

Werner Gnatzy · Ulrich Maschwitz

Pedestal hairs of the ant *Echinopla melanarctos* (Hymenoptera, Formicidae): morphology and functional aspects

Received: 12 July 2005 / Accepted: 3 October 2005 / Published online: 23 February 2006
© Springer-Verlag 2006

Abstract The South East Asian arboreal Formicine *Echinopla melanarctos*, as well as some other members of this genus possess a cuticular structure unique in ants, the pedestal hairs. In *E. melanarctos*, about 700 pedestal hairs are situated on the dorsal and lateral surfaces of the head, the alitrunk, the petiole and the gaster. They are arranged in a polygon-like figuration. On the summit of each of the up to 200- μm high pedestals, a single central hair inserts. This hair (up to 500- μm long) is innervated by a single bipolar mechanosensitive sensory cell. The lumen of each tube-like pedestal contains (1) epithelial cells (2) the sensory cell and the auxiliary cells of the central hair and (3) the long efferent ductules of up to ten isolated bicellular glandular units. Each glandular unit is composed of a secretory glandular cell and a duct cell, all of which are located at the base of a pedestal. The cytoplasm of a glandular cell contains a well-developed end apparatus and is characterised by stacks of smooth and granular endoplasmic reticulum, numerous polyribosomes, a lot of mitochondria and some up to 5- μm large secretory vesicles. The secretion of the gland cells is released on the apex of the pedestal wall via small pores. Approximately 30 μm below their summit, some pedestals possess additionally (up to six) mechanosensitive hairs that are arranged ray-like. We suppose that the pedestal hairs are important in nest-space protection and find that only in ants with high pedestals on the head (*Echinopla melanarctos* and *Echinopla pallipes*), the compound eyes are stalked thus overtopping the pedestals.

Keywords Pedestal hairs · Topography · Fine structure · Mechanoreceptors · Gland cells

Introduction

In ants (Formicidae), presence of conspicuous covers of long and dense hairs, on the exoskeleton is rare (Hölldobler and Wilson 1990). However, workers of species of the tropical ant tribes Basicerotini and Stegomyrmecini possess two dominant forms of setae on the dorsal surfaces of the body and outer surfaces of legs: longer ‘brush’ hairs with splintered distal ends, and shorter ‘holding’ hairs that vary among species from plumose to blade-shaped or filiform. According to Hölldobler and Wilson (1986), the two hair types usually but not invariably occur together to form a double layer. The brush hairs evidently scrape or otherwise capture fine particles of soil. In this way, the camouflaged workers can hardly be distinguished from the soil. Other well-documented special cuticular hair structures are the so-called ammochaetae, layers of long curved hairs situated on the lower surface of the head and on the mouthparts. They are found in various desert ants and used for cleaning the body cuticle and also for transport and soil digging (Wheeler 1910; Maidl 1933).

During ecological studies on the southeast-Asian arboreal formicine genus *Echinopla* (Maschwitz and Reichard, personal communication), we came upon *Echinopla melanarctos* (Smith 1857), an ant species living in **small colonies in dead hollow branches lying on the ground or hanging in the vegetation**. The habitus of this species is quite unique: head, alitrunk, petiole and gaster are dorsally fully covered with long black hairs, which are inserted in very obvious cuticular pedestals. These structures also surround the compound eyes of the species. As the eyes are sitting on stalks, they overtop the pedestal layer. Other species of *Echinopla* are also covered with a dense hair layer, partly with or without pedestal structures (Smith 1857; Hölldobler and Wilson 1990).

Here, we give a detailed morphological and fine structural analysis of the pedestal hairs of *E. melanarctos* that could contribute to future functional studies of

W. Gnatzy (✉) · U. Maschwitz
Zoologisches Institut, J.W. Goethe-Universität,
Siesmayerstr. 70, 60323 Frankfurt, Germany
E-mail: gnatzy@zoology.uni-frankfurt.de
Tel.: +49-69-79824713
Fax: +49-69-79824820

these unique structures. We used the techniques of light microscopy and scanning electron microscopy (SEM) to map the number, size and external structure of pedestal hairs and the gland cell-complexes associated with each of the pedestals.

We found on head, alitrunk, petiole and gaster (1) cuticular pedestals with a long hair (= central hair) inserting in the summit of each pedestal and (2) some pedestals which additionally possess shorter hairs (= secondary hairs) extending ray-like from the upper third of the pedestal. Using transmission electron microscopy (TEM), we found out that (3) the central and secondary hairs are cuticular mechanoreceptors of the ‘tactile hair’ type; i.e. each of these hairs is innervated by one bipolar sensory cell. Furthermore, (4) each tube-like pedestal contains in its lumen, the sensory cell and the auxiliary cells of the central hair and—if present—the sensory cells together with their auxiliary cells of the secondary hairs. Corresponding with the number of glandular units per pedestal, maximally ten efferent ducts pass through the pedestal lumen each of them opening at the summit of the pedestal in a single small pore. Also, (5) below the base of each pedestal floating in the haemolymph space are located between two and up to ten bicellular glandular units, (type class III according to Noirot and Quennedy 1974, 1991) each composed of a secretory cell and a duct cell.

Materials and methods

Animals

In all the experiments, adult workers of *E. melanarctos* Smith 1857 were used. They were obtained from a colony, which contained about 50 workers and brood. The ants were collected in the Pasoh Forest Reserve, a primary lowland dipterocarp forest in Negeri Sembilan in Peninsular Malaysia. The colony inhabited two hollow dead branches each about 20 mm in diameter. The branches lay 1.5 m apart from each other one on the ground and one hang loosely in the low vegetation. The colony was kept in a plastic container with a gypseous bottom layer where they lived within a bamboo culm 5–10 mm in diameter. As food supply, honey/water (1:1) was offered.

Image analysis and comparative morphology

The number and distribution of pedestal hairs on the exoskeleton of *E. melanarctos* ($n = 3$) were counted using a Wild M 5 microscope at a magnification of 500 \times . The quantitative data were expressed as means.

Additionally, the distribution of various hair types and the shape of compound eyes in workers of *E. melanarctos* and other three *Echinopla* species (*Echinopla lineata* Mayr 1862, *Echinopla pallipes* Smith

1857, *Echinopla striata* Smith 1857; collection W.H.O. Dorow, Forschungsinstitut Senckenberg, Frankfurt) were mapped using a Wild M 5 microscope at a magnification of 500 \times .

Ultrastructural studies

Workers of *E. melanarctos* were anaesthetised with carbon dioxide. Parts of the cuticle with pedestal hairs were sectioned oblique in a drop of buffer with a razor blade. These fragments were prepared for the SEM or the TEM.

Scanning electron microscopy

For SEM, all preparations were prefixed for several hours in 2% glutaraldehyde (in 80 mM sodium-cacodylate buffer and 3.9% sucrose, pH 7.25), postfixed for 2 h in 2% OsO₄ solution in the same buffer, finally dehydrated in a graded ethanol series. After critical point drying in a Polaron unit, using CO₂ and amyloacetate (2 \times 15 min), the samples were mounted vertically on aluminium holders using double-sided conductive carbon tape in order to allow an investigation of the

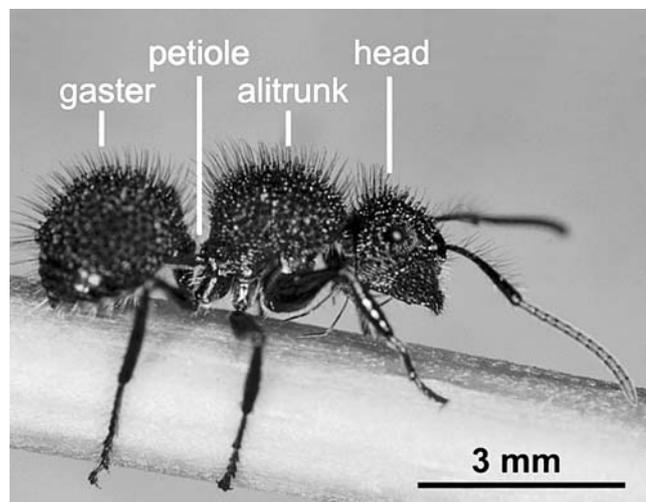


Fig. 1 Macro photo of a worker of *Echinopla melanarctos*, lateral view

Table 1 Distribution of pedestal hairs of *E. melanarctos*-workers ($n = 3$)

Location	Number of hairs
Head	$\bar{x} = 110$
Alitrunk (mesonotum)	$\bar{x} = 245$
Petiole	$\bar{x} = 15$
Gaster	$\bar{x} = 353$
	$\Sigma = 723$

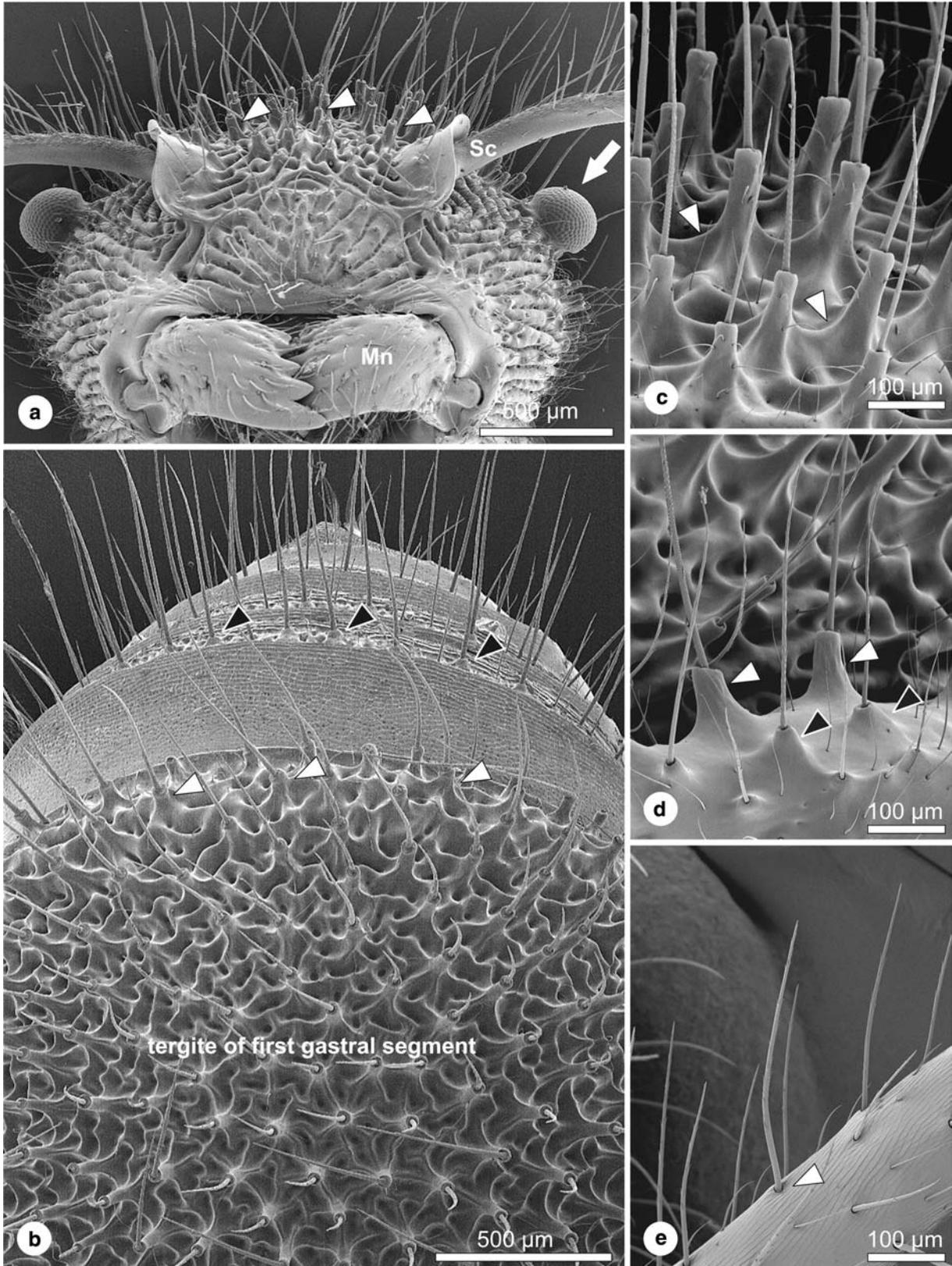


Fig. 2 a–e *Echinopla melanarctos*. General morphology and hair types of a worker. SEM pictures. **a** Head, frontal view. *White arrowheads* mark pedestal hairs, *arrow* marks stalked eyes. **b** Gaster, dorsal view. *White arrowheads* mark pedestal hairs on the huge tergite of the large first gastral segment, *black arrowheads* mark hairs with short pedestal on the remaining gastral tergites

c Tergite of first gastral segment, view from above. Note the arrangement of the pedestal hairs. Buttress-like cuticular ridges of pedestal bases *arrowheads*. **d** Hairs on the petiole with short (*black arrowheads*) and long pedestals (*white arrowheads*). **e** Bristle hairs on the leg of a worker ant without any pedestal (*arrowhead*). *Mn* Mandible, *Sc* base of scapus

inner and outer side of the specimens. Finally, the specimens were gold coated in an Agar Sputter Coater, then investigated with a field-emission SEM equipment (Hitachi S-4500) at an accelerating voltage of 1–5 kV. Some fragments were treated with hot 5% potassium hydroxide (KOH) for 10 min before SEM preparation. Additionally, some specimens were freed from wax with chloroform–methyl alcohol (2:1) at 60°C before SEM preparation (Brück and Stockem 1972).

Urticating effects

For testing the urticating effects of the pedestal hairs, living ants ($n=8$) with their pedestal hairs armed exoskeleton were brought in close contact to a human tongue and to the mucous membrane of the mouth.

Transmission electron microscopy

For TEM, all preparations were prefixed and fixed as described above for SEM. After rinsing in 80 mM cacodylate buffer plus 2.5% sucrose, the specimens were dehydrated subsequently in a graded alcohol series and embedded in Epon 812 resin (Serva) with propylene oxide as the bridging solvent. Orientated serial sections (~70 nm thick) were cut with a diamond knife, and collected on large (2×1 mm) formvar filmed grids. After lead citrate staining, the sections were investigated using a Hitachi H 500 TEM equipment at an accelerating voltage of 75 kV.

Semi-thin sections (1 µm) were stained with methylene blue, and analysed and documented using a SPOT digital camera (Reichert-Jung, Bannockburn, IL, USA). The pictures were processed with Adobe Photoshop software (Adobe Systems, San Jose, CA, USA).

Results

External morphology of *E. melanarctos*

The body length of the workers is \bar{x} 6.3 mm ($n=10$). The surface is shining and deep black in colour (Fig. 1). As typical for the genus, the first gastral segment is extremely large, accounting for more than half of the length of the gaster in the dorsal view or profile (Figs. 1, 2b). Especially striking are the numerous hair-carrying pedestals, which extend some distance beyond the cuticle (Figs. 1, 2a–d). They are located on the dorsal and lateral side of the head, the alitrunk, the petiole and the first gastral segment and make them look bristly. A further type of hairs, the secondary hairs, augments this impression; up to six hairs of this type can be found, most of which are arranged about 30 µm beneath the pedestal summit more or less ray-like around the pedestal wall (Figs. 2c, 3b). On the petiole and the gastral

Fig. 3 a–e *Echinopla melanarctos*. Glandular units of pedestal hairs in a worker. **a** Semi-thin longitudinal-section through a pedestal on tergite of first gastral segment. The course of the ductules within and out of the secretory gland cells (*Glc*) is indicated by white arrowheads. **b–c**. Low power SEM pictures. **b** Partly cut-off pedestal (*Pe*) with its gland cells (*Glc*). **c** Inner surface of a part of the pronotum. Note the arrangement of the gland cells (*Glc*). Arrows mark bundles of muscle fibres. **d** Inner surface of a part of the pronotum after KOH-treatment. Note that the openings into the lumina of the pedestals after the secretory glandular cells have been resolved are now visible (arrowheads). **e** Typical arrangement of gland cells (*Glc*) and its ductules (arrowheads) of a pedestal hair. Arrows mark nerve providing the sensory cells of pedestal. *Cu* cuticle of the pedestal, *Hlsp* haemolymph space, *Hs* hair shaft of central hair, *sH* secondary hairs

segments—except the first—up to 100-µm long hairs are located inserting on those pedestals measuring only 30 µm in height (Fig. 2b, d; cf Fig. 7). Furthermore, hairs, up to 550 µm length, without any pedestal base, inserting in a cuticular bulge only, frequently occur on the surface of legs and antennae (Figs. 1, 2e; cf Fig. 7). In *E. melanarctos*, the compound eyes are sitting on stalks of about 70 µm height and so they overtop the pedestal hair layer, a unique phenomenon in ants (Fig. 2a; cf Fig. 7).

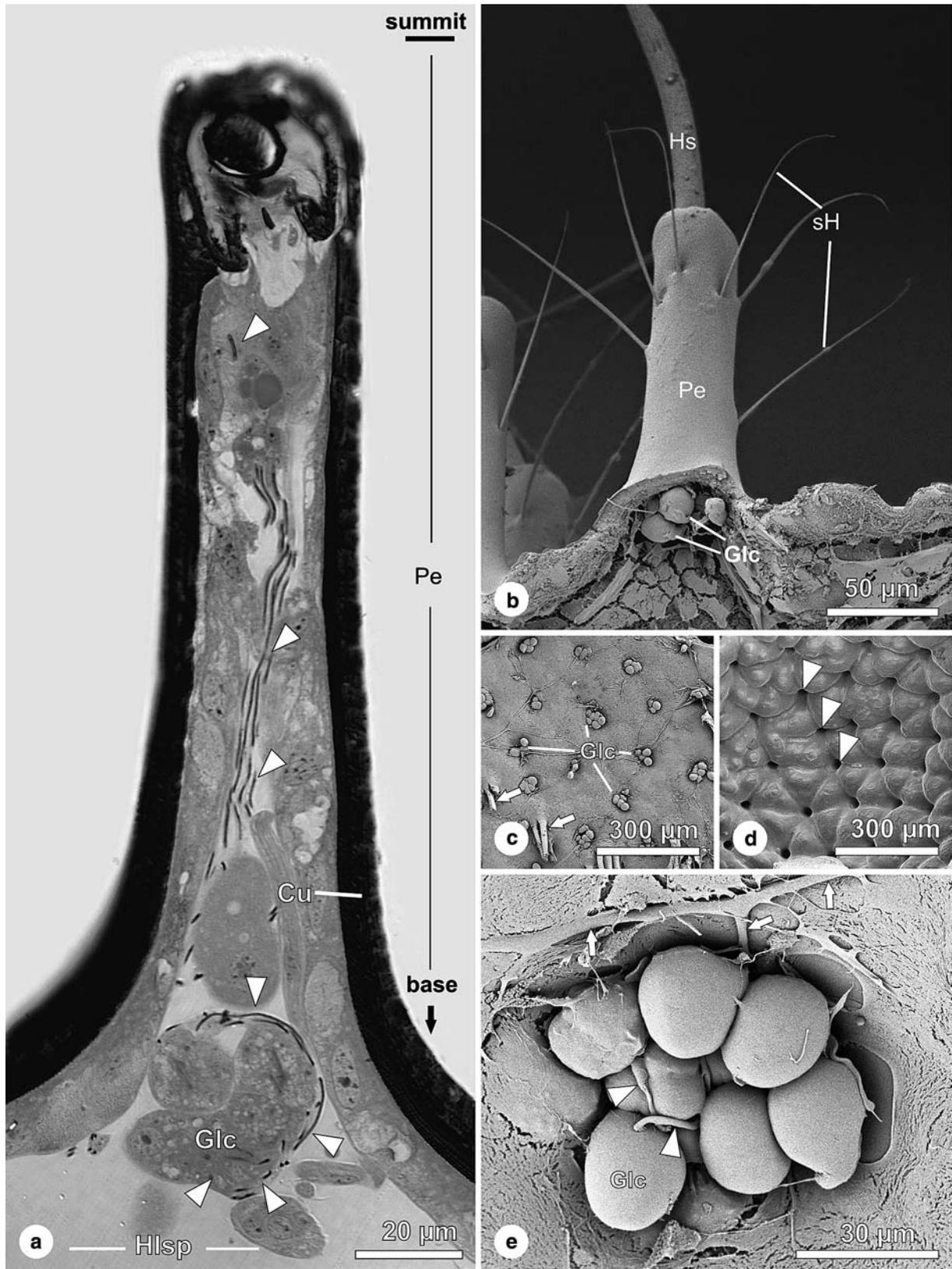
Number, size, topography the urticating effects of the pedestal hairs

All together, more than 700 pedestals are located on the worker body surface (Table 1). They are arranged mostly in a polygonal position 150–200 µm distant from each other, i.e. up to 30 mm⁻² (Figs. 2a, b, 3c, d). Most pedestals are located on the huge tergite of the large first gastral segment (= third abdominal segment) that constitutes three-fourth of the total gaster surface (Fig. 2b). At its summit, each pedestal carries a slightly outward curved central hair (Figs. 2a–c, 3b, 4a). No itching or urticating effects could be observed upon bringing the irritated workers on the mucous membranes (skin) in the human mouth (see Material and methods).

Fine structure of the pedestal hairs

The pedestal

The pedestals on the head, the alitrunk, the petiole and the first gastral segment in *E. melanarctos* look rather uniform. They consist of a smooth cuticular cylinder ca 35 µm in diameter. Its height is quite variable. While dorsally located pedestals are up to 200 µm in length, the laterally located pedestals are ca 100 µm. The pedestal base can be enlarged to about 50 µm, sitting on a stand of buttress-like cuticular ridges that extend about 100 µm (Fig. 2a, c). The solid pedestal wall is 5-µm thick, enlarging to 10 µm at the bottom (Fig. 3a).



A central hair arises from the slightly convex summit of each pedestal (Figs. 3b, 4a–c). The margin of the summit on the one side rises ca 5 μm higher compared with the

opposite margin. Near beyond this margin, up to ten orifices of glands terminate at the apical pedestal surface (Figs. 3b, 4a).

The central hair

Independently from the pedestal position on the head, the alitrunk, the petiole or the gaster, all central hairs are ca 500 µm in length. They are slightly curved outwards and possess longitudinal ridges (Figs. 2b–d, 4a, 5a). On these ridges, a few (4–10 per hair) spines arise (Inset Fig. 4a). At their base, the central hairs are 12.5 µm in diameter and continuously diminish apically (Figs. 2a–d, 5a). Whereas the lumen of the lower third of the hair is filled with a spongy cuticular material (Fig. 4b; lower inset, Fig. 5a), the upper part of the hair consists of a solid cuticle (upper inset, Fig. 5a).

Articulation of the central hair

The base of the central hair is asymmetric in shape (Fig. 4b). At one side, it extends approximately 12.5 µm into the pedestal lumen, however, on the opposite side, the extension is only 5 µm. The shape of hair articulation is also asymmetric (Fig. 4b). The base of the hair shaft is connected with the pedestal summit by a 0.75-µm thick cuticular joint membrane. Additional suspending fibres extending between hair articulation and hair base fix them flexibly at the pedestal summit (Fig. 4b).

Sensory supply

Each central hair is innervated by a single bipolar mechanosensitive sensory cell (Fig. 5a–g). The dendrite of the sensory cell is subdivided into an inner and outer dendritic segment by a short ciliary structure. At the level of the ciliary segment, the dendrite narrows and changes into the structure of a non-motile cilium (9+2+0 pattern in cross section; Fig. 5e). It is surrounded by a dendritic sheath, a secretory product of the thecogen cell (Gnatzy and Schmidt 1972a, b). The outer dendritic segment contains as a modality-specific structure, a tubular body (Figs. 4b, 5a) with an aggregation of densely packed microtubules (Gnatzy and Tautz 1980), which are interconnected by an electron-dense matrix and surrounded by a distinct peripheral layer of microtubules. Like other cuticular exteroceptors of insects (Gnatzy and Hustert 1989), each central hair possesses two extracellular spaces (Figs. 4b, 5b, e) (1) a large subcuticular cavity, the outer receptor lymph space, which is bordered by the apical membranes of the two outer auxiliary cells (Fig. 5b) and (2) a small inner receptor lymph space which extends around the ciliary base (Fig. 5e).

The secondary hairs, articulation and sensory supply

Each of the up to 100-µm long secondary hairs, inserts in a shallow depression in the outer pedestal wall; the tip of

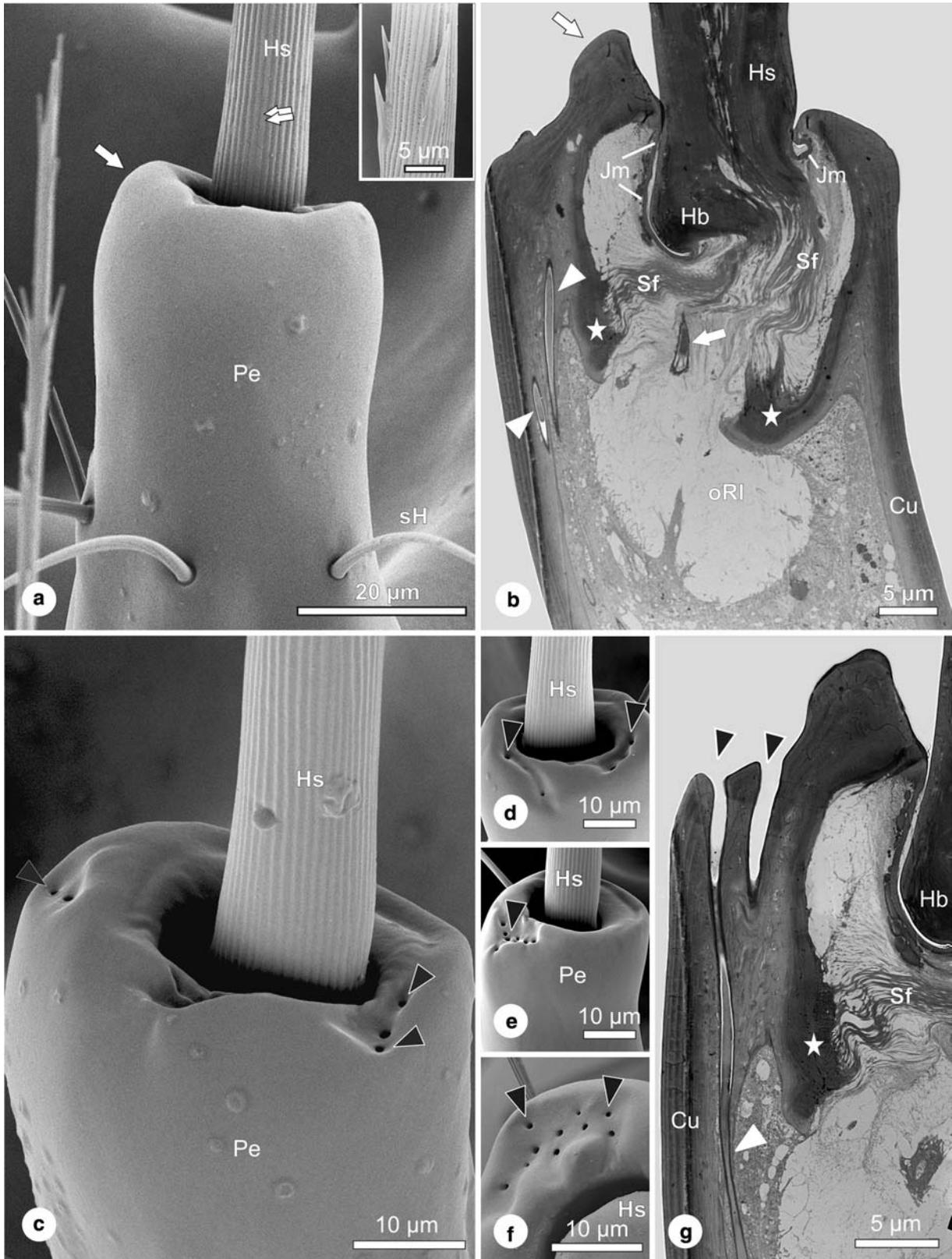
Fig. 4 *Echinopla melanarctos*. Pedestal and central hairs of a worker. **a** SEM. Summit of a pedestal, lateral view. Note that the top of the pedestal (*Pe*) in which the hair shaft (*Hs*) of the central hair inserts is asymmetrically formed, i.e. one margin is higher (*white arrow*) than the opposite, *asterisks* mark hair articulation. Surface of the hair shaft is sculptured by ribs (longitudinal ridges) (*double arrows*). Inset: Spines (4–10 per hair) arising more distally on the ridges of the central hair shaft. **b** TEM. Longitudinal section of articulation of a central hair shaft (cf Fig. 4a). Note that hair base (*Hb*) and articulation (*asterisk*) of the central hair shaft (*Hs*) follow outer asymmetrical geometry (*arrow*). Outer dendritic segment with tubular body are marked by *white arrow*, ductules of the gland cells by *arrowheads*. **c** SEM. Openings of gland cells ductules (*arrowheads*) at the summit of a pedestal (*Pe*) after pretreatment with chloroform–methanol. **d–f** SEM. Variations in number and location of pores from pedestal gland cells; pedestal (*Pe*) with pores (*arrowheads*). **g** TEM. Longitudinal section of a region like shown in Fig. 4c. Ductule (*white arrowhead*) running from the pedestal lumen enters the pedestal cuticle (*Cu*); pores of ductules at the summit of the pedestal are marked by *black arrowheads*. *Cu* cuticle of the pedestal, *Hb* hair base, *Hs* hair shaft of central hair, *Jm* joint membrane, *oRl* outer receptor lymph space, *Sc* Secondary hairs, *Sf* suspension fibres

these hairs points slightly downwards (Figs. 3b, 4a). Like the central hair (see above), they possess longitudinal ridges.

The shaft of each secondary hair is connected with the pedestal wall by a thick joint membrane. Because of the geometry of the articulation, the free play of the bristle is very small. Also, the central hairs the secondary hairs are innervated by only one bipolar mechanosensitive sensory cell. Their outer dendritic segment terminates immediately below the hair base and contains a small tubular body.

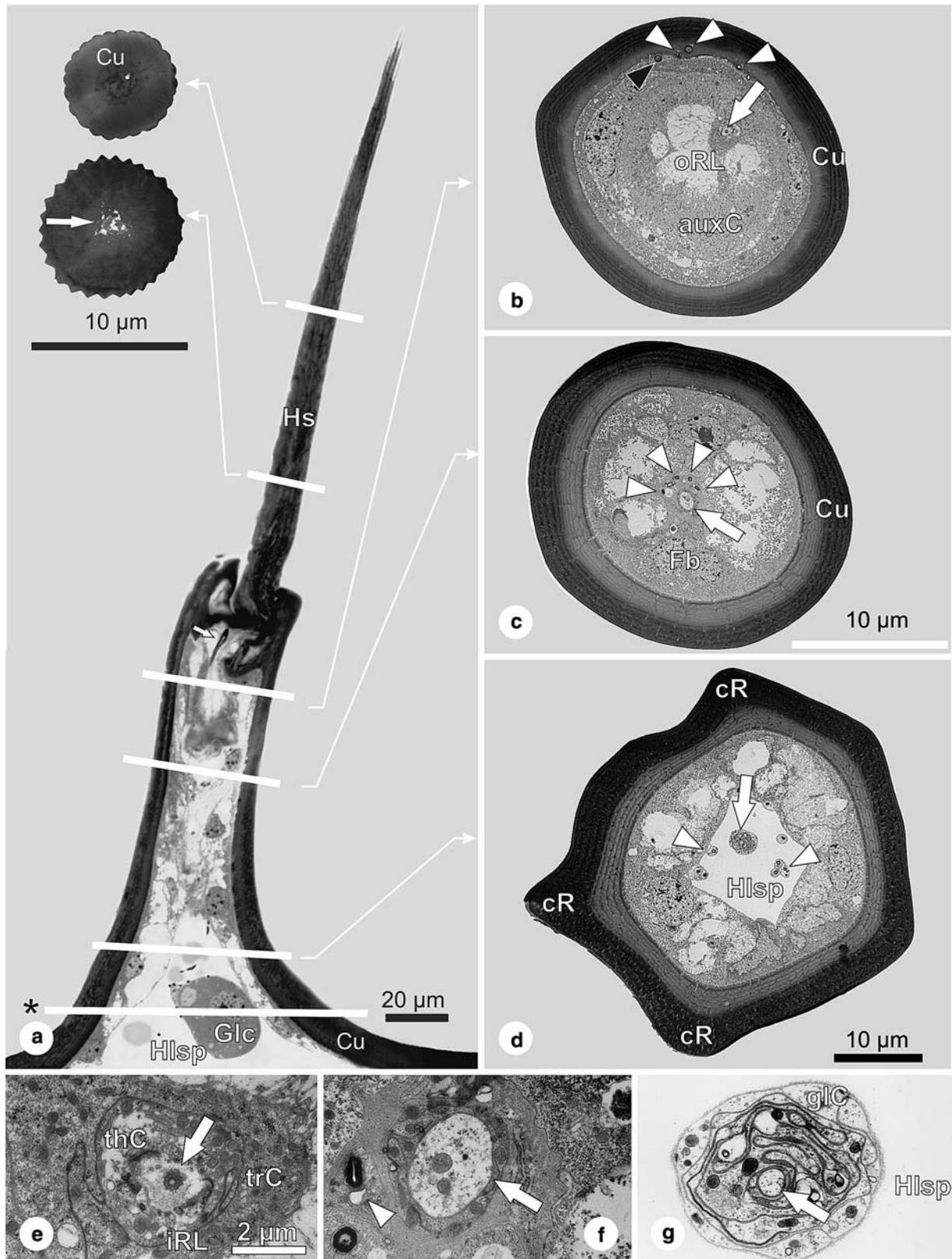
The gland complex

The lumen of each pedestal opens at its base in the direction towards the haemolymph space (Figs. 3a, 5a). Here, several bicellular glandular units (type-III glandular cells according to Noirod and Quennedey 1974, 1991) float in the haemolymph, each consisting of a large secretory cell (Figs. 3a–c, e, 5a, 6a, d) and an outermost duct cell (which produces the cuticular duct) (Figs. 3a, e, 6a, d). The number of glandular units per pedestal hair is variable, ranging from two to ten units (see Fig. 3c, e). The proper secretory cells are globular to fan-shaped and up to 30 µm large (Fig. 3e). Each secretory cell is provided with a large nucleus, an end apparatus located near the nucleus, stacks of smooth and granular endoplasmic reticulum, numerous polyribosomes, a lot of mitochondria and some up to 5-µm large vesicles which probably contain glycogen particles (Fig. 6a–d). The end apparatus is an internalised microvillar part of the plasma lemma, surrounding an efferent and blind-ending cuticular ductule (Fig. 6b, d) (Gnatzy and Volkandt 2001). Upon leaving the secretory cell, the epicuticle becomes much thicker and more compact without pores and forms the cuticular lining of the



ductule lumen in the duct cell. The duct cell is characterised by a reduced cytoplasm that surrounds the conducting canal throughout its entire length (Fig. 6d). On longitudinal sections, the extremely elongated

conducting canals within the lumen of the pedicel (cf Fig. 3a) can be followed until they reach their external cuticular pores (Fig. 4c–f). The distance between the secretory cells and the wall of the pedicel apex measures



approximately 200 µm (cf Fig. 3a). Approximately 20 µm below the pedestal summit, the conducting canals penetrate into the outer pedestal wall (Figs. 4b, 5b) ending on the pedestal wall surface with an up to 1-µm

wide pore (Fig. 4c–g). In SEM preparations, the pores are only visible after treatment with a chloroform–methanol solution (see Material and Methods) that resolves the lipid layer on the cuticle.

◀
Fig. 5 *Echinopla melanarctos*. Inner organisation of pedestal and its central hair in a worker. **a** Semi-thin longitudinal section of a pedestal with its central hair; arrow marks outer dendritic segment of the sensory cell innervating the central hair. *Upper inset*: Cross section of a central hair at a level as indicated in the longitudinal section. *Lower inset*: Cross section through the hair shaft at a level as indicated in the longitudinal section; arrow marks spongy cuticle. **b–g** TEM Cross sections. **b–d** Pedestal at a level indicated in **a**. **b** Arrow marks ciliary region of a central sensory hair (magnified in **e**). Note that some of the ductules being still in the epithel (*white arrowheads*) while one already has entered the pedestal cuticle (*black arrowhead*). **c** Arrow marks soma of sensory cell (magnified in **f**), *arrowheads* mark ductules. **d** Level of the buttress-like cuticular ridges (*cR*); arrow marks axon of a central hair (magnified in **g**), *arrowheads* mark ductules of gland cells within the haemolymph space (*Hlsp*). **e** Ciliary region of a central hair (*arrow*) showing thecogen cell (*thC*), trichogen cell (*trC*), inner receptor lymph space (*iRL*) and outer receptorlymph space (*oRL*), *arrow* marks ciliary neckledge. **f** Sensory cell soma of central hair (*arrow*), *arrowhead* marks ductule of pedestal gland cell. **g** Axon of central hair (*arrow*) enwrapped by a glial cell (*glC*). *auxC* auxiliary cells, *Cu* cuticle of pedestal, *Fb* Fat body cells, *Gcl* gland cell, *Hlsp* haemolymph space, *Hs* hair shaft, *oRL* outer receptorlymph space

Occurrence of pedestal hairs and stalked eyes in workers of *E. melanarctos* and three other *Echinopla* species

A comparison of the external morphology and topography of pedestal hairs, 'normal' hairs and compound eyes in *E. melanarctos* and three other *Echinopla* species (*E. lineata* Mayr 1862, *E. pallipes* Smith 1857 and *E. striata* Smith 1857) (Fig. 7) shows that all four species possess a layer of long and densely packed hairs (cf Figs. 1, 2a–d). In all investigated species, the hairs on antennae and legs seat directly in the cuticle surface. The only two of four investigated ant species with high pedestals on the head, namely, *E. melanarctos* and *E. pallipes*, also possess stalked compound eyes. Between hairs with high pedestal and 'normal' hairs, all transient stages could be found (see Fig. 7).

Discussion

The palaeotropical formicine genus *Echinopla* (Smith 1857) is distributed from the Nicobar Islands northwest of Sumatra through Sundaland and the Philippines to Northern Australia. It comprises about 30 described species, two of which certainly belong to the genus *Polyrhachis* (Reichardt 1997). A revision of the genus is still lacking.

Almost nothing is known about the biology of the genus *Echinopla*. As far as known, all the species are arboricolous (Forel 1910, Rosciszewski 1995). While investigating the biology of one unidentified species (*Echinopla* sp. R. found on the Malay Peninsula; see Reichardt 1997) we obtained few data from *E. melanarctos*. As far as necessary for a functional interpretation of the pedestal hairs, a short summary will be given on socioecology. **Both species were monogynous, nesting polydomously in hollow branches** mostly hanging loosely in the vegetation of dense forests, or rarely laying

on the ground. The censused colonies ($n=3$, *Echinopla* sp. R.; $n=2$, *E. melanarctos*) contained less than 400 and 100 workers, respectively. The colonies of the Australian *E. turneri*, Forel 1901 were monodomous and contained less than 100 workers (Taylor 1992). The nest cavities of *Echinopla* sp. R. and *E. melanarctos* were enlarged by gnawing in both species; however, no carton was produced for modification of the nest chambers or the entrance. Carbohydrate-containing fluids were collected by scouts from the surface of leaves using the outline-tracing strategy known from ants searching on plant surfaces (Jander 1990). **Both species did not visit any trophobionts. *Echinopla* sp. R. is a scavenger collecting small dead insects during foraging.** For exploiting experimental feeding sites, group recruitment was used in both species. The workers did not defend the feeding sites but hid upon disturbance or let themselves fall to the ground. Thus, both species can be classified as submissive according to a dominance hierarchy (Savolainen and Vepsäläinen 1988).

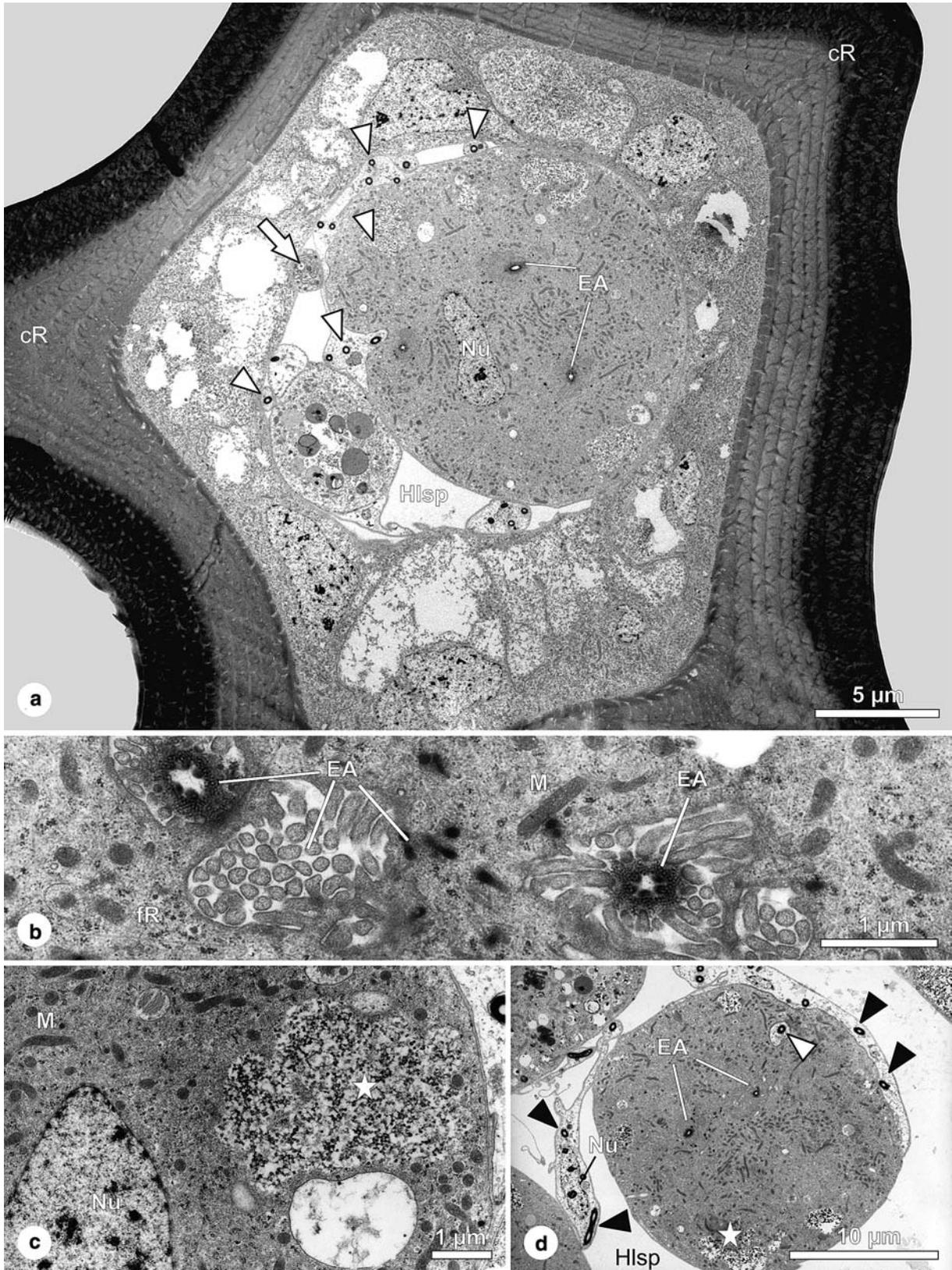
As our fine structural results show, the pedestal hairs of *E. melanarctos* are mechanosensitive. According to their exposed position on the exoskeleton, they encode primarily mechanical stimuli from the vicinity of the body. With respect to their external cuticular structures, the pedestal hairs of *E. melanarctos* belong to the type of tactile hairs (Gnatzy and Hustert 1989). Here, the hairs are moved by direct contact (with other animals, conspecifics or the substrate) through which the tip of the dendrite is mechanically deformed. In the case of the pedestal hairs, the hair shaft is inserted in the pedestal summit by means of a relatively thick joint membrane. The mechanical construction of the hair pedestal and the geometry of the hair base and their articulation signals that hair shaft deflection is allowed only in certain directions (see Gnatzy and Tautz 1980; Hustert et al. 1999).

In *E. melanarctos*, **more than 700 pedestal hairs occur in redundant patterns.** Thus, the parameters they encode should be very similar. This redundancy of similar sense organs increases the probability that stimuli are perceived. The density of the pedestal hairs on the exoskeleton of *E. melanarctos* may serve to recognise the location of the mechanical stimuli from above and lateral. Final conclusions as to the parameters encoded by the pedestal hairs can only be based on electrophysiological recording of their afferent signals to the CNS while natural stimuli are applied. Experiments of this kind are still missing.

For a functional interpretation of the pedestal hairs, in addition to their sensory properties further aspects have to be taken into account.

Chemical defensive function

Though small glands are ending on the pedestal apex near to the base of the hairs of *E. melanarctos*, any irritating and urticating function of the hairs on



mammals can be excluded. Correspondingly, no itching or urticating effects could be observed when bringing the irritated workers on mucous membranes (skin) in the

human mouth. Because of the lack of any closure and storage structures, the glands permanently release their lipophilic secretions on the hair base, which are dis-

◀
Fig. 6 *Echinopla melanarctos*. **a–d** Fine structure of glandular units of pedestal hairs in a worker. TEM pictures. **a** Cross section of pedestal base at a level indicated in Fig. 5a by an asterisk showing the nucleus with a nucleolus of a single secretory gland cell (*Nu*) and buttress-like cuticular ridges (*cR*) of the pedestal. *Arrowheads* mark ductules of several gland cells within the haemolymph space (*Hlsp*). **b** Secretory gland cell cytoplasm showing portions of the end apparatus (*EA*), mitochondria (*M*). **c** Nucleus (*Nu*) and cytoplasm of a secretory gland cell; *asterisk* marks presumed glycogen particles. **d** Secretory gland and duct cell of a pedestal hair. Nucleus of a duct cell (*Nu*); several cross-sectioned ductules within a duct cell (*black arrowheads*) and parts of the end apparatus (*EA*) within the gland cell, *asterisk* marks presumed glycogen particles. *Hlsp* haemolymph space

tributed over the hairs and other surface structures by themselves and by the cleaning behaviour of the ants. As *Echinopla* species possess a typical metapleural gland, which in ants produces generally antiseptic substances (Maschwitz 1974), an additional antibiotic function of the pedestal hair glands appears to be unlikely.

Mechanical protective function

When moving, resting or slightly enrolling upon the disturbance, the whole body of workers and queens including their legs and pedicells of their antennae is

fully hidden beneath a dense layer of long and stiff hairs. Mostly situated on long cylindrical pedestals in *E. melanarctos*, their position is further distally extended. Lateral hairs around some of the pedestals condense this hair cover. For overtopping this hair layer, the compound eyes correspondingly are elevated by stalks.

As our comparative studies revealed, the workers of all four species possess a layer of long and dense hairs. In three of these species (*E. melanarctos*, *E. pallipes* and *E. striata*), most of the hairs were located on high pedestals; in the other one species (*E. lineata*) they arose directly from the cuticle surface or on slightly elevated cuticular cups. Between such slight elevations and high pedestal structures all transient stages could be found. Thus, the pedestals can be interpreted as structures elevating the cuticular hairs. We suppose that the whole hair cover may serve as a shield against attacks of other arthropods, especially ants, which are highly common in the habitat of *E. melanarctos*. The sensory apparatus of the hairs gives exact information about contacts with the surroundings. The lipophilic secretions of the pedestal glands possibly function as lubricants that keep the non-living hair shafts intact, i.e. elastic and waterproof-like sebaceous glands or rump glands in mammals and birds, respectively. In the ever-moist tropical rain forests, arbicolours ants are highly diverse and abundant. Nevertheless only in the genus *Echinopla*, such a sophisticated

Location							
species	head	antenna	eyes	alitrunk	legs	petiole	gaster
<i>E. melanarctos</i>							
<i>E. lineata</i> (Coll. Dorow: 568)							
<i>E. pallipes</i> (Coll. Dorow: 572)							
<i>E. striata</i> (Coll. Dorow: 569)							

--	--	--	--	--

Fig. 7 Location of various hair types and occurrence of stalked eyes in workers of four *Echinopla* species

hair cover of the exoskeleton has developed. This indicates that in general, openly foraging tree ants cannot be protected against predators by such hairs. Therefore, we suppose that the hair cover of *E. melanarctos* is of special importance for protection of the colony members within the nest. All available information on nesting habits of all *Echinopla* species indicate that these ants use almost exclusively hollows varying in diameter and length and broken off branches hanging free in the lower vegetation. Also, rather rotten and labile branches are used. Thus, a wide variety of nesting possibilities are available. Nesting space is supposed to be a limiting factor in arboreal ants in ever-moist tropical forests (Hölldobler and Wilson 1990). **The workers do not build carton walls in their nests or close the unused branch openings with a carton.** Possibly, workers and queens of *E. melanarctos*, which according to their ecology are weak fighters, can use their hair cover to ward off direct attacks from other ants as well as to **protect nest chambers and brood with their hairy bodies against intruders, e.g. ant-predators like *Aenictus* army ants.** With more detailed future studies on nesting habits and defensive behaviour of *E. melanarctos*, especially in their nests this hypothesis could be tested.

Acknowledgements We wish to thank M. Jatho and C. Trömel for their numerous constructive suggestions to style the figures. We are grateful to W.H.O. Dorow (Forschungsinstitut Senckenberg, Frankfurt) for providing us with the *Echinopla* species from his collection. We thank O. Dittberner, B. Krebs, M. Stöhr and M. Ruppel for their excellent technical assistance.

References

- Brück E, Stockem W (1972) Morphologische Untersuchungen an der Cuticula von Insekten. I. Die Feinstruktur der larvalen Cuticula von *Blaberus trapezoides* Burm. *Z Zellforsch* 132:403–416
- Forel A (1910) Fourmis de Philippines. *Philipp J Sci Abt D* 5:121–130
- Gnatzy W, Hustert R (1989) Mechanoreceptors in behavior. In: Huber F, Moore Th, Loher W (eds) *Cricket behavior and neurobiology*. Cornell University Press, Ithaca, NY, pp 198–226
- Gnatzy W, Schmidt K (1972a) Die Feinstruktur der Sinneshaare auf den Cerci von *Gryllus bimaculatus* Deg. (Saltatoria, Gryllidae). IV. Die Häutung der kurzen Borstenhaare. *Z Zellforsch* 126:223–239
- Gnatzy W, Schmidt K (1972b) Die Feinstruktur der Sinneshaare auf den Cerci von *Gryllus bimaculatus* Deg. (Saltatoria, Gryllidae). IV. Die Häutung der langen Borstenhaare an der Cercusbasis. *J Microsc* 14:75–84
- Gnatzy W, Tautz J (1980) Ultrastructure and mechanical properties of an insect mechanoreceptor: stimulus transmitting structures and sensory apparatus of the cercal filiform hairs of *Gryllus*. *Cell Tissue Res* 213:441–463
- Gnatzy W, Volkmandt W (2001) Venom gland of the digger wasp *Liris niger*: morphology, ultrastructure, age-related changes and biochemical aspects. *Cell Tissue Res* 302:271–284
- Hölldobler B, Wilson EO (1986) Soil-binding pilosity and camouflage in ants of the tribes Basicertini and Stegomyrmicini (Hymenoptera, Formicidae). *Zoomorpholgy* 106:12–20
- Hölldobler B, Wilson EO (1990) *The Ants*. Harvard University Press, Massachusetts, pp 732
- Hustert R, Lodde E, Gnatzy W (1999) Mechanosensory pegs constitute stridulatory files in grasshoppers. *J Comp Neurol* 410:444–456
- Jander R (1990) Arboreal search in ants: search on branches. *J Insect Behav* 3:515–527
- Maidl F (1933) *Die Lebensgewohnheiten und Instinkte der Staatenbildenden Insekten*. Wagner, Wien
- Maschwitz U (1974) Vergleichende Untersuchungen zur Funktion der Ameisenmetapleuraldrüse. *Oecologica* 16:303–310
- Noirot C, Quennedey A (1974) Fine structure of insect epidermal glands. *Annu Rev Entomol* 19:61–80
- Noirot C, Quennedey A (1991) Glands, gland cells, glandular units: some comments on terminology and classification. *Annu Soc Entomol Fr* 27:123–128
- Reichardt A (1997) *Arborale Lebensstrategien von Ameisen am Beispiel der orientalischen Gattung *Echinopla* (Formicidae: Formicinae)*. Diploma Thesis, J.W. Goethe-University, Frankfurt
- Rosciszewski (1995) *Die Ameisenfauna eines tropischen Tieflandregenwaldes in Südostasien: Eine faunistisch-ökologische Bestandsaufnahme*. Dissertation, University of Frankfurt/M., pp 1–183
- Savolainen R, Vepsäläinen K (1988) A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* 51:135–155
- Smith Fr (1857) *Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A.R. Wallace*. *J Proc Linn Soc Lond Zool* 2:42–88
- Taylor RW (1992) Nomenclature and distribution of some Australian and Non Guinean ants of the subfamily formicinae (Hymenoptera: Formicidae). *J Aust Entomol Soc* 31:57–69
- Wheeler WM (1910) *Ants, their structure, development and behavior*. University Press, Columbia, NY