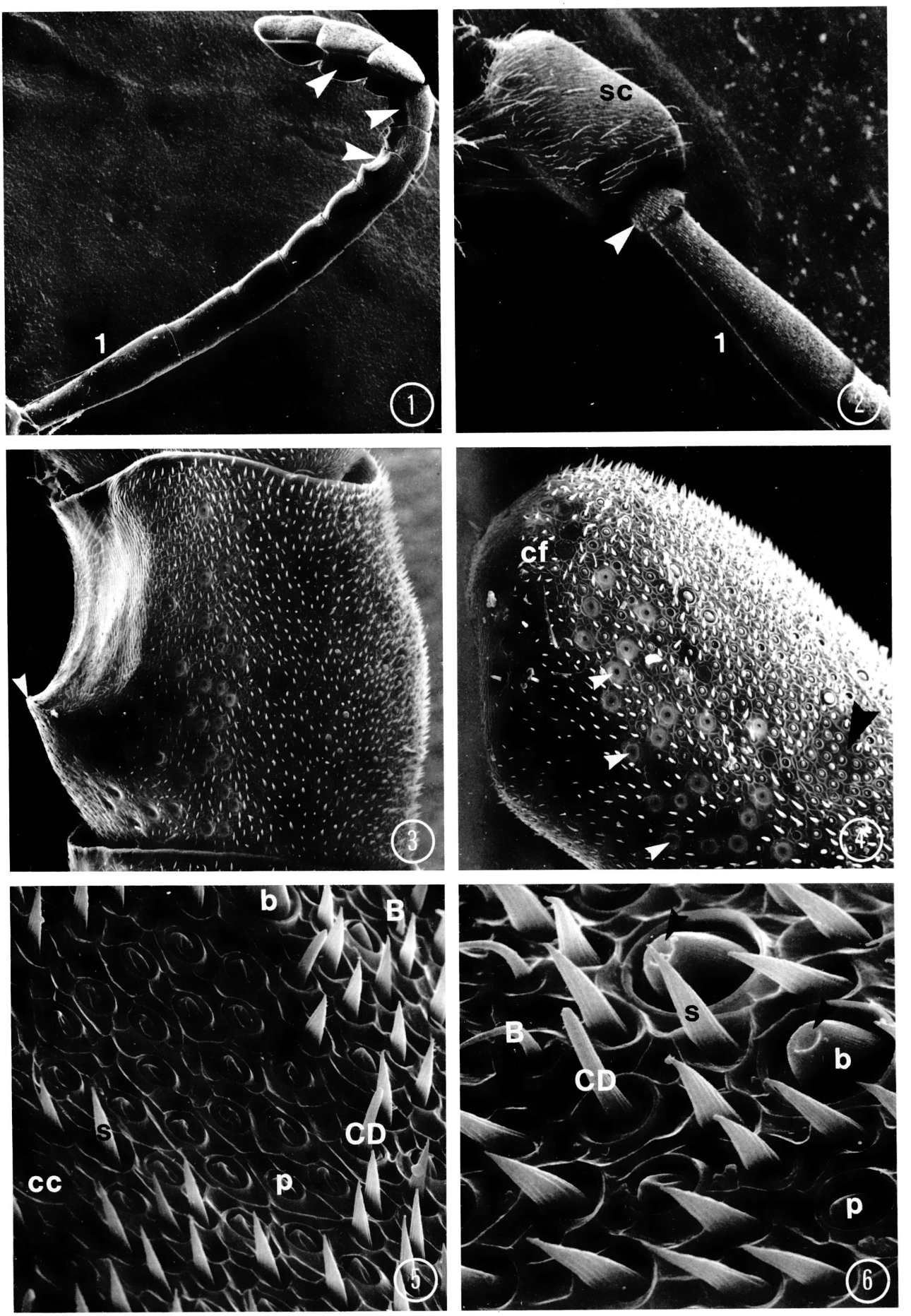
Results

Bembix rostrata

General morphology of antennae (Fig. 1). The dorsal, ventral and lateral sides of the antenna are difficult to identify due to the often twisted and bent shape of the flagellum. One clue is the black band on the otherwise yellow antenna. This band is dorsal on the scape and pedicel and seemingly dorsal on the flagellum as well.

Flagellar lengths are 4.8–5.4 mm in males and 4.5–5.0 mm in females. The scape is stout (Fig. 2) in both sexes. In the male, the three distal annuli are concave ventrally (Fig. 1) and have very few setae or sensilla. The ventral cuticle is imbricate, and, from fl^6 distally, has an angular edge towards the sensillum-rich part (Fig. 3). Fl^1 is long and thickened distally (Fig. 2). $Fl^{3–5}$ are smoothly bulbed ventrally (Fig. 1), bulb increasing in size distally. The female annuli are straighter and more cylindrical.

In males only, the distal part of the antenna from fl^6 outwards is formed into a hook (Fig. 1). When the antenna is fully flexed, the annuli of the hook, together with a transverse ventral ridge on fl^6 (Fig. 3), form a 'grip', grasping the female antenna during copulation (Tengö &



Figs. 1–6. Bembix rostrata male.—*1.* Right antenna inner/ventral aspect. Note the concave ventral area in the distal annuli (*arrows*). ×23.—*2.* Left antenna, dorsal aspect, with stout scape, small pedicel (*arrow*) and long fl^1. ×35.—*3.* Fl^6, inner/ventral aspect, the ventral side lacks sensilla almost entirely and is equipped with a ridge (*arrow*) which, together with the distal annuli, forms a grip upon folding of the antenna. ×180.—*4.* Left fl^{11}, dorsal aspect. *Black arrow* points to small s. placodeum zone, similar to that in Fig. 5; *white arrows* point to s. coeloconica. ×230.—*5.* Fl^{10}, dorsal aspect. Small zone with only s. placodea (wrinkled during the drying process). ×950.—*6.* Fl^9, dorsal aspect. S. basiconica with wide sockets and sunken tips (*arrows*). ×2100.

Ågren in prepn). The females' antennae do not have any corresponding special morphological features.

Sensillar zones. Setae, together with a few s. trichodea C/D, are the only pegs on the ventral surface (Fig. 3). Dorsally, setae and s. placodea are the most common, but are mixed with smaller numbers of other sensilla, including s. trichodea A and B (Fig. 4). Laterally between these surfaces is a zone with setae and s. trichodea. On the opposite lateral side is another zone with setae and pit organs.

On fl^8 to fl^{11} in the male there is a distinct small dorsal field facing laterally outwards. This field is composed exclusively of pore plates, numbering about 20–25 altogether (Fig. 5).

The flagellar apex has very few sensilla (Fig. 4).

The antennal dorsal cuticle is scabrous, the ventral side imbricate. In the 'grip' on fl^6 in males the scales are turned backwards and among the scales there are numerous small pores.

Setae. Setae are abundant over all the antennal surface distal to the base of fl^1, especially in the sensilla-poor ventral/proximal zone, but are also very common among the s. placodea. The setae are deeply ribbed, creating 10–15 longitudinal or elutely spiralled, rounded ridges (Figs. 5, 6), taper sharply at the tips, may be somewhat flattened laterally and are not erect, pointing distally in a slightly curved fashion. On the scape, the setae are thinner, in the 'grip' area they are short, stout, almost fang-like. Their sockets are not prominent, but the hairs are positioned in wide irregular craters.

Setae that obviously serve as mechanoreceptors for the flagellar posture are evident along the proximal margin of the annuli. They are somewhat thinner than ordinary setae.

Sensilla. Sensilla trichodea A, fewer than setae, are more numerous in females. They are glabrous (1–2 faint longitudinal institia may occur) and bent distally, with the tip pointed slightly up (Fig. 7). In both sexes they occur on all annuli from the distal part of fl^1 on the dorsal surface among s. placodea. The socket is round, and about twice as wide as the hair.

The small s. trichodea B are never abundant. They are distributed in the same zones as s. placodea (Fig. 6) and occasionally among the setae on all annuli. They are easily distinguished from other sensilla in being small and thin, elutely canaliculate, sharp and arched in an almost 90° angle (Fig. 8).

Sensilla trichodea C/D are sparsely scattered over the whole antenna (Figs. 5, 6), except in the 'grip' area of the males; in females, at least two sizes are found. The sensilla are long, erect, with the blunt tip oriented slightly upwards and backwards (Fig. 9). They are canaliculate, but not as coarsely as the setae. There is a pore at the tip. The socket is prominent.

Sensilla placodea are located in both sexes on the outer and dorsal sides of the flagellum, from mid fl^1 distally, together with setae, s. basiconica and other sensilla (Figs. 4–6). They have an unusual morphology in *B. rostrata*. The plates, situated in craters, are raised as low pegs, which may be somewhat more angular in females (Fig. 10). They are only 6–8 μm across, approximately half the size as is usual in Apidae (*s. lat.*). The pores are not arranged radially, as in bees (Ågren 1975), but irregularly. The centrifugal ring is sunken into the crater, and in air dried specimens a crevice surrounds it.

Pit organs occur in only one size and appear to be s. coeloconica, since their sunken peg can be seen (not possible in s. ampullacea). There are many on the lateral antennal surface (Figs. 3, 4), where they are arranged in a band along all annuli, from mid fl^1 in males and mid fl^2 in females. This band is broadest on the terminal annulus. The field around the pit, which is 3 μm in diameter, is nude and about 10 μm across (Fig. 5). Inside the pit, the inner raised cuticular ring is evident.

Sensilla campaniformia are distributed in the same regions as pit organs from mid fl^1 laterally on the outside. They also resemble pit organs in terms of surrounding field (Fig. 4). They have radial institia in the field, and the shape of the 'head' is irregular (Fig. 11).

Sensilla basiconica are prominent in both sexes (Figs. 4–6) from mid fl^1 in the male, proximal fl^1 in females. They measure approximately 7 μm across and only 8 μm in length and have indications of an apical pore. The peg wall is canaliculate, but the sunken (artifact of air drying?) tip appears regularly nodulate (Fig. 12). The socket is surrounded by a raised ring.

Argogorytes fargei

The antennal form, as well as the sensillar equipment, is generally similar to that of Apidae (*s. lat.*) (Esslen & Kaissling 1976), with the noted exception of the unusual s. placodea.

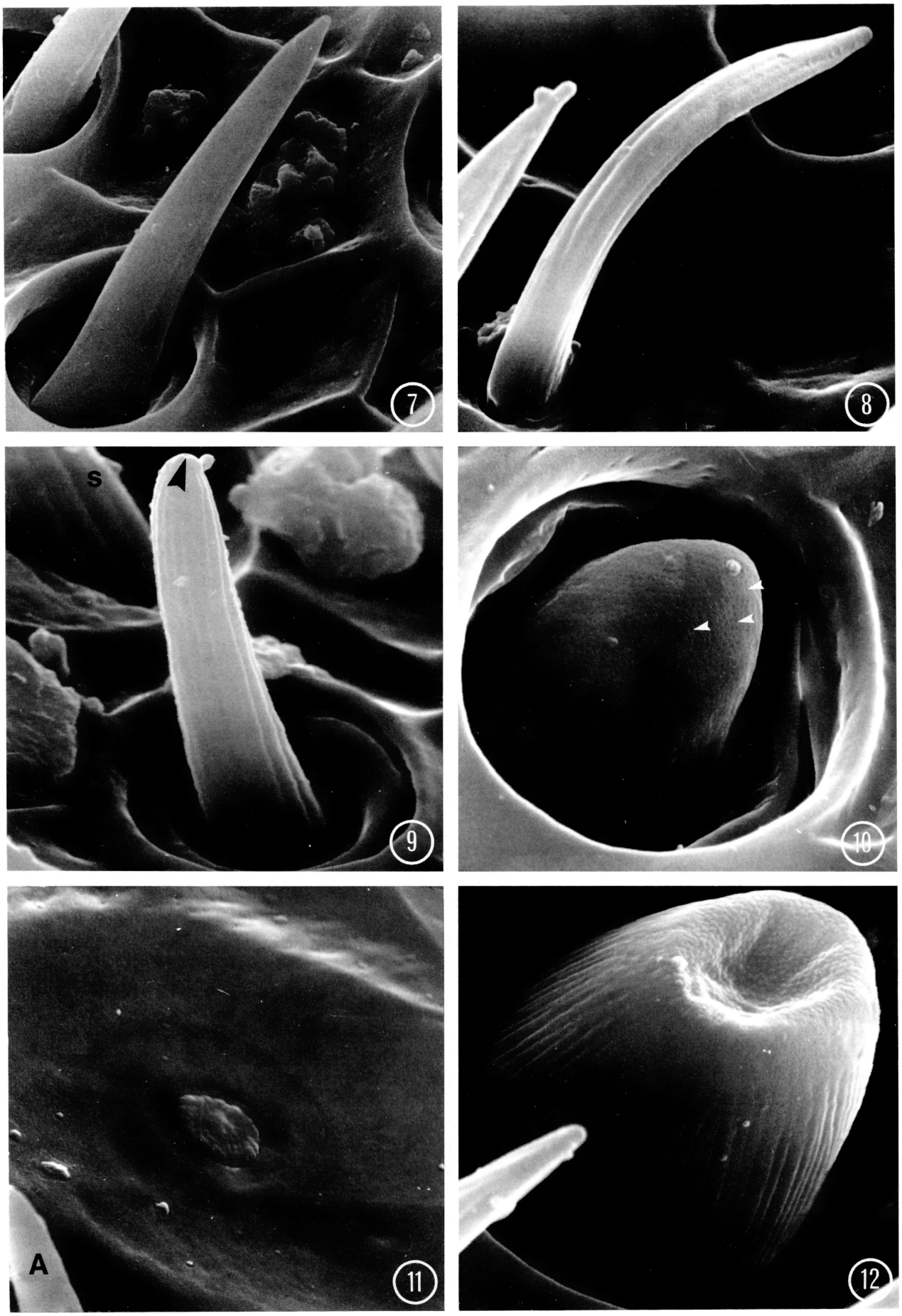
General morphology of antennae. The antennae have cylindrical annuli. The proximal annuli are somewhat longer than the distal ones, and the flagella are *c.* 4.5 mm long in both sexes. Pegs and setae are not all pointed in the same direction (terminally), but, depending on their position, are oriented towards the distal/dorsal side. The flagellar apex is densely packed with s. trichodea B and C/D. The cuticle surrounding the sensilla is rugose.

Sensillar fields. No bare zones are found here, with the sensilla and setae covering the whole flagellar surface. As in the other species, setae dominate ventral surfaces; s. trichodea A are found only dorsally.

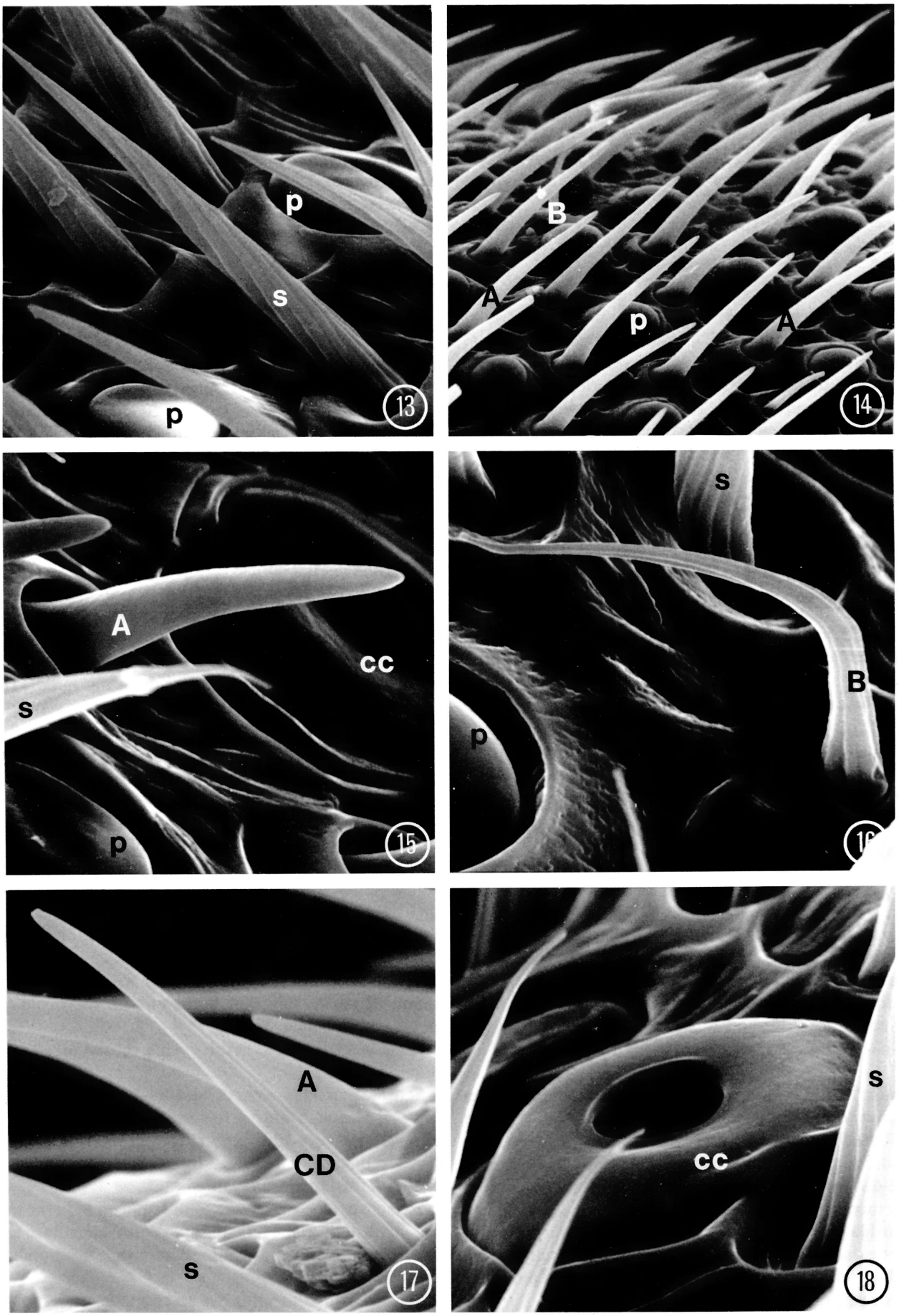
Setae. The setae are helically sculptured, like impala horns, and have a whip-like tip (Fig. 13). They occur on all annuli, but are somewhat less dense dorsally. Those in either the most proximal or ventral parts of the flagellum are less erect. The sockets are narrow.

As in *B. rostrata*, there are slender setae proximally on the annuli that apparently register the relative positions of the annuli at the joints.

Sensilla. Sensilla trichodea A are similar to those of Apidae (*s. lat.*) (Ågren 1975). They are slender and glabrous, without the S-form typical of *Apis* (Ågren 1975), and are found only on the dorsal surface. The



Figs. 7–12. Bembix rostrata.—7. Male, s. trichodeum A. ×7300.—*8.* Female, s. trichodeum B. Socket inconspicuous. ×12,700.—*9.* Male, s. trichodeum C/D. Wide socket, *arrow* points to pore at the tip. ×8500.—*10.* Female, s. placodeum. Note pores (*arrows*). ×12,800.—*11.* Female, s. campaniforme. ×9200.—*12.* Female, s. basiconicum (tip sunken during air drying). ×11,600.



Figs. 13–18. Argogorytes.—13. A. fargei male, fl^{10}, setae and s. placodea. ×3100.—*14. A. fargei* male, fl^{11} dorsal surface, note s. placodea. ×1300.—*15. A. fargei* female, fl^{8}, s. trichodeum A. ×6000.—*16. A. mystaceus* female, fl^{10}, s. trichodeum B. ×6800.—*17. A. fargei* male, fl^{11}, s. trichodeum C/D. ×4500.—*18. A. fargei* female, fl^{8}, s. coeloconicum. ×6000.

cuticle around the sockets is somewhat raised (Figs. 14, 15).

Sensilla trichodea B are present in generally increasing numbers distally; on the proximal annuli they occur only on the dorsal surface, but towards the apex also on the ventral side. They have longitudinal furrows, which stop before the tip as the peg tapers off sharply and ends like a whiptail. The sockets are narrow (Fig. 16, of *A. mystaceus*).

Sensilla trichodea C/D are rather evenly dispersed all around the flagellum. They are canaliculate, *c.* 22 μm long and erect (Fig. 17).

Sensilla placodea occur distally from the proximal border of fl^1. At first they are found only on the dorsal side, but from approximately fl^4 around the whole antenna, although more sparsely on the mid-ventral surface. The plate is raised and resembles a hemispherical dome separated from the surrounding surface by a crevice (Fig. 14). This cleft may either be an artifact of the air drying or correspond to a lower point at which the plate rim is fastened to the cuticle. The outer rim of the sensillum is raised; radial rows of pores are discernable on the plate surface.

Sensilla coeloconica are situated primarily along the ventral midline, but also dorsally/medially in increasing number from around fl^5 distalwards. The pits are 4–6 μm across (Fig. 18) and encircled by a smooth flat field 11–13 μm in diameter, raised above the surrounding cuticle. The peg is canaliculate and situated in an internal caldera-like structure.

Sensilla campaniformia were not observed.

Sensilla basiconica are restricted to females, where they are slender and aggregated distally/dorsally from approximately fl^4 distalwards. They display a distinct bulge at the tip, presumably indicating the location of a pore, and have wide sockets.

Argogorytes mystaceus

General morphology of antennae. The flagella of males (*c.* 7.8 mm long) are 2/3 longer than those of *A. fargei*, hence there is space for more sensilla, and the annuli are slightly curved. In females (flagella 4.2 mm long) the annuli are approximately 35% shorter than in males. Fl^{11} is long and club-like in both sexes.

Sensilla. Sensilla trichodea A occur most proximally on fl^1, close to the scape. On the remaining annuli they are distributed in a dorsal zone shared with s. placodea. The sensilla, generally S-bowed in bees (Ågren 1975), are here more downwardly curved at the tip. The socket is relatively inconspicuous.

Sensilla placodea. Males: compared to *A. fargei*, the s. placodea seem to be somewhat denser ventrally in the distal annuli. Females: none found ventrally in a narrow zone or ventrally/distally on fl^{10}.

Sensilla coeloconica. Males: in low numbers, on ventral surface of fl^{7-11}. Females: for all annuli distally/dorsally, fewer laterally, somewhat higher in number distally. The nude field around the pit is large.

Sensilla campaniformia were observed only on fl^9 close to s. coeloconica in a single female. No prominent field surrounded the central bulb.

Sensilla basiconica were recorded only in females among the s. placodea from fl^5 outwards, in greater numbers distally. They appear in different sizes and are carinulate. A trace of an apical pore suggests a function as taste organs. The socket is large and, as in s. placodea, the cuticle is raised around the sensillum. The membranous socket is shrunken in the fixation processes.

With respect to other sensilla this species is similar to *A. fargei.*

Cerceris rybyensis

General morphology of antennae (Fig. 19). The antennae are filiform, with most female flagella having a circumference up to 150% of that in males (flagella 2.4–2.8 mm long in males, 2.6–2.9 mm in females). In males the annuli are evenly cylindrical and quite short; fl^1 is somewhat asymmetrical. The scape is less stout than in *B. rostrata.* Female annuli are distinguished by being more bulbous.

There is a small sensillum-free area at the antennal apex. The ventral hairs and pegs on fl^{10} of the female are all centred towards a point proximal to this sensillum-free area. The flagellar cuticle is rugose.

Sensillar fields. Females have more sensilla than males due to the greater size of their antennae. As in other species above, s. trichodea A and s. placodea are aggregated into a dorsal field that begins at the middle of fl^1 (Fig. 20). Additionally, females possess a ventral pit organ field.

Setae. These are present in all annuli, being especially dense on the ventral surface and proximally on the dorsal surface. As in the species above, they have a spiralled appearance (Figs. 21, 22) and the small setae occur on the most proximal part of the distal annulus at the flagellar joints.

Sensilla. Sensilla trichodea A occur dorsally on all annuli and in greater density in females.

Sensilla trichodea B (Figs. 20, 23) are numerous on all annuli of the female, but occur only in the distal-most annulus of the male.

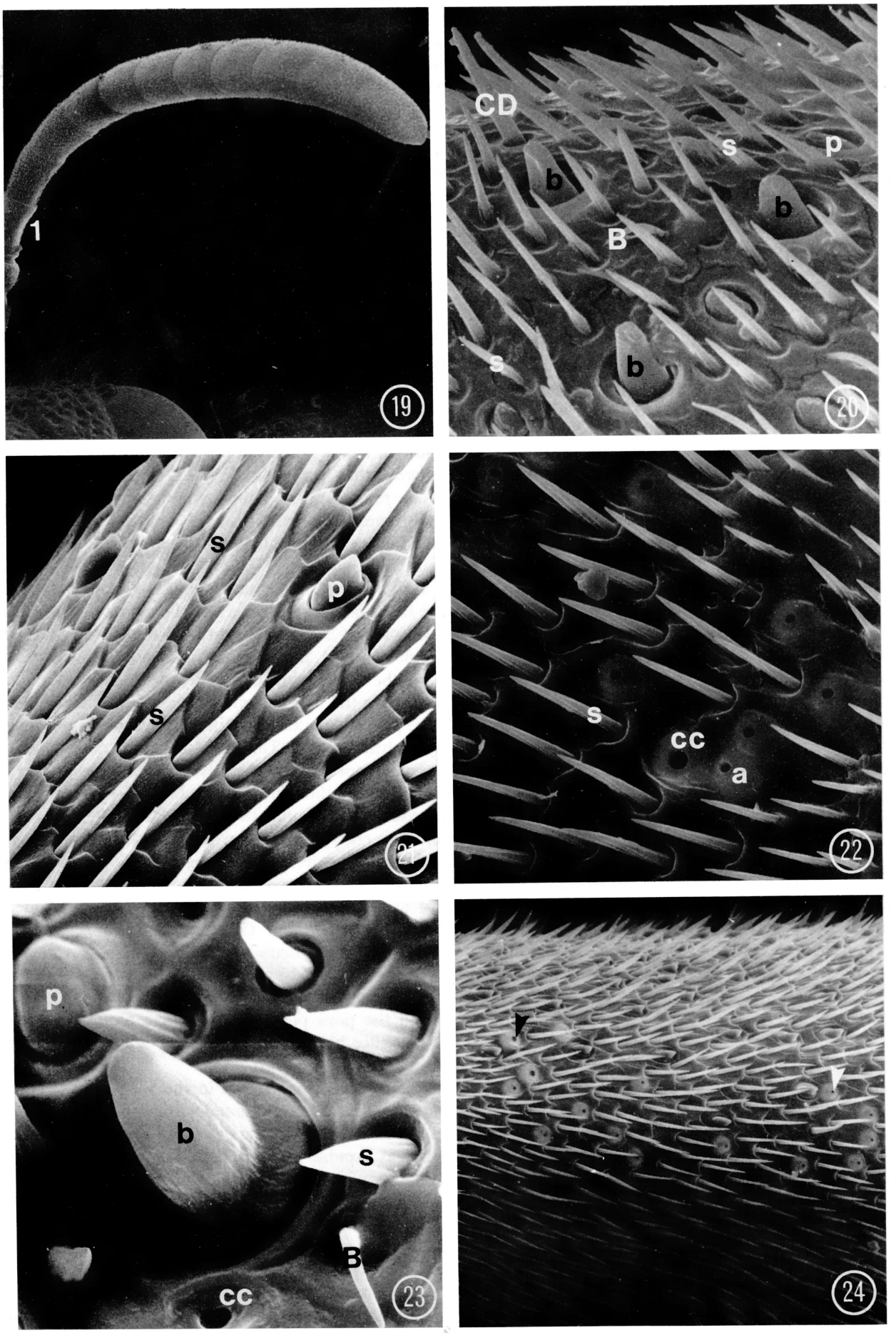
Sensilla trichodea C/D are evenly spread on all annuli (Figs. 20, 23).

Sensilla placodea occur on all annuli in both sexes (Figs. 20, 24), although only a few on fl^1 (Fig. 21). They are formed like very low pegs (Figs. 21, 23) with the tip directed distally. They seem to circle the antenna in the males; in the females they do not.

Sensilla coeloconica were found only on fl^4 in the male, from fl^2 distally in the female. They form fields close to the ventral midline and are intermixed with s. ampullacea (Figs. 22, 24).

Sensilla campaniformia are scattered in small numbers in the vicinity of pit organs on the most proximal annuli and also on the very tip of the flagellar apex.

Sensilla basiconica were found dorsally from fl^2 in females, fl^3 in males, increasing in number distally. They are thick, but not longer than surrounding s. trichodea



Figs. 19–24. Cerceris rybyensis.—19. Male, whole antenna. ×45.—*20.* Male, fl^{11} dorsal aspect. ×1500.—*21.* Female, fl^{1} distally, dorsal aspect. ×1400.—*22.* Female, fl^{8} proximally, pit organs. ×1400.—*23.* Female, fl^{10}, s. basiconicum (note wide socket). ×3700.—*24.* Female, fl^{4}, ventral aspect. *Black arrow*, s. coeloconicum, *white arrow*, s. ampullaceum. ×400.

(Fig. 20). The surface is sculptured longitudinally with many thin furrows (Fig. 23). The tip collapses during air drying. The socket is about as wide as the length of the peg, creating a wide membranous bridge between the peg and the surrounding cuticle.

Discussion

General morphology of antennae

The antennal form of the four sphecid species investigated is similar to that in Apidae (*s. lat.*) (Ågren 1975, 1977, 1978; Ågren & Svensson 1982), with the striking exception of *Bembix rostrata*. In the males of this species the flagellum is provided with an area that upon folding forms a 'grip', which, as behavioural studies (Tengö & Ågren in prepn) indicate, is associated with copulation, serving as a mechanostimulatory tool for intersexual communication. During copulation the male grips the base of the female antennae with his antennae, closes the hook outwards into a noose and slowly pulls the female antennae through this repeatedly. Another case of antennal modification in males associated with tactile communication while in copula has been noted in the aphelinid wasp *Encarsia* (Viggiani & Mazzone 1980). Although the sexual drive of *Argogorytes* males is exploited by *Ophrys* orchids to achieve pollination (Kullenberg 1961), no indication of any particular morphological traits in response to this specialized interaction was observed.

In Apidae (*s. lat.*) the cuticular surface around the dorsal sensilla is usually nude, especially in the s. placodea zones (Ågren 1975; Ågren & Svensson 1982). The Sphecidae studied have sculptured cuticle all around the antennae.

The flagellum does not contain any muscles; instead, antennal movements are controlled by muscles within the scape and between the scape and tentorium (Chapman 1971). In both male and female *Bembix rostrata* the scape is thick and stout, indicating the presence of well developed extensors and flexors. These represent an adaptation to this insect's extensive use of the antennae as probing organs (Tengö & Ågren in prepn).

Sensilla patterns

The general distribution patterns of the setae and of the individual sensillum types do not differ markedly from those in Apidae (*s. lat.*). Setae are located on the ventral surface and in a proximal ring around each annulus (also abundant dorsally in *B. rostrata*). Sensilla are situated dorsally and in increasing numbers terminally. Pit organs, in contrast to other sensilla types, tend to be aggregated into distinct fields, which typically have a mid-ventral, and in some bees also a dorsal, position.

In many Apidae (*s. lat.*) there is a nude ventral zone on the terminal annulus (Ågren & Svensson 1982). However, in the Sphecidae examined this varies. In *Cerceris rybyensis* this area is very small, whereas in the two *Argogorytes* species and *Bembix rostrata* females it is densely packed with setae and sensilla. In *B. rostrata* males this bare zone falls within the 'grip' area.

Variation of the patterns among the three sphecid genera is of a magnitude similar to that reported for the interfamily (*s. str.*) level in Apidae (*s. lat.*) (Ågren 1975, 1977, 1978; Ågren & Svensson 1982). Intrageneric comparisons of sensillar distribution, examined only for the two species of *Argogorytes*, revealed similar patterns. This contrasts with the striking dissimilarities observed at the intergeneric level. Readily discerned intrageneric (non-gender related) variation in Aculeata has been reported only for *Sphecodes* (Halictidae *s. str.*) (Ågren & Svensson 1982).

Sensilla types

All the sensilla types observed in the Sphecidae wasps have their homologous counterparts in Apidae (*s. lat.*). Conversely, the Apidae (*s. lat.*) sensillum sets match those of the Sphecidae completely, with the restriction that s. ampullacea were found only in *Cerceris rybyensis* and that it was not possible to distinguish with the SEM between the s. trichodea C and D of the Sphecidae. The setae, pit organs, s. trichodea and s. campaniformia are indistinguishable from those in Apidae (*s. lat.*). Placoid and basiconical sensilla, however, deviate morphologically.

Bulbous s. placodea and stout s. basiconica, typical of the four Sphecidae species, are the main sensillar characteristics that consistently differ from those observed in Apidae (*s. lat.*). In the latter, s. placodea have plates that are either level with, or slightly above, the surrounding cuticle. In the four sphecid species, the s. placodea have pore plates elevated in a different fashion. As discussed by Walther (1983) "The elevation of the pore plates . . . has developed independently several times . . . in . . . different families of the Aculeata." Furthermore, s. placodea differ among the Sphecidae. In *Bembix rostrata* and *Cerceris rybyensis* they form broad, low pegs within wide sockets, whereas in *Argogorytes fargei* and *A. mystaceus* they are dome-shaped. The arrangement of pores is not as rigidly ordered as in bees. The s. placodea in *Bembix rostrata* and *Cerceris rybyensis* resemble the "niedergelegten Haare" (fallen hairs) in ants, which have been suggested to be an intermediary form between plate organs and hairs (Kürchner 1969). Wacker (1925) considered the pore plates in Sphecidae as intermediate in appearance between those of Vespoidea and Apidae (*s. lat.*).

The s. basiconica found in the four sphecids are all stout, cylindrical and situated within wide sockets. Males of *Bembix* and *Cerceris* possess basiconical sensilla, whereas Apidae (*s. lat.*) males never do. These facts, together with the morphological characteristics of the sensilla, agree with the view that the Sphecidae ". . . is regarded the more primitive of the two families, Sphecidae and Apidae (*s. lat.*) . . ." (Lomholt, 1975). This is expressed by Walther (1983), who states that "sensilla basiconica with short and cylindrical pegs which are standing in the center of a socket with a great diameter are more primitive than those with slender and long pegs placed on small sockets", and ". . . the males in the Hymenoptera often show the more primitive expression of a character".

Considering the sensillar pore equipment and drawing from observations made in parallel investigations of *Apis* (Lacher 1964), one can make inferences on the modalities of each sensillum type. Accordingly, s. placodea and s. trichodea A may function as odour receptors, s. basiconica and s. trichodea C/D as taste and mechanoreceptors, s. trichodea B and some setae (especially at annular joints) as touch mechanoreceptors, s. campaniformia as hygro- and thermoreceptors (Yokohari 1983), and pit organs as receptors for CO_2, temperature and humidity.

The flagellar sensillar equipment as a taxonomical tool

The following aspects of shape and distribution of flagellar sensilla (supposedly plesiomorph character given first) might be of value in characterizing interspecific differences within the Sphecidae:

s. placodea like low pegs or dome-shaped;

s. basiconica in both sexes or only in females;

s. coeloconica over the whole flagellum or only terminally;

s. ampullacea present or not;

s. campaniformia over the whole flagellum or only terminally (or absent);

s. placodea and other sensilla also ventrally or only dorsally;

apex nude or setous.

Given these characteristics, the *Argogorytes* wasps share the least with the others and with Apidae (*s. lat.*), *A. fargei* diverging most. The similarities between *Bembix* and *Cerceris* — belonging to different tribes — are stronger than between *Bembix* and *Argogorytes* — members of the same tribe. Thus, in the studied organs, intraspecific specializations in response to behavioural or physiological evolutionary pressures obscure the taxonomic lines.

In conclusion, there is no evidence for a taxonomic hierarchy based on flagellar sensillar patterns.

Acknowledgements

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Abbreviations used in figures

A	s. trichodeum A
B	s. trichodeum B
CD	s. trichodeum C or D
a	s. ampullaceum
b	s. basiconicum
cc	s. coeloconicum
cf	s. campaniforme
p	s. placodeum
s	seta
sc	scape
1	fl^1

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