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Micromorphology of the model species pea aphid *Acyrtosiphon pisum* (Hemiptera, Aphididae) with special emphasis on the sensilla structure

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Abstract

The pea aphid complex [*Acyrtosiphon pisum* (Harris 1776)] (Hemiptera, Aphididae), listed among the 14 aphid species of the greatest economic importance, is a globally distributed key pest of pulse crops. Since the pea aphid is a well-studied model organism, an enormous amount of literature has been published about this species. However, comprehensive morphological analyses using scanning electron microscopy (SEM), focused on all body parts of adult viviparous and sexual generations of *A. pisum*, are lacking. Thus, we present the first detailed morphological description of all body parts of adult wingless and winged viviparous females (parthenogenetic generation) as well as oviparous females, winged and wingless males (sexual generation), representing the most common *A. pisum* pea biotype. In particular, the sensilla of the body surface, antennae, mouthparts, legs and male genitalia are mapped by the high-resolution scanning electron microscope. The morphological diversity of sensilla is discussed in the context of their function and the biology of aphids.

Keywords: *Aphids, morphs, pea biotype, SEM, sensory organs*

Introduction

The pea aphid complex [*Acyrtosiphon pisum* (Harris 1776)] comprises 11–15 distinct host races, associated with different legumes (Leguminosae or Fabaceae) (Simon et al. 2003; Peccoud et al. 2009). *A. pisum*, representing tribe Macrosiphini of the subfamily Aphidinae (Hemiptera, Aphididae), is an aphid pest of major agronomical importance, which feeds on cultivated species (annual or perennial) such as pea, broad bean, chickpeas, lentils, alfalfa, red clover as well as wild legume species. The pea aphid not only inflicts direct injury through feeding on its host plants but also transmits viral diseases, among others the pea enation mosaic virus (PEMV) and bean leaf roll virus (BLRV) (Blackman & Eastop 2000; Van Emden & Harrington 2017). It is a globally distributed key pest of pulse crops, causing significant yield losses (Ryalls et al. 2013; Megersa 2016; Paudel et al. 2018).

Acyrtosiphon pisum, like other aphid species, is characterized by a complex life cycle and the presence

of various morphs through the season (cyclic parthenogenesis). Briefly, the generation of the stem mother hatches from the overwintering eggs in early spring, on young leaves of host plants. In the next generations, both winged and wingless females are produced by parthenogenesis. A generation of winged viviparous females disperses to other host plants. Then, they produce a generation of wingless females, which in turn produce a generation of winged and wingless females. This cycle continues until late summer or early autumn, when winged females fly back to their overwintering host crops (i.e. the perennial broad bean plants) and produce males and wingless oviparous females. The sexuales mate and the oviparous females lay fertilized eggs on the leaves and stems of perennial legumes (Ogawa & Miura 2014; Bogdan 2018).

The pea aphid is a model organism and the first hemipteran and one of the first insect genomes sequenced (The International Aphid Genomics Consortium 2010). An enormous amount of literature has been published about this species, including investigation of the production of various morphs by the

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same genotype in response to environmental or genetic factors (Ogawa et al. 2012; Ogawa & Miura 2014). In the pea aphid, the so-called wing (wingless versus winged viviparous females or wingless versus winged males) and reproductive (asexual versus sexual generation) polymorphism/polyphenisms are observed (Brisson et al. 2007; Brisson 2010; Srinivasan & Brisson 2012). However, comprehensive morphological analyses using scanning electron microscopy (SEM), focused on all body parts of adult viviparous and sexual generations of *A. pisum*, are lacking. The exception was an investigation of the head and thoracic structures of the third to fifth instar for winged and wingless lines of viviparous generation (Iskikawa & Miura 2007), development of the flight apparatus of males (Ogawa et al. 2012), morphology of antennal, legs and labial sensilla of the adult wingless viviparous females (De Biasio et al. 2015), morphology of tarsi of the adult wingless viviparous females (Friedmann et al. 2015) or morphology of hind tibia of nymphal instars, adult wingless viviparous females and oviparous females (Murano et al. 2018) of various *A. pisum* biotypes. The obtained results of micromorphological investigations were also the basis for behavioural and electrophysiological studies. In the case of the pea aphid complex, which is an example of sympatric speciation through host specialization (Frantz et al. 2010; Peccoud & Simon 2010), such detailed study will also help to resolve systematics and evolutionary biology of these insects. Therefore, the objective of this paper is to provide (1) a general morphological description of all body parts of adult wingless viviparous females, winged viviparous females, oviparous females, and winged and wingless males; (2) comparative study of the structure and distribution of sensilla on the body surface, antennae, mouthparts and legs in these morphs representing the *A. pisum* pea biotype (Auclair 1978) under a scanning electron microscope.

Material and methods

Insects

Aphid cultures were started with insect material originally collected from fields of *Pisum sativum* in Poland near Gliwice or Poznań. In the laboratory, the insects were reared in plastic cages on *Pisum sativum* var Tarchalska as the host plant in the climatic chamber KKS 240/240 TOP+ with a phytotron system (POL-ECO-APARATURA SP.J., Wodzisław Śląski, Poland). Firstly, the viviparous generation (adult wingless and winged females) were reared in the conditions of a long day photoperiod of 16:8 D/N, temperature 20°C (+/-1°C) and humidity 70% (+/-10%). Then, isolated colonies of pea aphids were maintained in the

conditions of a short day photoperiod of 8:16 D/N, temperature 15°C (+/-1°C) and humidity 70% (+/-10%) in which they produced a sexual generation of oviparous females and winged males. Wingless males were maintained in the short-day conditions from the separate strain, associated with *P. sativum* var Cysterski.

Scanning electron microscopy

Specimens for SEM analysis (two wingless males and five individuals for each remaining adult morphs) were preserved in 70% ethyl alcohol. Preserved samples were transferred into a 6% phosphotungstic acid (PTA) solution in 70% ethanol for 24 h. Dehydration of the samples was performed using serial baths of 80%, 90% and 96% ethyl alcohol for 10 min each, and two baths of absolute alcohol 10 min each. Dehydrated specimens were subsequently dried in a series of baths of a ratio of 1:3, 1:2; 2:3 hexamethyldisilazane (HMDS) and absolute alcohol for 30 min each, followed by two 30-min baths in the undiluted fluid. Whole samples of wingless and winged viviparous females, oviparous females and wingless and winged males were dried in a Leica CPD 300 critical point dryer (Leica Microsystems, Vienna, Austria). Samples were mounted on aluminium stubs with double-sided adhesive carbon tape and sputter-coated with gold in a Pelco SC-6 sputter coater (Ted Pella Inc., Redding, CA, USA) to obtain a layer approximately 25 nm thick. Whole samples were coated with chromium in a Quorum 150 T es plus sputter coater (Quorum technologies, Laughton, UK) with a 30 nm layer. Coated samples were imaged and measured with a Hitachi SU8010 field emission scanning electron microscope (Hitachi High-Technologies Corporation, Tokyo, Japan) at 5.0, 7.0 and 10.0 kV accelerating voltage with a secondary electron detector.

Sensilla nomenclature and types follow basic results on insect, including aphids (Slifer 1970; McIver 1975; Bromley et al. 1979, 1980; Shields 2010).

Results

General morphological characters

Acyrtosiphon pisum is a rather large aphid with wingless viviparous females with the body length 2.20–5.10 mm (Figure 1a-c) and winged viviparous females with the body length 2.30–4.40 mm (Figure 1d-e). Oviparous females are of similar length as winged viviparous females (Figure 1f-g), whereas winged males (Figure 1i-j) are distinctly smaller than winged viviparous females. The smallest adult morphs are wingless males with the body length 1.10–1.40 mm (Figure 1h). The surface of all body parts is covered by a very thin wax layer. The head of the wingless morphs

(wingless viviparous females, oviparous females and wingless males) is well separated from the pronotum and is characterized by well-developed, rather smooth antennal tubercles and a U-shaped frons (Figure 2a,i). The lateral side of the head bears big and rounded, well-developed compound eyes with well-visible ocular tubercles with a triommatidium on the distal end of the eye (Figure 2b). The compound eye is about 137–152 μm high and about 123–137 μm in diameter. Ommatidia in the compound eye are rounded, 5.80–9.40 μm in diameter and form regular diagonal rows. The ocular tubercle is protuberant, rounded, 28–34 μm high in the basal part and 25–30 μm wide, with a wrinkled surface. The three ommatidia are

visibly bigger than those in the compound eye (Figures 2c,d; 10a).

The head of the winged morphs (winged viviparous females and winged males) is similar in its general morphology as in the wingless morphs with slightly lower antennal tubercles and a wider frons. Three ocelli are clearly visible: one on the frons and two on the dorso-lateral side. Additionally, the latter two are located on slightly raised cuticle (Figure 2e). All three structures are visible also from the lateral side of the head (Figure 2f–h). The compound eyes are more rounded as in wingless viviparous females and oviparous females, 155–160 μm high and 130–140 μm in diameter, with rounded and hexagonal ommatidia

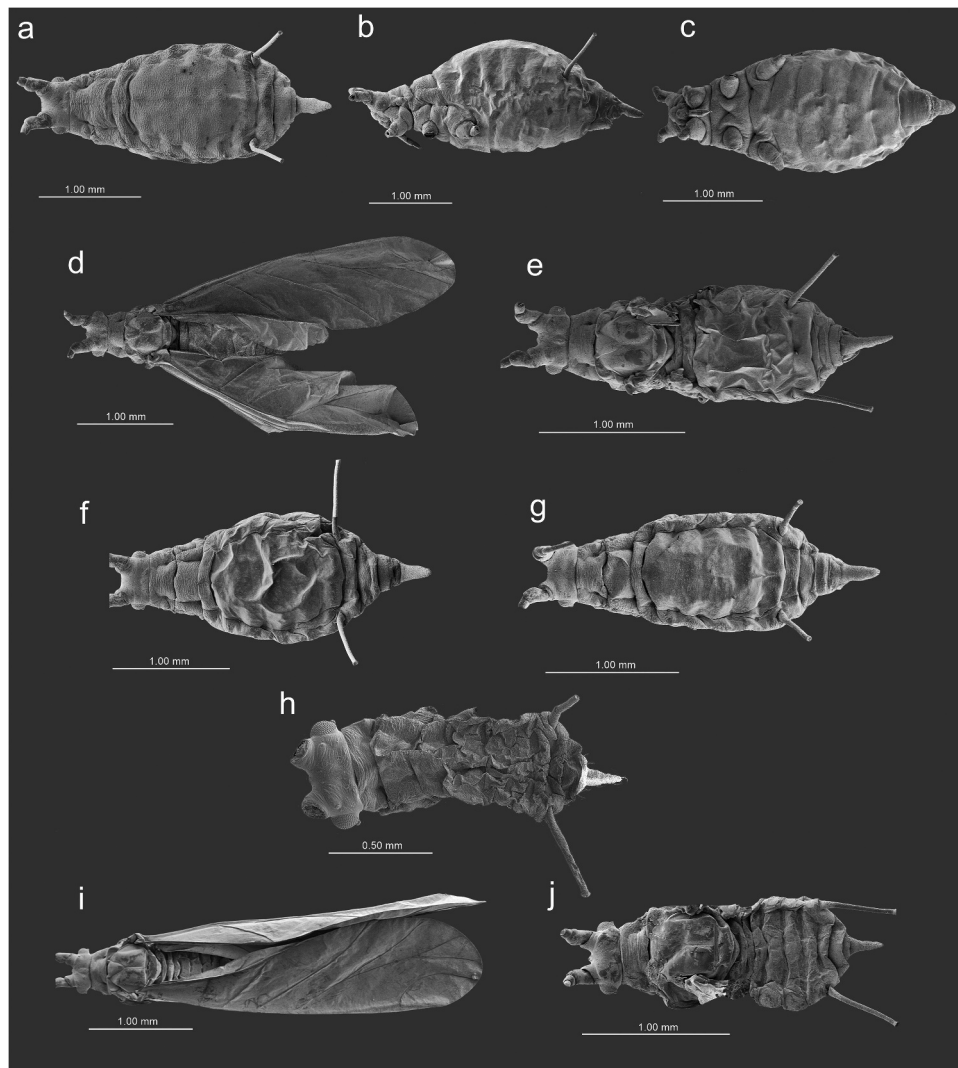


Figure 1. SEM of the whole specimens of the examined morphs of *A. pisum*: (a) dorsal side, (b) lateral side, (c) ventral side of wingless viviparous female, (d) winged viviparous female, (e) winged viviparous female with wings removed, (f) oviparous female before oviposition, (g) oviparous female after oviposition, (h) wingless male, (i) winged male, (j) winged male with wings removed.

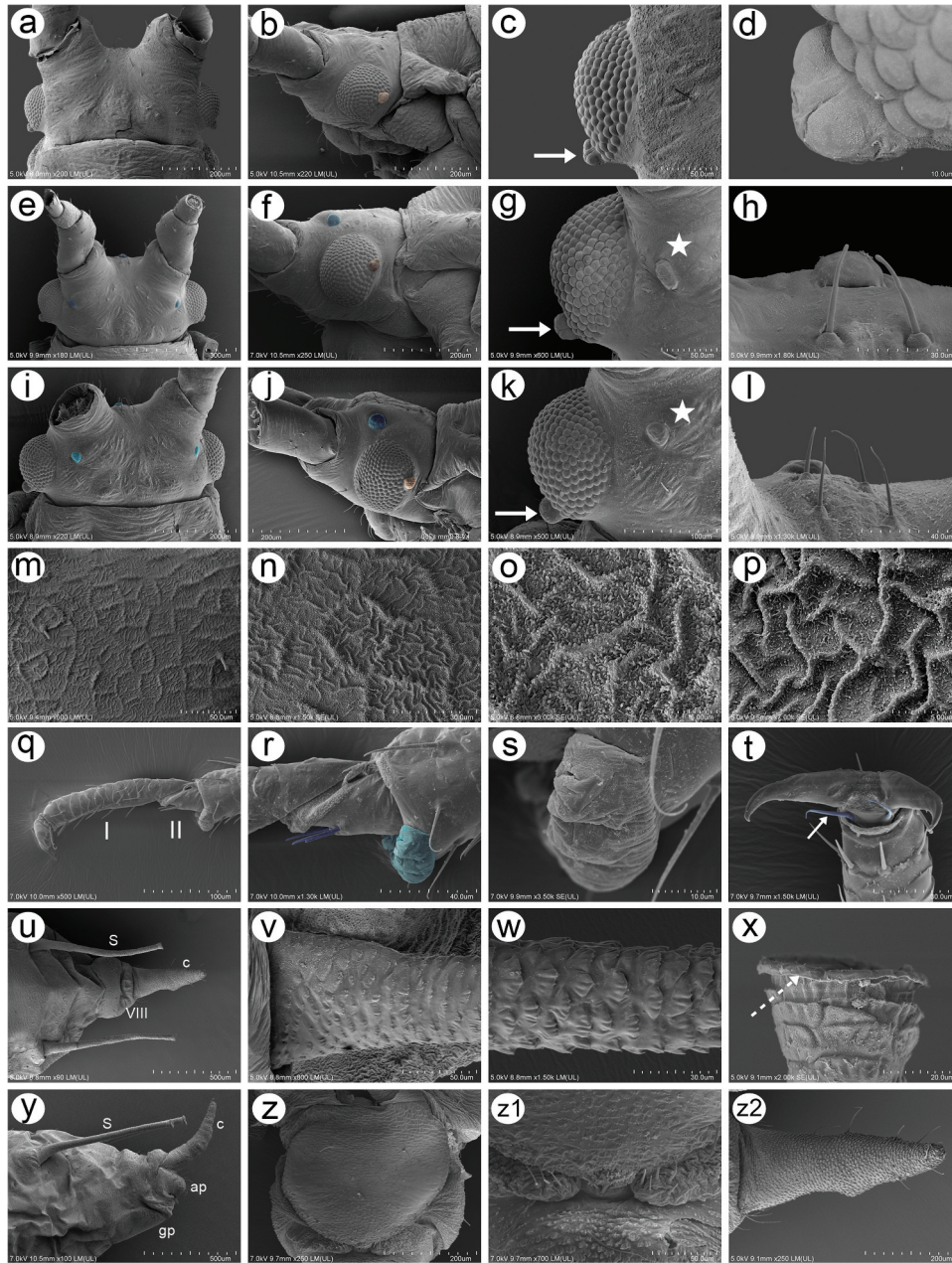


Figure 2. General morphological characters shared by the examined morphs of *A. pisum*: (a) dorsal side of the head of wingless viviparous female with well-developed antennal tubercles and U-shaped like front, (b) lateral side of the head of oviparous female with well-developed compound eye and triommatidium (light orange), (c) structure of the compound eye of wingless viviparous female with triommatidium on well-developed ocular tubercle (arrow), (d) structure of the ocular tubercle with three ommatidia (triommatidium) of wingless viviparous female, (e) dorsal side of the head of winged viviparous female with well-developed antennal tubercles, wide U-shaped frons and three ocelli (blue), (f) lateral side of the head of winged viviparous female with well-developed compound eye, dorso-lateral ocellus (blue) and triommatidium (orange), (g) structure of the compound eye, triommatidium (arrow) and ocellus (star) of winged viviparous female, (h) structure of the frontal ocellus of winged viviparous female, (i) dorsal side of the head of wingless male with three ocelli (blue), (j) lateral side of the head of winged male with ocellus (blue) and triommatidium (orange), (k) structure of the compound eye, triommatidium (arrow) and ocellus (star) of the wingless male, (l) structure of the frontal ocellus of wingless male, (m) dorsal abdominal cuticle of wingless viviparous female, (n) structure of the dorsal cuticle sculpture, showing two kinds of undulations: bigger (macrosculpture), forming polygons, and smaller (microsculpture) inside the polygons in the form of more or less regular zigzag in wingless viviparous female, (o) structure of the microsculpture of wingless viviparous female with sharp edges and abundant wax secretions in the form of small flats, (p) structure of the microsculpture of oviparous female with more gentle edges and less wax secretions in the form of minute bars, (q) morphology of the hind tarsus of wingless and winged morphs showing two segments: small triangle first segment (I) and elongated second segment with two claws (II), (r) end of hind tibia with well-developed tibial attachment pad (blue) and first segment of tarsus with three ventral setae (violet), (s) structure of the tibial attachment pad, (t) end of second segment of hind tarsus with two claws and parempodia with rounded bases and flat apices (violet), (u) dorsal end of abdomen of viviparous (wingless and winged) morphs: c – cauda, s – siphunculi, VIII – abdominal segment VIII, (v) imbrication structure of the basal part of siphunculi, (w) structure of imbrication of the middle part of siphunculi, (x) apical end of siphunculi with little-developed flange (arrow), (y) lateral end of abdomen of viviparous morphs (wingless and winged female): ap – anal plate, c – cauda, gp – genital plate, s – siphunculi, VIII – abdominal segment VIII, (z) genital plate of wingless and winged viviparous female with rudimentary gonapophyses, (z1) structure of the rudimentary gonapophyses, (z2) cauda.

about 12–17 μm in diameter. The ocular tubercle is about 29–33 μm high and 24–26 μm wide. The frontal ocellus is more protuberant, semi-circular, 10–12 μm high and 21–23 μm wide, whereas the dorsolateral ocelli are more discoidal and oval, 4–6 μm high, 27–29 μm long and 10–12 μm wide. The examined wingless males were characterized by the possession of mixed features of wingless and winged morphs (Figure 2i,j). Besides the compound eyes (also more rounded) with triommatidia, three well-developed (but slightly smaller than in the winged male) ocelli were visible (Figure 2k,l). In the wingless male, the compound eyes are about 130–146 μm high and 70–93 μm wide from the dorsal side. The ocelli are less protuberant, 23–26 μm in diameter, while those in winged males are about 37–40 μm . Single ommatidia is about 7.80–10.00 μm in diameter and are similar to those in winged males (9.40–11.60 μm).

The dorsal body cuticle (especially visible in wingless viviparous and oviparous females) is characterized by two kinds of sculpture forming more or less regular ornamentation (Figures 2m, 10b). The sculpture may be divided into a thick edged macrosculpture in the form of quadrangles and pentagons and a microsculpture in the form of more or less regular zigzags inside the macrosculpture (Figure 2n). Small differences can be noted between the microsculpture of wingless viviparous females and oviparous females. Wingless females are characterized by sharp edges of the microsculpture and additionally greater wax secretion (Figure 2o) than the sexual females, in which the microsculpture is clearly gentle-edged with less wax secretion (Figure 2p). The lateral side of the abdomen is characterized by ruffled or wrinkled cuticle with well-visible oval spiracle openings, surrounded by more or less developed sclerotic tubercles (Figure 10c).

Aphids' legs are adapted for walking. The first segment of the tarsus is short, almost triangular, with three ventral trichoid sensilla, whereas the second segment is elongated (Figure 2q,r). Distal ventral ends of the tibiae bear a well-developed tibial attachment pad (Figure 2s). The proximal part of the second segment of the tarsus (near the connection with the first segment of the tarsus) bears one rounded campaniform sensillum (Figure 11c). Its distal end is characterized by normal-shaped (pointed) claws and long, well-developed tubular parmpodia with flattened apices (Figure 2t). Siphunculi are tubular, tapering and clearly imbricated (Figure 2u). The imbrication is differentiated on a particular part of the siphunculus: from small with many small denticles near the basal part (Figure 2v), well-developed and slightly protuberant with transverse

furrows in the middle (Figure 2w) to wide plates near the apex (Figure 2x). The apical part of the siphunculi additionally ends in a small, inrolled flange (Figure 2x). The cauda in dorsal view is tongue-shaped, sometimes with a little-developed indentation in the middle (Figure 2u,z) and bent up in the lateral view (Figures 2y, 10d,f). The genital plate of viviparous morphs (wingless and winged viviparous females) is almost rounded, imbricated on almost the whole surface with a slightly narrowing posterior end. Its anterior part bears only two setae, which are more numerous but poorly visible on the posterior edge (Figure 2z). Three rudimentary gonapophyses can be found between the posterior part of the genital plate and the anterior part of the anal plate, of which the two laterals are slightly bigger than the central one. All gonapophyses bear 3–5 short and rigid trichoid sensilla (Figures 2z1, 10e).

Wings of viviparous females and males have morphology typical for aphids, with well-visible cubital veins and pterostigma and slightly visible media and radial sector (Figure 3a). The forewing membrane is covered by a very thin wax layer and is smooth on most of its surface. The central part of the membrane bears very few, small, triangular or slightly trapezoid scale-like elements, 1.00–1.60 μm long and about 0.63–0.90 μm wide (Figure 3b, c). The membrane area near the wing edges bears more, evidently longer, mostly wide crescent-shaped or almost straight and also more regularly distributed scale-like elements, 2.50–3.50 μm long (Figure 3d, e). Basal part of wings (near the wing articulation), pterostigma and subcosta bear rounded campaniform sensilla which structure, size and shape are the same as in those on pedicel and legs. Hindwings have a well-developed part of the claval apparatus in the form of an area with numerous scale-like elements and four rolled up hamules (Figure 3f,g). The scale-like elements in the claval area are mostly C-shaped, often with an additional lateral branch (Figure 3h).

Oviparous females are characterized by numerous small, rounded, sometimes forming eight-shaped scent plaques (pseudosensoria) on most of the length of hind tibiae (Figure 4a). The scent plaques are mostly protuberant, similar in size, 9–11 μm in diameter (Figure 4b), and their whole surface is covered by numerous very small, rounded or slightly elongated pores, about 18–22 per 1 μm^2 (Figure 4c). The end of the abdomen in oviparae is characterized by much more developed rudimentary gonapophyses, and the surface of the body is more membranous between them and the genital plate (Figure 4d), which is additionally bigger and wider than in the viviparous females and also more setose with longer and well-developed posterior setae (Figure 4e).

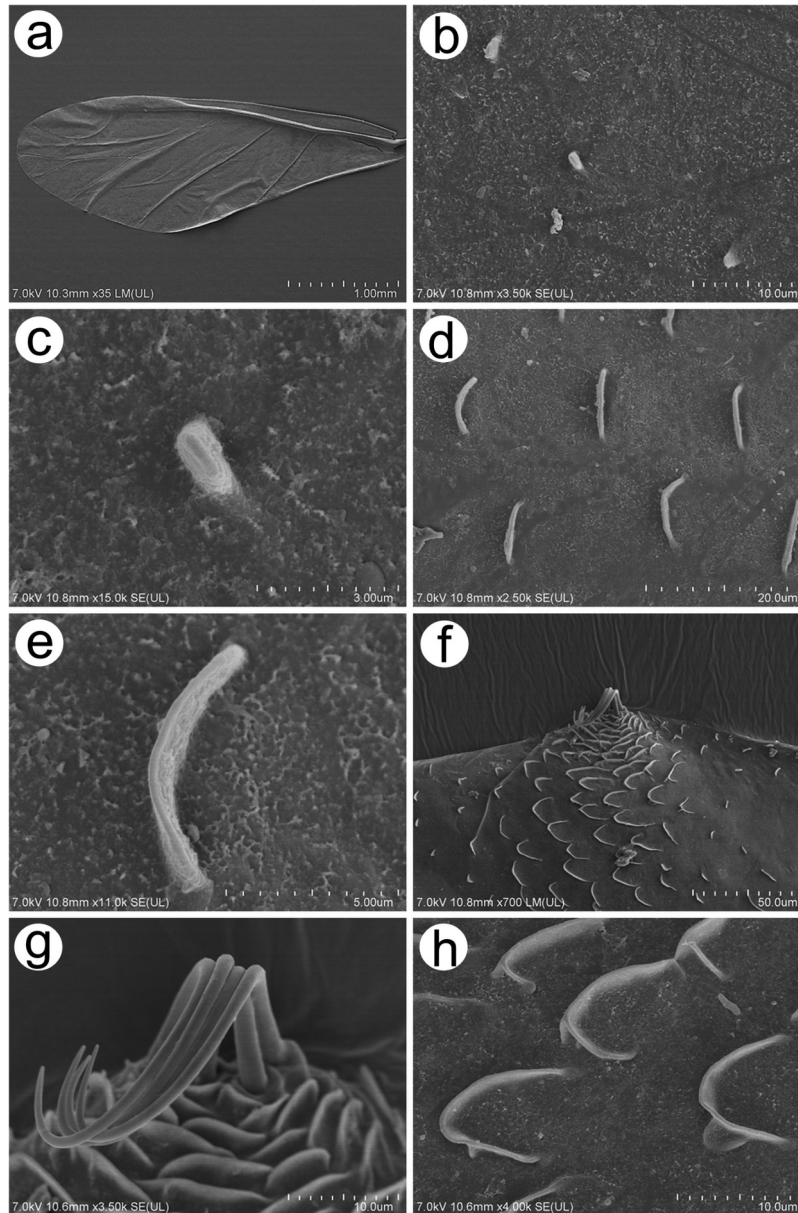


Figure 3. Wing characters of winged morphs (winged viviparous female and winged male) of *A. pisum*: (a) general view of forewing, (b) surface of main part of the wing membrane with very thin wax layer and very small scale-like elements, (c) structure of wax layer on the wing membrane and the scale-like element, (d) surface of the wing membrane near edges and pterostigma with very thin wax layer and long, crescent-shaped scale-like elements, (e) structure of the long, crescent-shaped scale-like element, (f) part of the claval apparatus on the hindwing with four hamules, (g) structure of the hamules on hindwing, (h) structure of semi-oval scale-like elements near the hamules on hindwing.

The males (both wingless and winged) differ from wingless and winged viviparæ by the presence of sclerotized genitalia on the ventral end of the abdomen, formed by paired, setose parameres and the basal part of the phallus, surrounded by a sclerotized part of genital capsule (Figure 4f). Setae on parameres of both wingless and winged males are long, fine and pointed (Figure 4g, h), in

contrast to the basal part of the phallus, covered by numerous rounded cavities with minute structures resembling peg-like sensilla (Figure 4h). In both winged and wingless males, the whole surface of the genital area is densely covered by sculpture-forming trident processes with the exception of the smooth surface of the basal part of the phallus (Figure 4g, h).

Body and leg sensilla

Body and leg sensilla appear to be trichoid sensilla with well-developed sockets. On the dorsal side of the body, the sensilla rise almost perpendicularly to the cuticle surface or aslant in different directions. Trichoid sensilla are rather short, tubular, thick and rigid with more or less capitate apices (Figure 5a-d), about 16–30 μm long in wingless morphs and up to

35–40 μm long in winged morphs. Their surface is mostly smooth without any sculpture (Figure 5e), but in many cases, the capitate apex is wrinkled, sometimes very clearly (Figure 5c, f). The sockets of dorsal body sensilla are rounded from the top and trapezoid from the lateral view, 6.50–7.50 μm in the basal diameter and 2.50–2.80 μm in the diameter of the opening. On the legs, trichoid sensilla are more

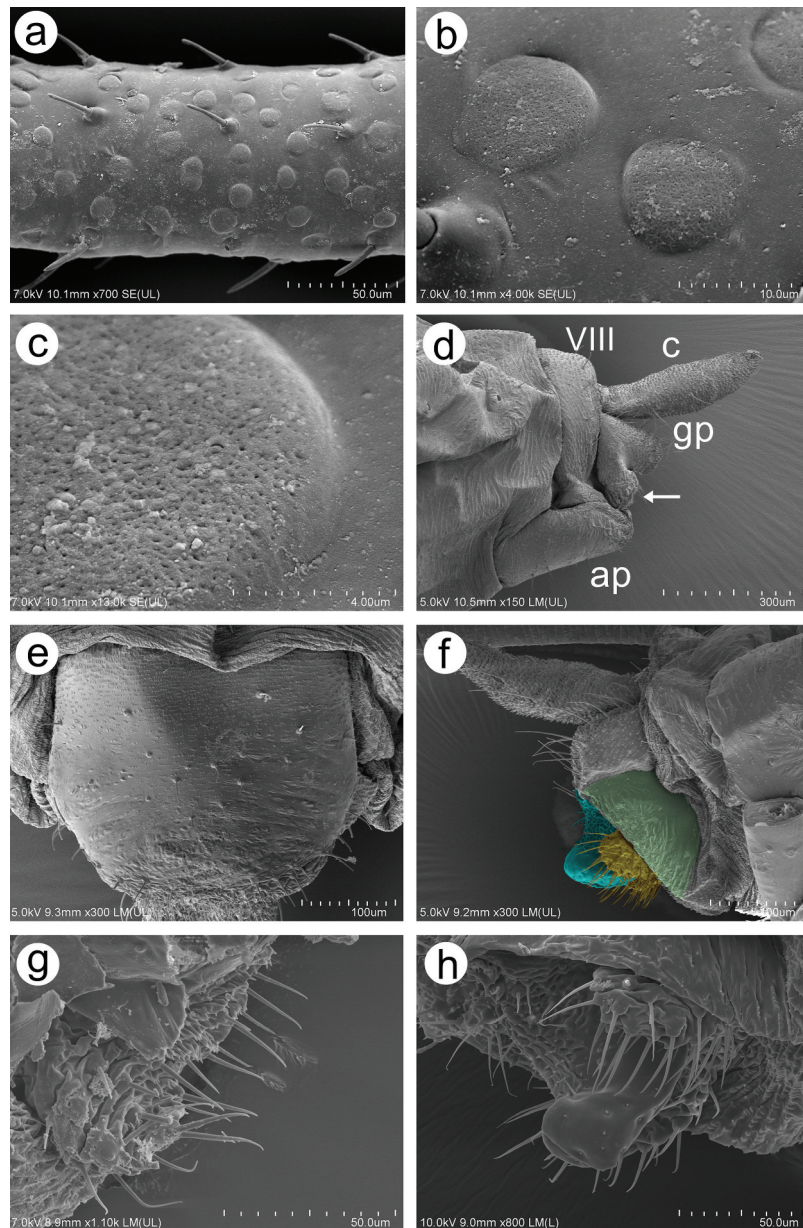


Figure 4. Characters of sexual morphs (oviparous females and males) of *A. pisum*: (a) part of hind tibia of oviparous female with numerous scent plaques (pseudosensoria), (b) rounded and slightly protuberant scent plaques with numerous small pores, (c) structure of the porous surface of scent plaque, (d) lateral end of abdomen of oviparous female: ap – anal plate, c – cauda, gp – genital plate, VIII – abdominal segment VIII, dotted arrow – big rudimentary gonapophyses, (e) structure of genital plate of oviparous female, (f) winged male genitalia lateral view: basal part of the phallus (turquoise), paramere (yellow), sclerotized part of the genital capsule (green), (g) structure of the paramere of wingless male, (h) structure of basal part of the phallus of winged male.

varied, mostly in the length and the apices' shape. Sensilla on femora are rather short, 15–30 μm long with slightly capitate apices (sometimes simply blunt with a gentle rounded apex and arising mostly at an acute angle in the distal direction (Figure 5g, h)). Their surface is also smooth, but often wrinkled (sometimes strongly) apices are observed (Figure 5i). On the other hand, sensilla of tibiae are very long, thick and rigid, 30–40 μm long with capitate or blunt apices (mostly the dorsal side of tibiae and from the proximal part to the middle of their length) (Figure 5j, k) or strongly thick and rigid with pointed or dagger-like apices (mostly ventral and distal part of the tibiae) (Figure 5l–n). Sockets of the sensilla of the legs are rounded from the top and trapezoid from the lateral view but, opposite to those on the dorsal side of the body, they take the distal direction as the sensilla, losing their lateral symmetry (Figure 5o). There are no differences in the length and shape of sensilla between parthenogenetic and sexual morphs (Figure 5p–r).

Besides trichoid sensilla, internal side of trochantera and very proximal parts of femora of legs of all examined morphs of *A. pisum* bear groups of 3–4 campaniform sensilla, usually 3–5 μm in diameter. They are unevenly distributed, usually rounded and with small, sometimes poorly visible pore in the middle of the sensillum plate (Figure 11b–d).

Antennal sensilla

Coeloconic, campaniform and placoid sensilla. Three kinds of sensilla may be found on selected antennal segments in all morphs of *A. pisum*. In the presented example, the pedicel of wingless viviparous and oviparous females bears one single rhinariolum on the ventral side, which in all examined specimens is located on a small protuberance, 2.50–3.60 μm in diameter. In all cases, only the opening (2.00–2.40 μm in diameter) is visible, always without any protruding peg (Figure 6a, b). In the winged viviparous females and winged males, the opening (of the same diameter) of the rhinariolum may be found also on the ventral side but directly on the pedicel cuticle without visible protuberances (Figure 6c). In all examined morphs one campaniform sensillum can be found on the dorsolateral side of the pedicel (Figures 6d, 11a). The external ring of the sensillum is about 10–11 μm in diameter while the internal ring is 4.70–5.50 μm in diameter.

Placoid sensilla can be found in all morphs in different numbers and locations, almost in all cases on antennal segments III (secondary rhinaria), V and VI (primary rhinaria). In wingless viviparous females,

usually two small multiporous placoid sensilla near the basal part of antennal segment III (Figure 6e) are present. They are in forms of rather rounded and often flat discs, 8.90–15.00 μm in diameter, lying in cuticle cavities with gentle edged (Figure 6f) or well-developed and ragged (Figure 6g, h) edges with very small projections, 0.50–0.90 μm long.

In winged viviparous females more numerous, small multiporous placoid sensilla are distributed on the whole length of antennal segment III in one single row, are mostly rounded and slightly protuberant, about 11–18 μm in diameter (Figure 6i, j). Similarly, as in wingless viviparous females, they are lying in a cuticle cavity, surrounded by a slightly raised cuticle flange or ring with very short projections, 0.38–1.15 μm long (Figure 6k, l).

In antennal segment III of oviparous females, if possessing any placoid sensilla, they are often more residual than in other examined morphs. These multiporous placoid sensilla in the sexual females are rather small or very small and seem to be residual (Figure 6m). Two kinds of these sensilla have been found in oviparae: big and irregular in size and shape, 7.00–9.50 μm in diameter, lying deep in the cuticle cavity with an irregular ring, and very small, spherical, 2.00–2.50 μm in diameter with a rounded but thick ring (Figure 6n). The bigger sensillum surface is characterized by numerous very small pores, whereas the surface of the small sensillum is smooth (Figure 6o, p). Antennal segment III (as well as segments IV and V) of the winged male bears numerous small multiporous sensilla, which are located on the whole length of the segments and almost always in two or three more or less regular rows (Figure 6q, r). Small multiporous sensilla are different in size and shape, mostly rounded or oval, 6.50–15.00 μm in diameter and are surrounded by a raised sclerotic ring, almost without or with very short projections, 0.31–1.50 μm long (Figure 6s, t). The sensilla of wingless males are the same in their characters as in the winged ones, but the placoid sensilla in the examined specimens were observed only on antennal segment III (Figure 6u) and antennal segment V (Figure 6w), while the fourth segment was characterized only by trochoid sensilla (Figure 6v). The small placoid sensilla are of the same shape and very similar in diameter as those in the winged males (Figure 6y).

In all morphs on antennal segments V and VI sensilla known as the primary rhinaria are visible and they are all characterized by numerous short and long projections of the cuticle. Antennal segment V bears one rounded or slightly oval big multiporous placoid sensillum near the distal end

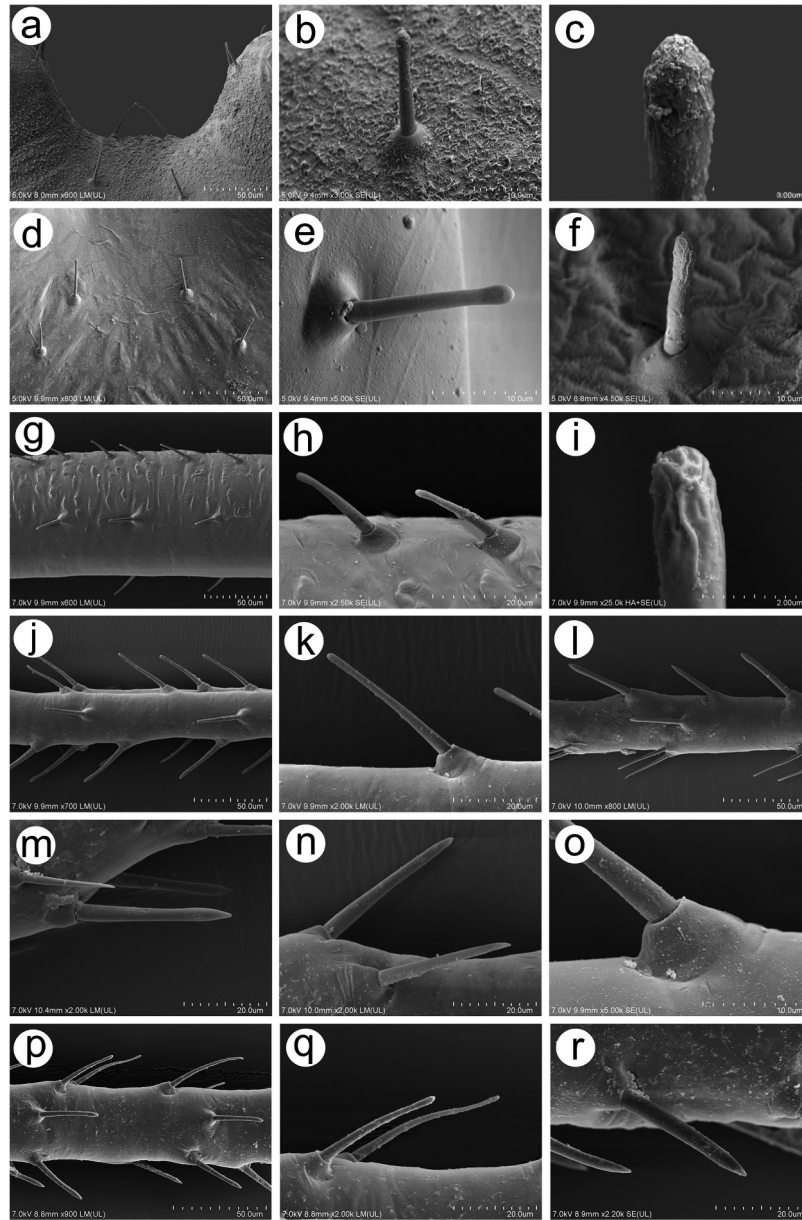


Figure 5. Body and leg trichoid sensilla of *A. pisum*: (a) short trichoid sensilla on antennal tubercles and frons of wingless viviparous female, (b) fine structure of head trichoid sensillum of wingless viviparous female, (c) fine structure of the very slightly swollen apical part of the trichoid sensillum, (d) trichoid sensilla on the head of winged viviparous female, (e) trichoid sensillum on thorax, (f) trichoid sensillum of abdomen with ruffled apical part, (g) part of hind femur of wingless viviparous female with general view of short and blunt trichoid sensilla, (h) structure of wingless viviparous female femoral trichoid sensilla with slightly capitate apices, (i) fine structure of the ruffled surface of the apical part of the sensillum, (j) mid part of hind tibia of wingless viviparous female with two kinds of long, thick trichoid sensilla: with blunt apices on the dorsal side and with dagger-like apices on the ventral side, (k) structure of trichoid sensilla with blunt or slightly capitate apices, (l) end of tibia of winged viviparous female with almost all long, thick trichoid sensilla with mostly dagger-like and pointed apices, (m) structure of the sensilla on the ventral part, (n) structure of the sensilla on the dorsal part, (o) fine structure of the socket of trichoid sensilla, (p) mid part of hind tibia of wingless male with capitate and pointed trichoid sensilla, (q) structure of trichoid sensilla with capitate apices, (r) structure of the sensilla with pointed apices on the ventral side of the tibiae.

of the segment (Figure 7a), 14–17 μm in diameter (when rounded) or 29–32 μm wide and 17–20 μm long (when oval). The big multiporous placoid sensillum on antennal segment V lies in a wide sclerotic cavity surrounded by two kinds

of about 30–40 ring projections: short, single and pointed, 0.50–1.75 μm and long, thick single or forked, 3–7 μm (Figure 7b, c, m). The surface of the sensillum is often covered by a thin wax layer (Figure 7d). The antennal segment VI area,

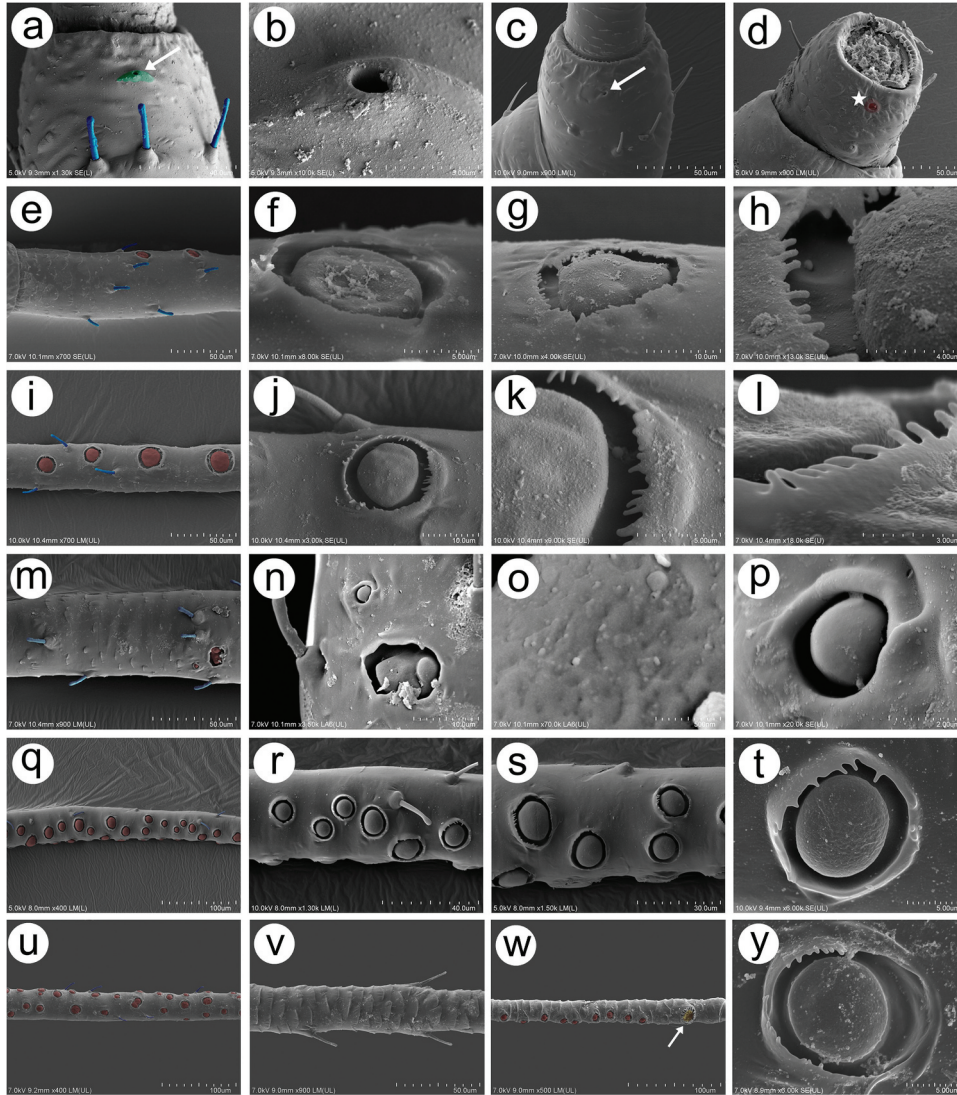


Figure 6. Antennal sensilla of *A. pisum*: (a) ventral side of pedicel of wingless viviparous female with one rhinariolium on a raised area (green) and trichoid sensilla (blue), (b) fine structure of the rhinariolium showing the rounded opening, (c) ventral side of the pedicel of winged viviparous female with a small rhinariolium without raised area (arrow), (d) dorsal side of the pedicel of oviparous female with campaniform sensillum (orange, star), (e) part of antennal segment III of wingless viviparous female near the base with small placoid multiporous sensilla (secondary rhinaria) (red) and type I trichoid sensilla (blue), (f) structure of small placoid sensillum with gentle edges of cuticle, (g) structure of small placoid sensillum with slightly ciliated cuticle edge, (h) fine structure of the ciliated cuticle edge, (i) part of antennal segment III of winged viviparous female with small, wide multiporous placoid sensilla (secondary rhinaria) (red) and type I trichoid sensilla, (j, k) structure of small placoid sensillum with ciliated cuticle edge, (l) fine structure of lateral view of small placoid sensillum showing porous surface, (m) part of antennal segment III of oviparous female near the base with small placoid multiporous sensilla (secondary rhinaria) (red) and type I trichoid sensilla (blue), (n) structure of different sized small placoid sensilla, (o) fine structure of the porous surface of the bigger sensillum, (p) fine structure of the second smaller sensillum, (q) part of antennal segment III of winged male with numerous small multiporous sensilla (secondary rhinaria) (red) and type I trichoid sensilla (blue), (r, s) structure of placoid sensilla with partly ciliated cuticle edge, (t) fine structure of small placoid sensillum and the cuticle edge, (u) part of antennal segment III of wingless male with numerous small multiporous sensilla (secondary rhinaria) (red) and type I trichoid sensilla (blue), (v) part of antennal segment IV with only trichoid sensilla, (w) part of antennal segment V of wingless male with numerous small multiporous sensilla (secondary rhinaria) and big multiporous placoid sensillum (primary rhinarium) (arrow), (y) fine structure of small placoid sensillum and the cuticle edge of wingless male.

between the basal part and terminal process, is characterized by the presence of three kinds of sensilla: a big multiporous placoid sensillum (major rhinarium), two small multiporous

placoid sensilla and four sunken coeloconic sensilla (all together with small placoid sensilla called accessory rhinaria), which are lying very close to each other and form a nest. Each

sessillum lies in an independent cavity and is surrounded by mostly independent ring projections which may fuse, especially in the central part of the sensilla nest (Figure 7e). The big multiporous placoid sensillum is rounded, very similar to that on antennal segment V, 10–13 µm in diameter and located on the external lateral side of the sensilla nest. Small multiporous placoid sensilla are oval or irregular in diameter and mushroom-shaped, 5–6 µm long and 3–4 µm wide (Figures 7f, 11e). From the four sunken coeloconic sensilla two are of type II, characterized by 8–11 long, tightly adjoining projections (Figure 7g), and two of type I with 10–12 very short projections forming a rounded rosette (Figures

7h, 11f,g). The sunken coeloconic sensilla are separated into two groups: one coeloconic sensillum (type I) in the most distal location, above big and small multiporous placoid sensilla, and the three others near each other from the centre of the nest and between small multiporous placoid sensilla (type I coeloconic sensillum) to an external lateral position (type II coeloconic sensilla). In winged morphs, all sensilla on antennal segments V and VI are characterized by similar morphological features (Figure 7i) and location on the segments. In winged viviparous females and winged males, a small difference in mutual location of sensilla on antennal segment VI is found. The big multiporous placoid sensillum is in an external lateral

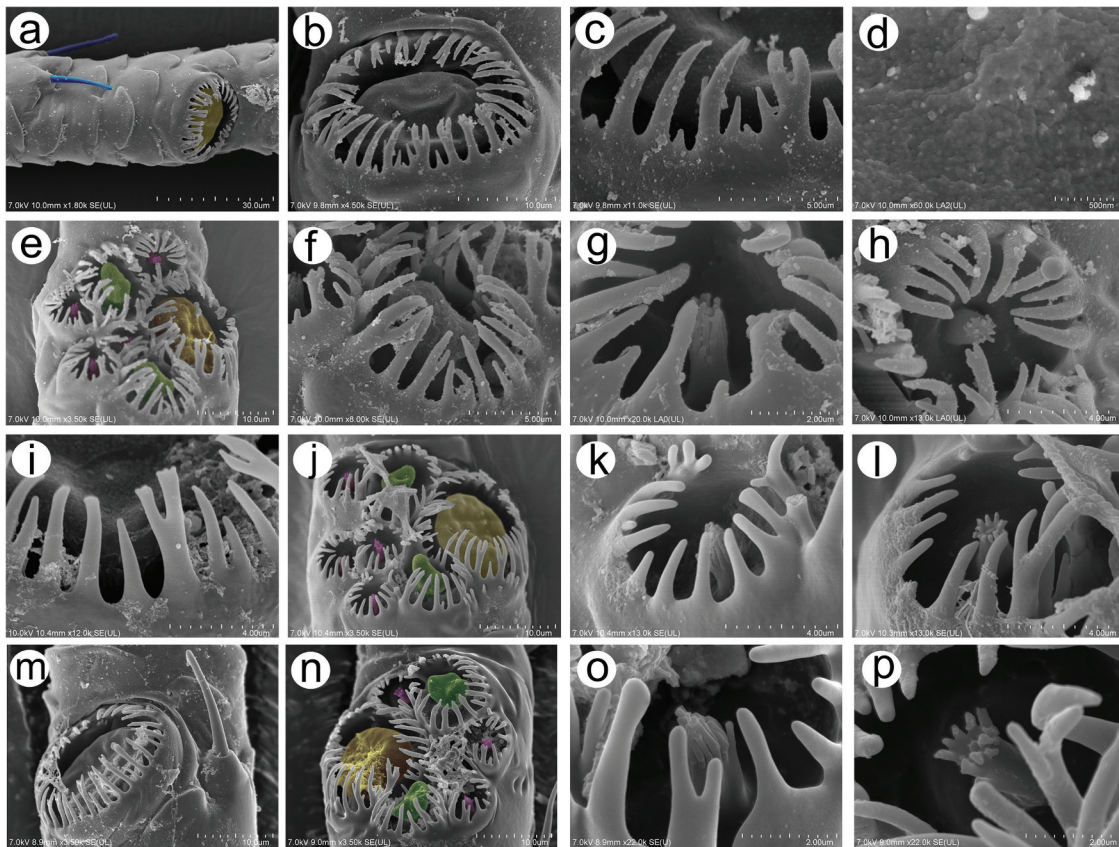


Figure 7. Antennal sensilla of *A. pisum*: (a) apical part of antennal segment V of wingless viviparous female with type I trichoid sensilla and big multiporous placoid sensillum (yellow) with ciliated cuticle edge, (b) structure of the big placoid sensillum, (c) fine structure of the ciliated cuticle edge projections, (d) fine structure of the sensillum surface, (e) sensilla of the apical part of antennal segment VI base and basal part of terminal process of wingless viviparous and oviparous female: big multiporous placoid sensillum (yellow), two small multiporous placoid sensilla (green) and three visible sunken coeloconic sensilla (pink), (f) fine structure of the small placoid sensillum, (g) fine structure of type II sunken coeloconic sensillum, (h) fine structure of type I sunken coeloconic sensillum, (i) fine structure of ciliated cuticle edges and big placoid sensillum surface, (j) sensilla of the apical part of antennal segment VI base and basal part of terminal process of winged viviparous female: big multiporous placoid sensillum (yellow), two small multiporous placoid sensilla (green) and sunken coeloconic sensilla (pink), (k) fine structure of type II sunken coeloconic sensillum, (l) fine structure of type I sunken coeloconic sensillum, (m) structure of the big placoid sensillum of wingless male, (n) sensilla of the apical part of antennal segment VI base and basal part of terminal process of the wingless male: big multiporous placoid sensillum (yellow), two small multiporous placoid sensilla (green) and sunken coeloconic sensilla (pink), (o) fine structure of type II sunken coeloconic sensillum, (p) fine structure of type I sunken coeloconic sensillum.

location, two small multiporous placoid sensilla are in the nest centre in polar positions (one slightly higher and one slightly lower from the big placoid sensillum) and all four sunken coeloconic sensilla in an external lateral position: one type I in the distal end, a second type I and one type II in the middle, and finally one type II in the proximal end of the nest (Figure 7j, n). Their morphology is the same as in wingless morphs (Figure 7k, l) and there are no differences between them in the parthenogenetic and sexual generations (Figure 7o, p).

Trichoid sensilla. Trichoid sensilla are present on all antennal segments and represent two kinds: type I trichoid sensilla from antennal segment I to the base of antennal segment VI and type II trichoid sensilla on the antennal segment VI terminal process. Antennal trichoid sensilla type I are very similar to those which were found on the dorsal side of the studied morphs' body. They are rather short, 18–22 μm long on the pedicel and 10–13 μm on antennal segments III–V, thick, 1.70–2.20 μm and with more or less capitate apices, which often have a wrinkled surface on antennal segments I–V (Figure 8a, b). On the base of antennal segment VI they are visibly longer, 16–17 μm long, slender, 1.20–1.80 μm , with blunt but also wrinkled apices (Figure 8c). The surface of the sensilla is smooth but very often covered by wax secretion, slightly longer in winged morphs but all slightly curved towards the antennal cuticle (Figure 8d–f). Sockets of the sensilla are rounded and trapezoid in lateral view, in all cases taking the distal direction.

Type II trichoid sensilla may be found in different numbers along the terminal process (Figure 8g, j, m) and typically four always on its tip (called apical setae) (Figure 8h, k, n). They are very similar within all examined morphs, very short, straight, rigid and blunt or slightly rounded on apices in a general view, but often they are slightly spherical, pointed or flat (Figure 8i, l, o). Sockets of these sensilla are similar to those in type I trichoid sensilla but are much more slender and protuberant. High-resolution images of the sensilla structure, their sockets and apices are given in Figure 12.

Mouthparts sensilla

The rostrum (labium) is short with five segments which are short and similar in length to the visible type I trichoid sensilla in a general view (Figure 9a–

d). The last rostral segment is fused from segments IV and V without any visible border (its common name is the ultimate rostral segment) (Figure 9a), besides the slightly visible, narrower area at the apical dorsal part (Figure 9c). The ultimate rostral segment is slightly elongated, triangular with type I and type II trichoid sensilla, and type II and type III basiconic sensilla (Figures 9a–c; 13). The type II trichoid sensilla are shorter than trichoid sensilla type I, 19–25 μm , lying in the middle of the ultimate rostral segment on both the dorsal and ventral side, are tubular with rounded apices (Figure 9e). The type I trichoid sensilla are visibly longer, 27–130 μm , located in the distal part of the ultimate rostral segment as three pairs of so-called primary setae. They are also characterized by narrower and pointed apices (Figure 9f). Sockets of both types of trichoid sensilla are rounded or oval from the top and flat trapezoid, 7–8 μm in diameter (Figure 9g). Trichoid sensilla are mostly smooth, but in some cases of type I trichoid sensilla, numerous irregularities may be seen (Figure 9h). The type II basiconic sensilla are located on the very proximal part of the ultimate rostral segment, always two in number, shorter in the wingless morphs, 5–6 μm (Figure 9i, j) and longer in winged morphs, 9–11 μm (Figure 9k, l). They are also characterized by more protuberant sockets, 5–6 μm in diameter. The type III basiconic sensilla are visible on the very distal part of the ultimate rostral segment (Figure 9m, q) as very short, tapering pegs without sockets, lying in small cavities. In all morphs they are mostly present in eight pairs, 3.18–5.70 μm long and with a very clearly visible moulting pore in their basal part (Figure 9n, o, p, s, t). The moulting pores are more or less visible in basal parts of almost all type I trichoid sensilla on rostral segment IV (Figure 9r).

Table I presents a comparison of the terminology of various types of sensilla in relation to their function and the terminology of morphological characters, traditionally used in the taxonomy of aphids.

Discussion

The pea aphid is a species that possesses both wing polyphenism and a genetic wing polymorphism (Brisson 2010; Ogawa et al. 2012). The wing polyphenism applies to the parthenogenetic viviparous generation – wingless females produce genetically identical winged offspring in response to environmental factors such as poor food quality, overcrowding or predation risk (Purandare et al. 2014). In contrast, wing production in males is environmentally insensitive and

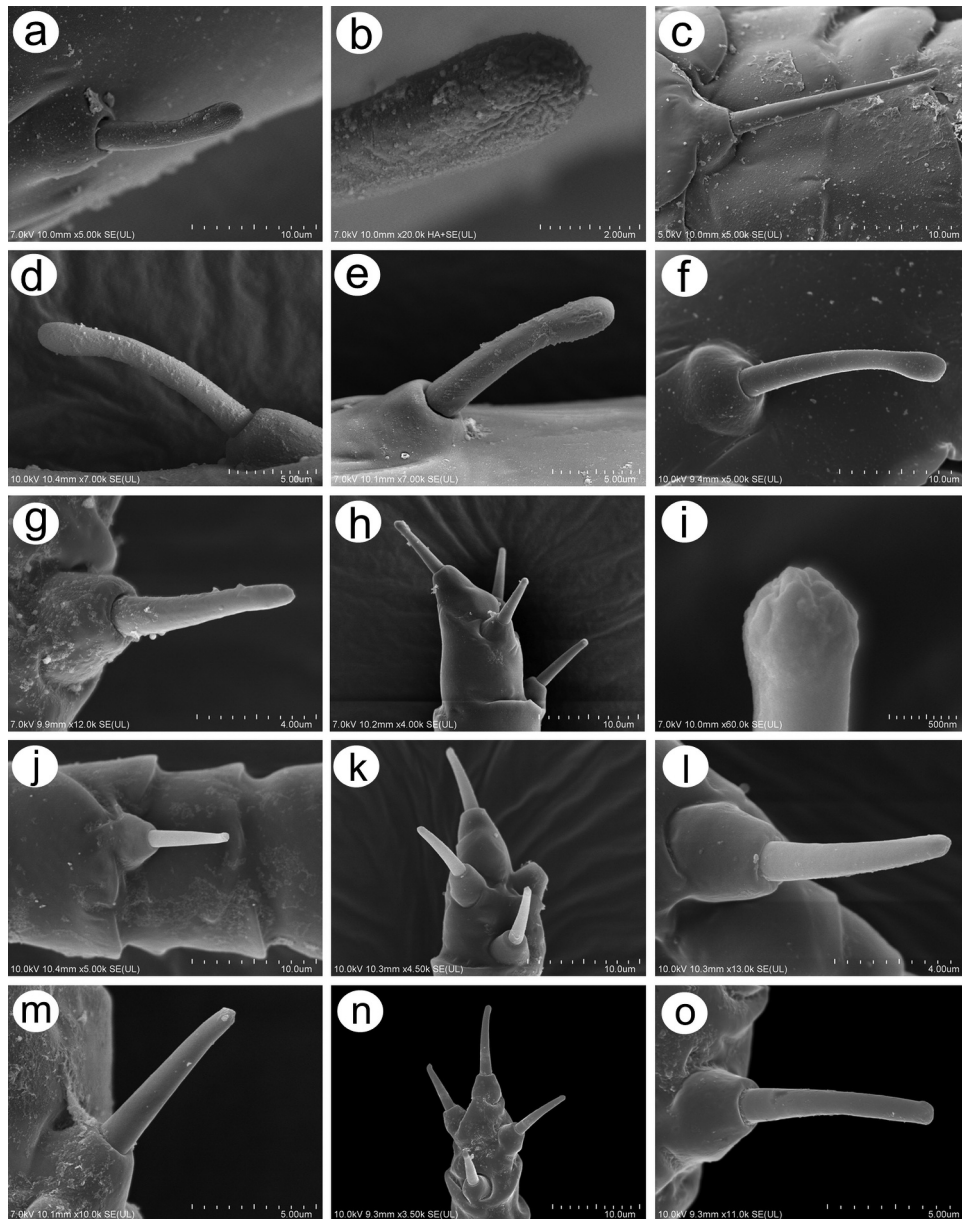


Figure 8. Antennal sensilla of *A. pisum*: (a) type I trichoid sensillum on of antennal segment III of wingless viviparous female, (b) fine structure of the trichoid sensillum apical part, (c) type I trichoid sensillum on of antennal segment V of wingless and winged morphs, (d) type I trichoid sensillum on of antennal segment III of winged viviparous female, (e) type I trichoid sensillum on of antennal segment III of oviparous female, (f) type I trichoid sensillum on antennal segment III of wingless and winged male, (g) type II trichoid sensillum on terminal process of wingless viviparous female, (h) type II trichoid sensilla on the apical part of terminal process of wingless viviparous and oviparous female, (i) fine structure of the apex of the sensillum, (j) type II trichoid sensillum on terminal process of winged viviparous female, (k) type II trichoid sensilla on the apical part of terminal process of winged viviparous female, (l) structure of the sensillum, (m) type II trichoid sensillum on terminal process of winged male, (n) type II trichoid sensilla on the apical part of terminal process of winged male, (o) structure of the sensillum.

controlled by the sex-linked, biallelic locus, *aphicarus* (*api*) (Braendle et al. 2005).

Despite the fact that the genotypes are identical, they are phenotypically different. The head of both wingless and winged females is similar in its general morphology, with the exception of slightly lower

antennal tubercles and a wider frons in winged females and the larger head width in the distance between the eyes in the wingless females. Winged females possess slightly bigger compound eyes with ommatidia rounded and hexagonal with a diameter almost twice as large as that of wingless females. In

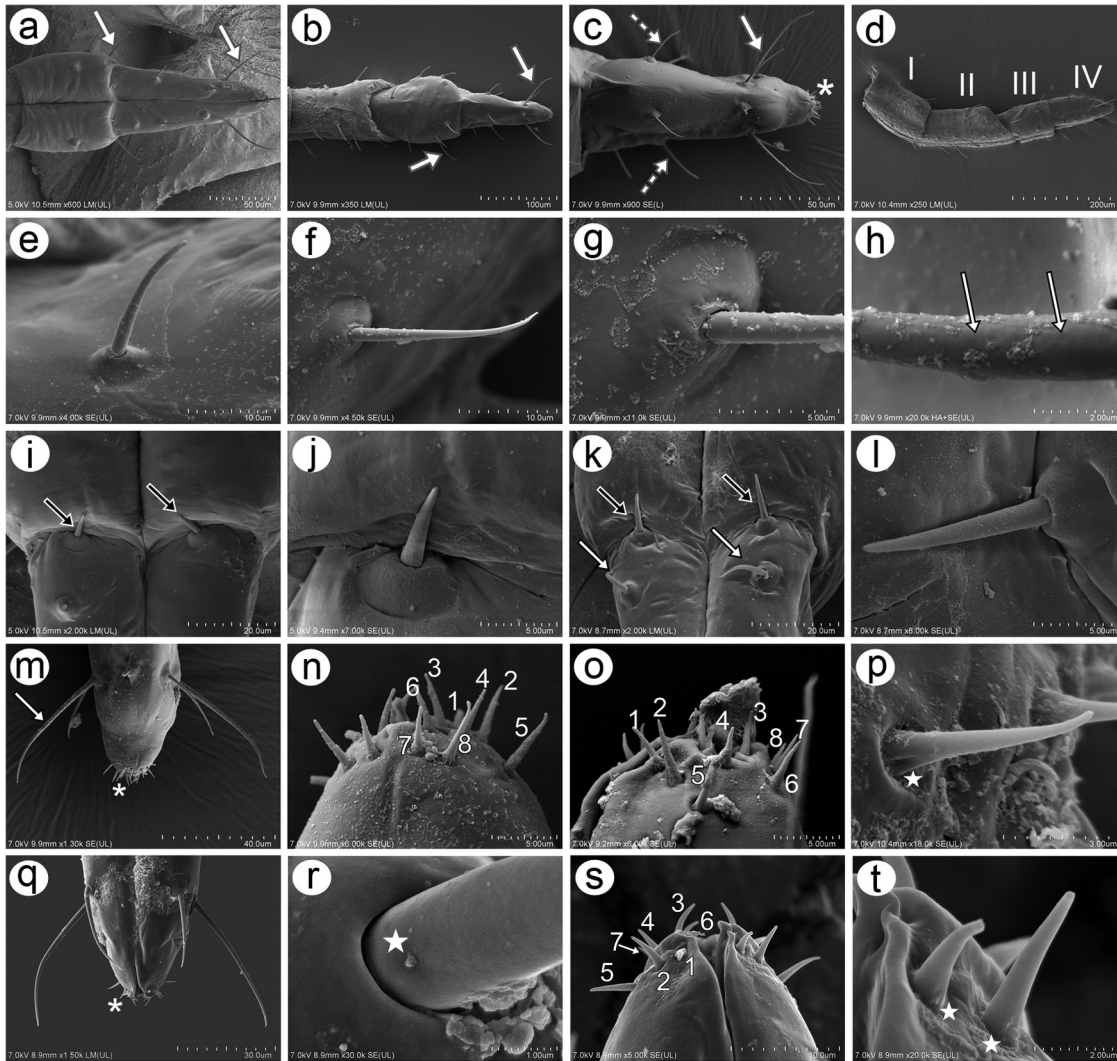


Figure 9. Mouthparts sensilla of *A. pisum*: (a) ventral side of rostral segments III and IV of wingless viviparous female with visible trichoid sensilla (arrows), (b) dorsal side of rostral segments III and IV of winged viviparous female with visible trichoid sensilla (arrows), (c) latero-dorsal side of rostral segment V of oviparous female with trichoid sensilla as accessory setae (dotted arrow), as primary setae (solid arrow) and type III basiconic sensilla (asterisk), (d) lateral side of rostrum of winged male showing all four (I–VI) segments, (e) structure of the type I trichoid sensillum on rostral segment III, (f) structure of type I trichoid sensillum on rostral segment IV, (g) fine structure of the basal part of type I trichoid sensillum and its socket (e–h wingless viviparous female) (h) fine structure of the surface of type I trichoid sensillum on rostral segment IV with visible immersions (arrows), (i) proximal (basal) part of rostral segment IV of wingless viviparous female with type II basiconic sensilla (arrows), (j) structure of the basiconic sensillum, (k) proximal (basal) part of rostral segment IV of winged viviparous female with type II basiconic sensilla (black arrows) and visible type I trichoid sensilla (white arrows), (l) structure of the basiconic sensillum, (m) distal (apical) part of rostral segment IV of wingless viviparous female with long type I trichoid sensilla (arrow) and type III basiconic sensilla (asterisk), (n) apex of rostral segment IV of wingless viviparous female with eight pairs of type III basiconic sensilla, (o) apex of rostral segment IV of winged viviparous female with eight pairs of type III basiconic sensilla, (p) fine structure of type III basiconic sensillum with moulting pore on the basal part (star), (q) distal (apical) part of rostral segment IV of wingless male with long type I trichoid sensilla (arrow) and type III basiconic sensilla (asterisk), (r) fine structure of the surface of type I trichoid sensillum on rostral segment IV with visible moulting pore (star), (s) apex of rostral segment IV of wingless male with seven pairs of basiconic sensilla type III, (t) fine structure of type III basiconic sensilla with moulting pore on the basal part (stars).

both winged and wingless morphs, ommatidia on the ocular tubercle are visibly bigger than those in the compound eye. In contrast, the frontal and dorsolateral ocelli are the unique structures of winged females within the viviparous generation. Such

a photoreceptor system, consisting of the compound eye, used for image formation, and the ocelli, responsible for recognition of light intensity, are typical for insects, including aphids (Kring 1977). However, a bigger compound eye with larger

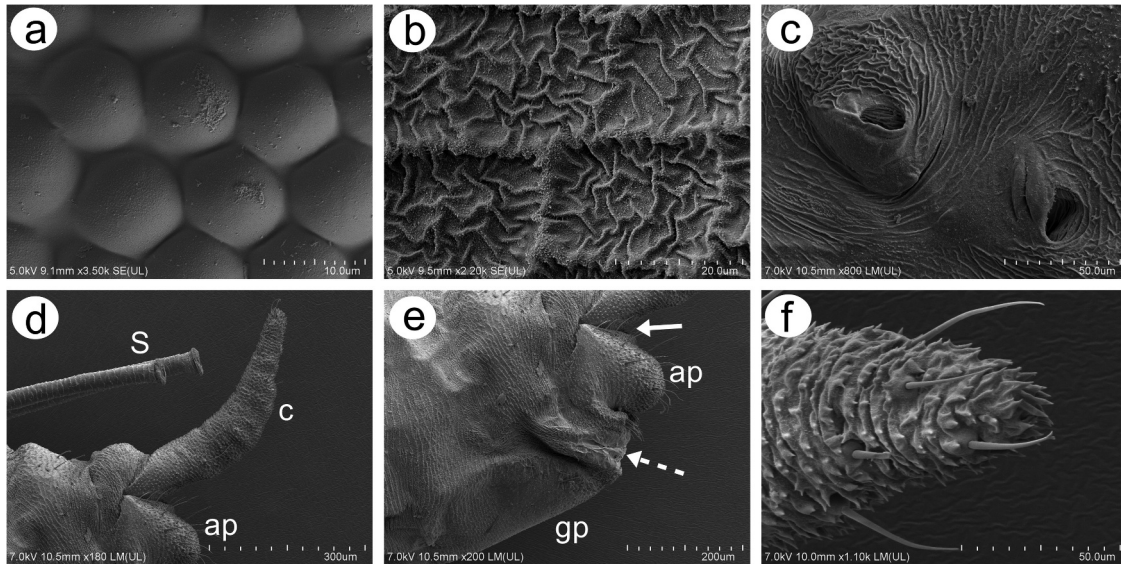


Figure 10. Detailed characters of the general morphology of *A. pisum*: (a) fine structure of the ommatidia of compound eye; (b) fine structure of dorsal cuticle sculpture; (c) structure of abdominal spiracles; (d, e) lateral side of the end of the abdomen of apterous viviparous female showing perianal structures: S-siphunculi, c-cauda, ap-anal plate, gp-genital plate, rg-rudimentary gonapophyses, arrow-genital pore, dotted arrow-genital pore; (f) structure of the cuticle and trichoid sensilla on the cauda.

ommatidia is, therefore, the adaptation of winged morphs for dispersion and host plant location. Similar characters of the photoreceptor system were observed in the viviparous generation of the broad bean biotype of *A. pisum* (Iskikawa & Miura 2007). Moreover, winged pea aphids can change their phototactic responses, which help them to disperse during their pre-breeding period and to prevent them from flying away from the host plants during the period of their reproduction (Zhang et al. 2016).

The male wing polymorphism is determined by a single gene locus on the X chromosome: *aphicarus* (*api*) (Braendle et al. 2006). Three *api* genotypes are present in natural populations: clones homozygous for the *api*-winged allele that produce all winged males, clones homozygous for the *api*-wingless allele that produce all wingless males and clones heterozygous for *api* that produce winged and wingless males in equal proportions. Although all three possible *api* genotypes may occur on the same host plant species, several studies suggest that male morph production may correlate with host plant range and persistence. In the pea biotype of *A. pisum* studied, both the strain producing solely winged males and the strain producing winged and wingless males were available. In winged and wingless males, both the compound eye with triommatidium and the frontal and dorsolateral ocelli are present. These structures are slightly larger in winged males; nevertheless, in addition to the

function of dispersion and host finding, the photoreceptor system can play an important role in mate selection.

In the case of aphids, the olfactory and gustation system plays a similar or even more important role in such behaviour. In aphids, different types of sensilla are located on the antennae, mouthparts, legs and genitalia (Dunn 1978; Bromley et al. 1979, 1980; Wiczorek et al. 2019) (Table I). The antennal sensilla are distributed on the pedicel and the flagellum. Scanning electron microscopy observations of the pea aphid antennae mostly highlighted differences in the distribution of sensilla in the studied morphs. The most important differences relate to the distribution of sensilla in winged and wingless morphs; that is, the latter possess numerous multiporous placoid sensilla distributed on the whole lengths of antennal segments III, IV and V. In wingless morphs, both asexual and sexual females are characterized by the presence of a few placoid sensilla on antennal segment III, whereas wingless males have the same type of sensilla on the whole lengths of antennal segments III and V. In general, the largest number of this type of sensilla occurs in winged males, while the sensillum with the largest diameter occurs in the winged females. The morphology of antennal sensilla across all the studied morphs is similar; that is, three kinds of sensilla were found – one campaniform sensillum on the pedicel, numerous small multiporous placoid sensilla on antennal segments III–V

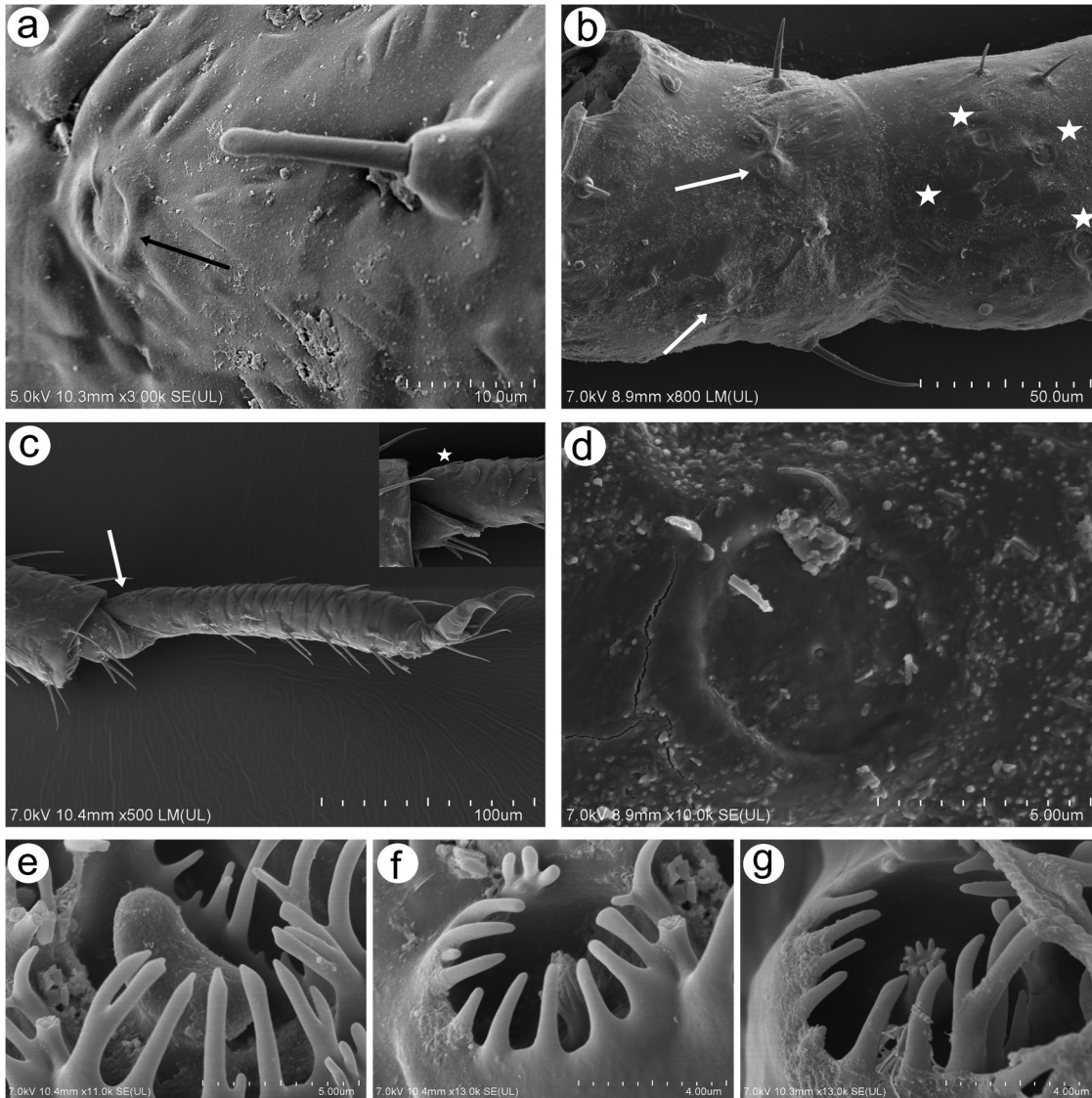


Figure 11. Detailed structure of the campaniform, placoid and coeloconic sensilla of *A. pisum*: (a) structure of type I trichoid and campaniform sensillum on the pedicel; (b) campaniform sensilla on the internal side of trochanter (arrows) and proximal part of femur (asterisks); (c) campaniform sensillum (arrow and asterisk) on dorsal proximal part of second segment of tarsus; (d) fine structure of campaniform sensillum on femur; (e) fine structure of small multiporous placoid sensillum on ANT VI (accessory rhinarium); (f) fine structure of type II sunken coeloconic sensillum; (g) fine structure of type I sunken coeloconic sensillum.

(secondary rhinaria), a large single multiporous placoid sensillum on antennal segments V and VI (primary rhinaria), the latter surrounded by two small multiporous placoid sensilla, and four coeloconic sensilla of type I and II. Among aphid species studied so far, such sensilla arrangement on antennal segments V and VI seems to be constant (Bromley et al. 1979, 1980; Ban et al. 2015; De Biasio et al. 2015; Kanturski et al. 2017; Bruno et al. 2018). In aphids, the antennal sensory system is supplemented by trichoid sensilla of two types – trichoid sensilla of type I distributed along the

whole antenna, from antennal segment I to the base of antennal segment VI, and trichoid sensilla of type II on the terminal process of antennal segment VI. In the pea biotype of *A. pisum* studied, trichoid sensilla are similar across the morphs (short and thick with capitate apices of type I and short, rigid with pointed apices of type II). However, the number, shape and distribution of trichoid sensilla, as well as placoid sensilla, are of great diagnostic value and importance in aphid taxonomy (Yang et al. 2009; Kanturski et al. 2015, 2018; Barjadze et al. 2018). More

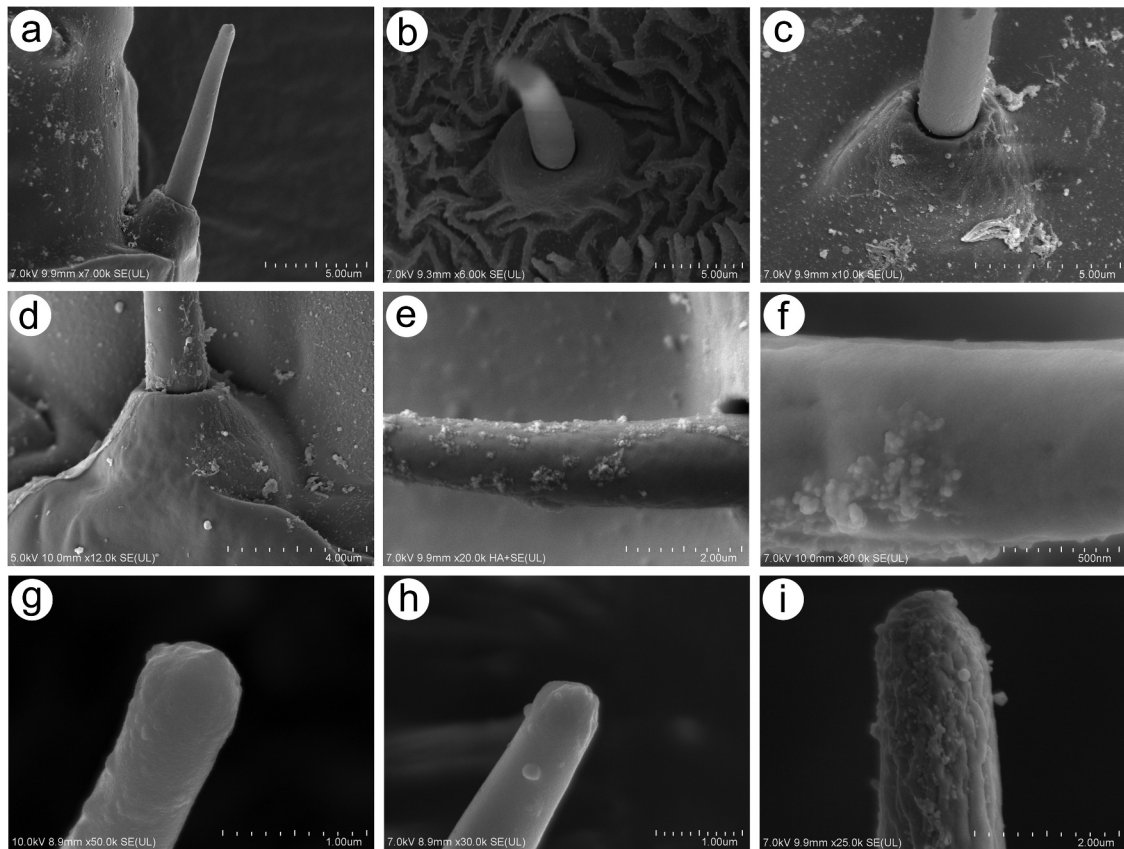


Figure 12. Detailed structure of the body and legs trichoid sensilla of *A. pisum*: (a) type II trochoid sensillum on terminal process; (b, c, d) fine structure of sockets and basal parts of type I trochoid sensilla; (e, f) fine structure of the surface of type I trichoid sensilla; (g, h) fine structure of apical parts of type II trichoid sensilla; (i) fine structure of apical part of type I trichoid sensillum.

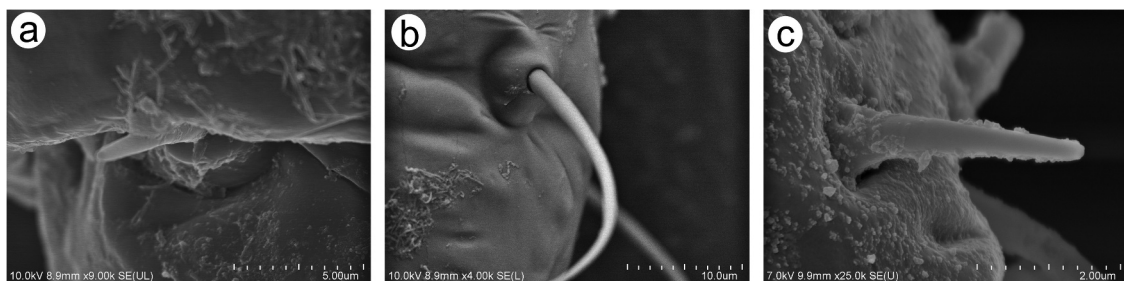


Figure 13. Detailed structure of the mouthparts sensilla of *A. pisum*: (a) fine structure of type II basiconic sensillum; (b) type I trichoid sensillum socket on the mouthparts; (c) fine structure of type III basiconic sensillum.

importantly, the morphological diversity of sensilla is reflected in their function. Primary and secondary rhinaria, constituted by placoid sensilla, function as chemoreceptors. In all morphs, they are responsible for the identification of plant volatile compounds and recognition of the specific host plant whereas the large placoid sensillum of antennal segment VI is sensitive to the alarm pheromone (Zhang et al. 2017). However, in winged morphs equipped with a much larger number of secondary

rhinaria, it is the adaptation to host plant location during dispersal (viviparous females) or recognition of sex pheromones (winged and wingless males). Coeloconic sensilla of the primary rhinarium are specialised thermo- and hygrometers whereas the campaniform sensillum provides the information of the position of the antennae. In general, campaniform sensilla on different parts of the body (pedicel, trochanter, femur, second segment of hind tarsus and wings) have been described and

Table I. Comparison of the terminology of various types of sensilla and their function in relation to the terminology of morphological characters traditionally used in the taxonomy of aphids.

Body part	Terminology of sensilla	Terminology of morphological characters of aphids	Putative function
Dorsum	type I trichoid sensilla	setae	mechanoreceptors
Antennal segment I	type I trichoid sensilla	antennal setae	mechanoreceptors, probably
Antennal segment II	type I trichoid sensilla	antennal setae	chemoreceptors
	coeloconic sensillum	rhinarium	higroreceptor
	campaniform sensillum	–	prioprioreceptor
Antennal segment III	type I trichoid sensilla	antennal setae	mechanoreceptors
	small multiporous placoid sensilla	secondary rhinaria	chemoreceptors (olfactory function)
Antennal segment IV	type I trichoid sensilla	antennal setae	mechanoreceptors
	small multiporous placoid sensilla *	secondary rhinaria *	chemoreceptors (olfactory function)
Antennal segment V	type I trichoid sensilla	antennal setae	mechanoreceptors
	small multiporous placoid sensilla *	secondary rhinaria *	chemoreceptors (olfactory function)
	big multiporous placoid sensillum	primary rhinarium	chemoreceptor (olfactory function)
Antennal segment VI base	type I trichoid sensilla	antennal setae	mechanoreceptors
	big multiporous placoid sensillum	primary rhinarium (major)	chemoreceptor (olfactory function)
	small multiporous placoid sensilla	accessory rhinaria	chemoreceptors (olfactory function)
	type I sunken coeloconic sensilla	–	higroreceptors, probably also thermoreceptors
	type II sunken coeloconic sensilla	–	higroreceptors, probably also thermoreceptors
Antennal segment VI terminal process	type II trichoid sensilla	setae along terminal process setae on the tip of terminal process (apical setae)	mechanoreceptors, additionally chemoreceptors
Labium (rostrum) segments I–III	type I trichoid sensilla	rostral setae	mechanoreceptors with most probably gustatory function
Labium (rostrum) segments IV +V	type II basiconic sensilla	–	–
(ultimate rostral segment)	type I trichoid sensilla	ultimate rostral segment accessory setae	–
	type I trichoid sensilla	ultimate rostral segment primary setae	–
	type III basiconic sensilla	–	–
Trochanter, femora, tibiae, tarsi	type I trichoid sensilla	femoral, tibial, tarsal setae	mechanoreceptors with probable gustatory function
	campaniform sensilla	–	prioprioreceptors
Cauda	type I trichoid sensilla	caudal setae	mechanoreceptors
Parameres**	type I trichoid sensilla	parameres setae	mechanoreceptors
Basal part of the phallus	peg-like sensilla	–	mechanoreceptors

* winged morphs, ** males.

examined in a few aphid species so far, e.g. in the *Mindarus* Koch and *A. pisum* (Montagno & Favret 2016) or *Pseudosigella* Hille Ris Lambers (Kanturski et al. 2017) and are accepted to be proprioceptive organs which convert forces into electrical discharge by detecting strains or deformations in the cuticle (Pringle 1937; Bromley et al. 1980). Trichoid sensilla of type I are putative mechanoreceptors and specialized sensilla of type II are putative chemoreceptors with a gustatory role (Bromley et al. 1979, 1980; Sun et al. 2013).

In insects in general and in aphids in particular, other body structures besides the antennae are related to chemoreception (Bruno et al. 2018). Aphids, like other hemipterans, are characterized by highly specialized piercing-sucking mouthparts consisting of the labium, labrum, maxillae and mandibles. Two types of trichoid sensilla (type I and II) and two types of basiconic sensilla (type II and III) are located on the labial segments. Labial sensilla mostly play a putative role in mechanically sensing the feeding sites or provide the information of the position of the other mouthpart

components. However, our SEM observations confirm the presence of a moulting pore in the basal part of the type III basiconic sensilla (eight pairs of short peg sensilla), distributed on the tip of the ultimate rostral segment and type I trichoid sensilla on ultimate rostral segment IV in all adult morphs studied, which indicates most probable their chemoreceptor function.

In addition to olfactory and visual stimuli, insects' mechanosensory structures on legs also play an important role not only in walking and in the detection of substrate-borne vibrations but also in regulation of the first phase of feeding behaviour or mating (reviewed by Tuthill & Wilson 2016). According to De Biasio et al. (2015), legs of broad bean *A. pisum* biotype present numerous trichoid sensilla, uniform in size, shape and distribution. In the pea biotype of *A. pisum* studied, there are also no fundamental differences between individual morphs in these trichoid sensilla. However, sensilla on tibiae are the longest, thick and rigid, with capitate or blunt apices on the dorsal and proximal part or with pointed or dagger-like apices on the ventral and distal parts of the tibiae. In aphids these sensilla are most probably mechanoreceptors; however, ultrastructural studies have shown that one of the trichoid sensilla (ventral seta) of the first tarsal segment is typical of a contact chemoreceptor (Van Emden & Harrington 2017). Like the number, shape and distribution of trichoid sensilla on antennae, these structures on legs are also of a great diagnostic value and importance in aphid taxonomy (Blackman 2010). Among the tested morphs, only the oviparous females possess numerous small, rounded (or sometimes forming eight-shaped) scent plaques (pseudosensoria) on most of the length of the hind tibiae. Similar structures were observed in the broad bean *A. pisum* biotype (Murano et al. 2018). In aphids scent plaques are responsible for the secretion of monoterpene sex pheromones, detected by males' placoid sensilla (secondary rhinaria), distributed on antennal segments III–V (Birkett & Pickett 2003). Reproductive polyphenism involves cyclical switching between asexual and sexual reproduction in response to environmental factors such as day length and temperature conditions. The presence of scent plaques on the hind tibiae of oviparae is a universal feature of these morphs, also present in aphids with a shortened life cycle, when the sexual generation appears at the beginning of summer (Wieczorek et al. 2014). On the other hand, such a universal feature in males is the presence of varied modified genital structures (Wieczorek et al. 2011, 2012). The pea aphid is a good example of comparing these structures, as winged and wingless males of *A. pisum* pea biotype were available in the current SEM observations. In both winged and wingless

males, the whole genital area is covered by clear microsculpture and long type I trichoid sensilla, the longest and the most densely distributed on parameres. In contrast, the surface of the basal part of the phallus is smooth and covered by numerous rounded cavities with minute structures resembling peg-like sensilla. Similar results were obtained in the case of previously studied aphid species. However, the number and shape of peg-like sensilla significantly differ among the species studied so far (Wieczorek et al. 2011, 2012). Interpretation of the function of these sensilla (mechanoreceptors or chemoreceptors) only on the basis of scanning electron micrographs is speculation – especially since recent research concerning the mapping of odorant-binding proteins' (OBPs – soluble proteins mediating chemoreception in insects) expression profiles have shown that sensilla on antennae or mouthparts of aphids are not the only contact chemoreceptors (Sun et al. 2013; De Biasio et al. 2015; Zhang et al. 2017; Bruno et al. 2018; Wang et al. 2019).

Our results, concerning the detailed SEM study of adult morphs of *Acyrtosiphon pisum* clones, representing the common pea biotype, are of general interest. However, they can be the basis for further immunochemical and ultrastructural research, primarily in understanding the role and function of various types of sensilla in the perception process in different morphs, representing various biotypes or species. The results also underline the importance of micromorphological investigations in insect systematics and evolutionary biology.

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