

## ORIGINAL ARTICLE

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**Comparative study of the metatibial gland in ants (Hymenoptera, Formicidae)**

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**Abstract** A novel glandular structure is described within the metatibia in ants of the poneroid group. This metatibial gland has been considered a major synapomorphic character of the subfamilies belonging to the doryline section. Histological investigations combined with scanning electron micrograph studies revealed a remarkably complex gland, consisting of a glandular epithelium and a cuticular pore plate, the morphology of which varies considerably between the species. This gland is also present in species of the genera *Diacamma* and *Pachycondyla* (Ponerini). Based on the morphology of glandular epithelia and pore plates, it is not possible to decide whether this structure is homologous or analogous to that of the doryline section subfamilies. In workers of certain species of the genus *Diacamma*, the secretions of this gland are involved in sexual calling behavior.

**A. Introduction**

In recent years, the study of chemical communication in ants has received new impetus by the discovery of many hitherto unknown exocrine glands (Hölldobler and Wilson 1990; Billen 1993). In particular, detailed histological investigations of the legs have revealed a variety of new glandular structures, such as the basitarsal glands associated with the cleaning apparatus in the forelegs of all ant species studied (Schönitzer and Lawitzky 1987; Schönitzer and Dott 1989; Hölldobler et al. 1992), the specialized basitarsal glands in the hindlegs of species of the genera *Onychomyrmex* and *Prionopelta* (see Hölldobler and Palmer 1989a; Hölldobler et al 1992) which serve in

trail communication and orientation behavior, the arolium gland present in the pretarsus of front, middle, and hindlegs in all ant species studied (Hölldobler and Palmer 1989b; Billen 1993), and the specialized footprint glands in the pretarsus of the hindlegs of *Amblyopone australis* Erichson, 1842 (Hölldobler and Palmer 1989b). In addition, Schoeters and Billen (1993) described glandular structures found inside the coxae of *Pachycondyla obscuricornis* Emery, 1890. In species of the genus *Crematogaster* (Myrmicinae), the workers lay trails with secretions from a special tibial gland (Fletcher and Brand 1968; Leuthold 1968), the morphology of which has been studied by Pasteels et al. (1979) and Billen (1984).

In a number of ant genera belonging to the Cera-pachyinae, Dorylinae, Aenictinae, and Ecitoninae, Bolton (1990) describes “an apparently glandular area on the worker hind tibia, located ventrally on the leg segment immediately behind the metatibial median spur”. Bolton considers these four subfamilies to be a monophyletic lineage and refers to them as the doryline section (sensu Bolton 1990) of the poneroid group of ants. According to Bolton, the metatibial structure represents an important synapomorphy for the doryline section. A similar structure was found on the metatibia of some Ponerini (Ponerinae), but Bolton thinks these are not homologous to those found in the doryline section.

In the present paper, we report the results of a histological investigation of this structure in at least one representative species from each of the four subfamilies belonging to the doryline section. We confirm that this is, indeed, an exocrine gland which can vary considerably in size and morphology between species of the doryline section. We also investigated this gland in several species of the genera *Diacamma* and *Pachycondyla* (Ponerinae).

**B. Material and methods**

The histological investigations of the legs followed the techniques described in Hölldobler et al. (1992). The scanning electron micrographs (SEM) were prepared with a DSM 962 Zeiss scanning electron microscope. The following species from doryline section sub-

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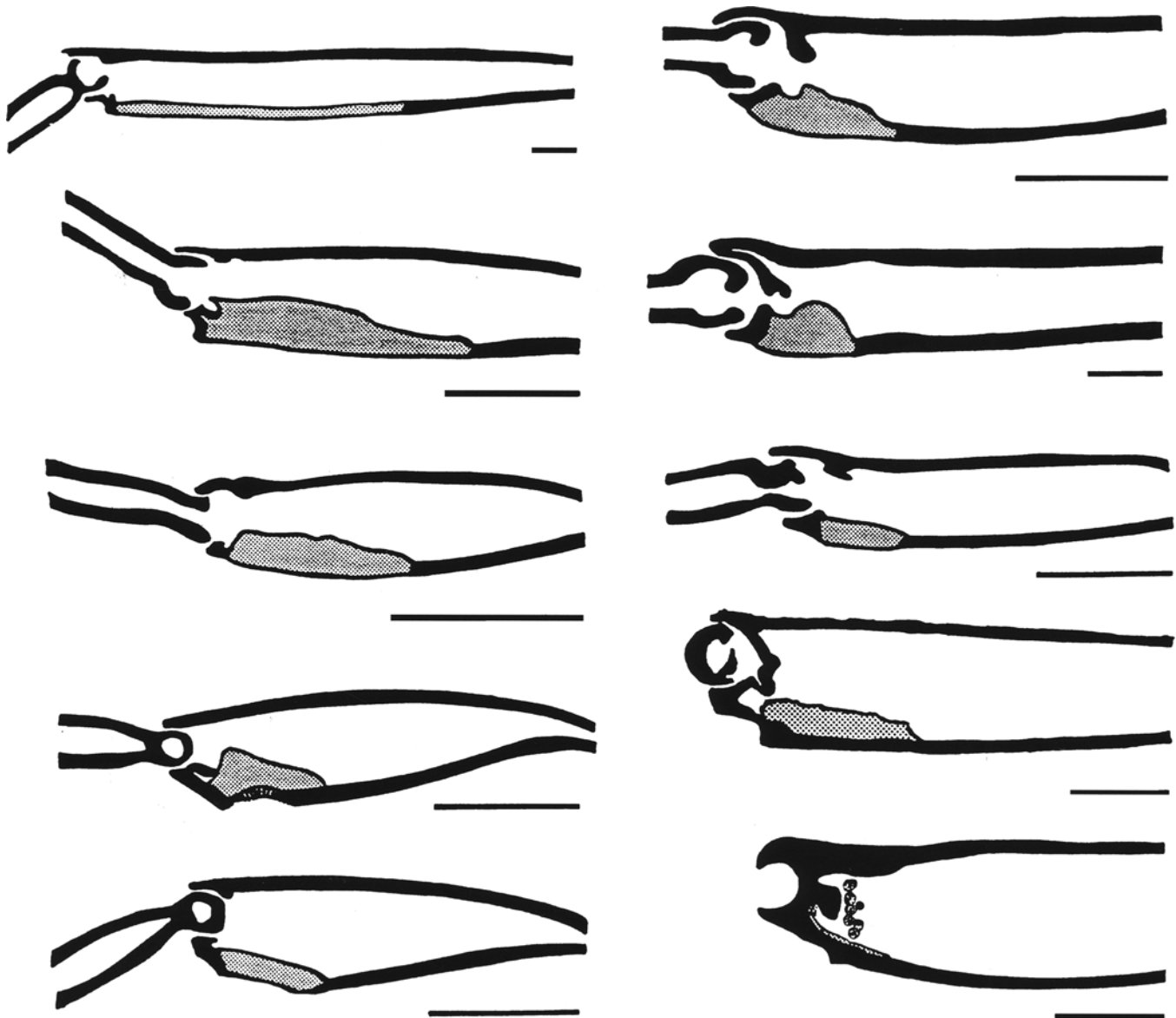
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families<sup>1</sup> were investigated: Cerapachyinae: *Cerapachys turneri* Forel, 1902, *C. biroi* Forel, 1907, *Sphinctomyrmex steinheili* Forel, 1900; Dorylinae: *Dorylus nigricans* Illiger, 1802; Ecitoninae: *Eciton hamatum* (Fabricius, 1782, *Neivamyrmex nigrescens* Cresson, 1872; Aenictinae: *Aenictus ceylonicus* (Mayr, 1866). In addition, we studied the Ponerini (Ponerinae) *Pachycondyla villosa* (Fabricius, 1804), *P. rufipes* (Jerdon, 1861), *P. tessierinoda* (Emery, 1877), *P. crenata* (Roger, 1861), *P. tridentata* (F. Smith, 1858), *Pachycondyla* [= *Paltothyreus*] *tarsata* (Fabricius, 1798), *Diacamma* sp. (from India)<sup>2</sup>, *Diacamma* sp. (from Malaysia), and *Diacamma* sp. (from Japan). Voucher specimens of the *Diacamma* species have been deposited in the Museum of Natural History (London) and the Museum of Comparative Zoology of Harvard University (Cambridge, Massachusetts).

<sup>1</sup> Nomenclature and group designations according to Bolton (1990)

<sup>2</sup> Peeters et al (1992) refer to this species as *Diacamma vagans*

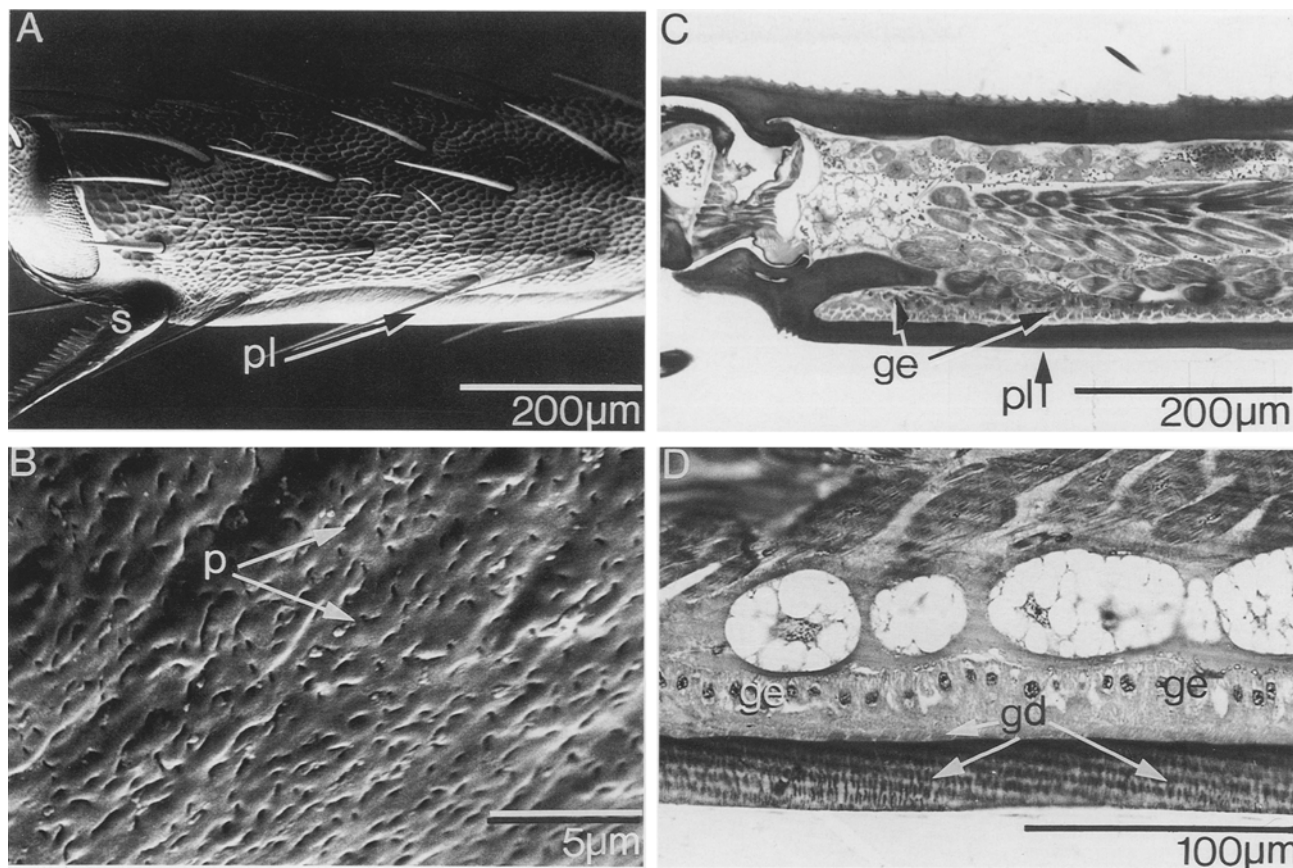
**Fig. 1** Schematic illustration of the anatomical proportions of the metatibial glands (shaded area) in ants. Left side from top: *Eciton hamatum*, *Neivamyrmex nigrescens*, *Aenictus ceylonicus*, *Cerapachys turneri*, *Sphinctomyrmex steinheili*. Right side from top: *Diacamma vagans*, *Diacamma* sp. (from Malaysia), *Diacamma* sp. (from Japan), *Pachycondyla rufipes*, *Pachycondyla* (= *Paltothyreus*) *tarsata*. Bars on the left side represent 200  $\mu$ m, on the right side 400  $\mu$ m



## C. Results

### I. Metatibial gland of doryline section subfamilies

We fully confirm Bolton's (1990) macroscopic description of the external morphology of the metatibial gland in species belonging to doryline section subfamilies. Bolton writes that "in its presumed most generalized form the gland appears as an elongate strip, running from close behind the spur towards the base of the tibia ... the length and width of the gland varies considerably through the doryline section ...". The variation of the dimensions of the gland in the different species, as revealed by our histological investigations, is presented in Fig. 1. The gland consists of a layer of epithelial secretory cells, but height, width, and longitudinal dimensions of the glandular tissue vary considerably among the species studied. For example in *Eciton hamatum*, the glandular epithelium is relatively thin, but extends more than three-quarters of the length of the tibia. A similar situa-



**Fig. 2A–D** Metatibial gland of *Eciton hamatum* worker. **A** Scanning electron micrograph (SEM) showing the slightly convex pore plate (*pl*); spur (*s*). **B** SEM showing pores (*p*) on the pore plate. **C** Sagittal section through metatibia, making the glandular epithelium (*ge*) of the metatibial gland visible. **D** Close-up of the glandular epithelium (*ge*) and cuticle with glandular ducts (*gd*)

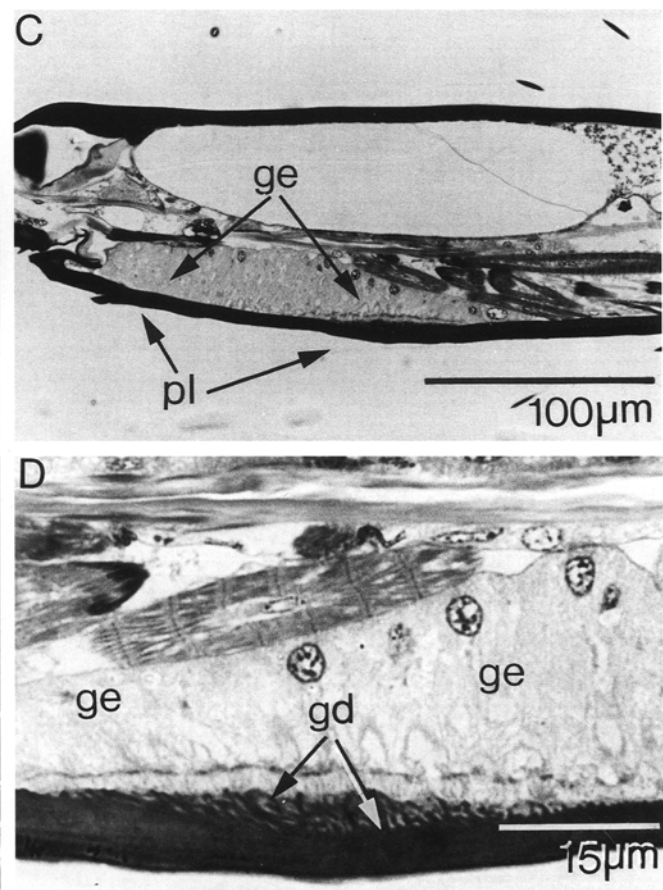
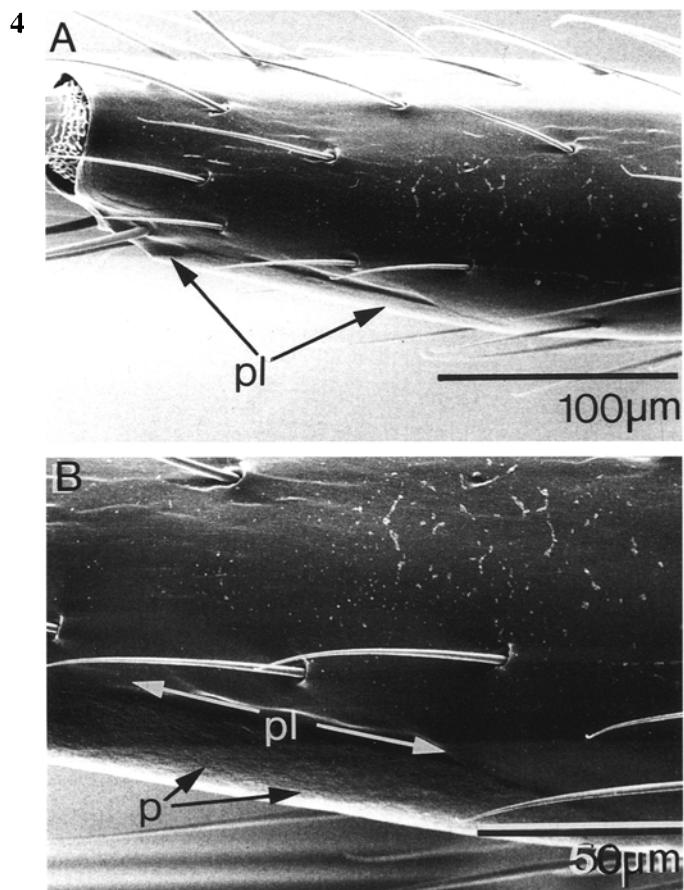
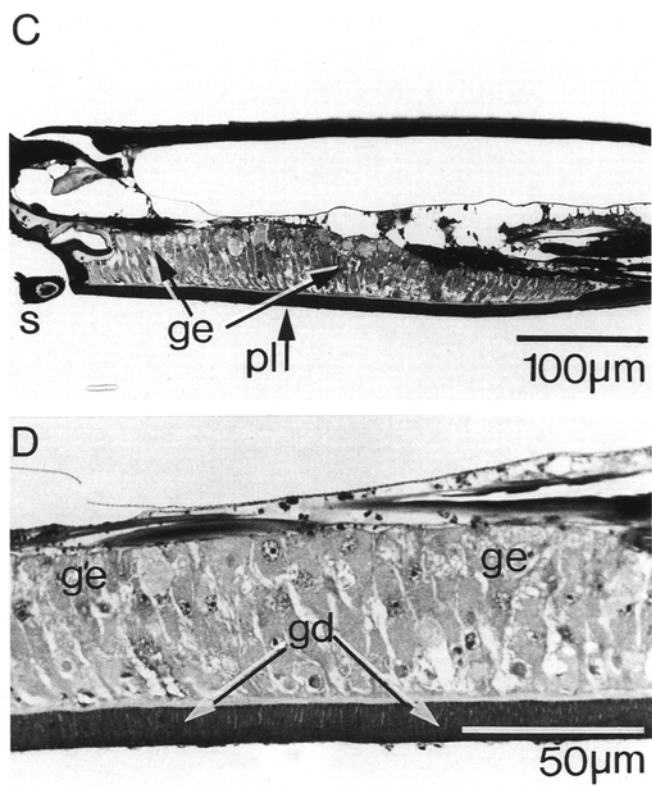
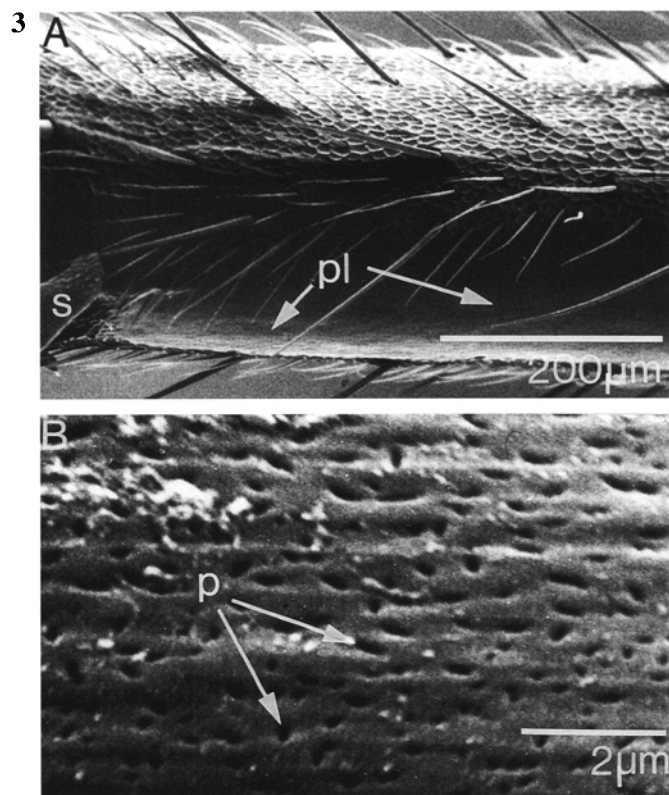
tion was found in *Dorylus nigricans* (not illustrated). In *Neivamyrmex nigrescens* and in *Aenictus ceylonicus*, the relative length of the metatibial gland is approximately one-half of the length of the tibia, but the epithelium consists of relatively large cylindrical cells. In *Cerapachys turneri* and *Sphinctomyrmex steinheili*, the glandular structure is more compact, extending about one-quarter of the length of the tibia. In its presumed most generalized form, Bolton described the external appearance of the glandular area on the tibia as “filled with or roofed by whitish to yellowish modified cuticle which appears relatively dull, frequent granular to spongiform tissue.” Under SEM inspection, this glandular area in *Eciton hamatum* is revealed as a long, hairless strip, perforated by many slit-shaped pores (the pore plate). Histological sections show that these pores are the openings of cuticular ducts which directly connect to the cells of the glandular epithelium (Fig. 2). In *Neivamyrmex nigrescens*, we found the same basic pattern, however, the glandular epithelium is more pronounced (Fig. 3). Similarly in *Aenictus ceylonicus*, the metatibial gland consists of a large pore plate associated with a thick glandular epithelium. In a particular area of the pore plate (~35  $\mu$ m

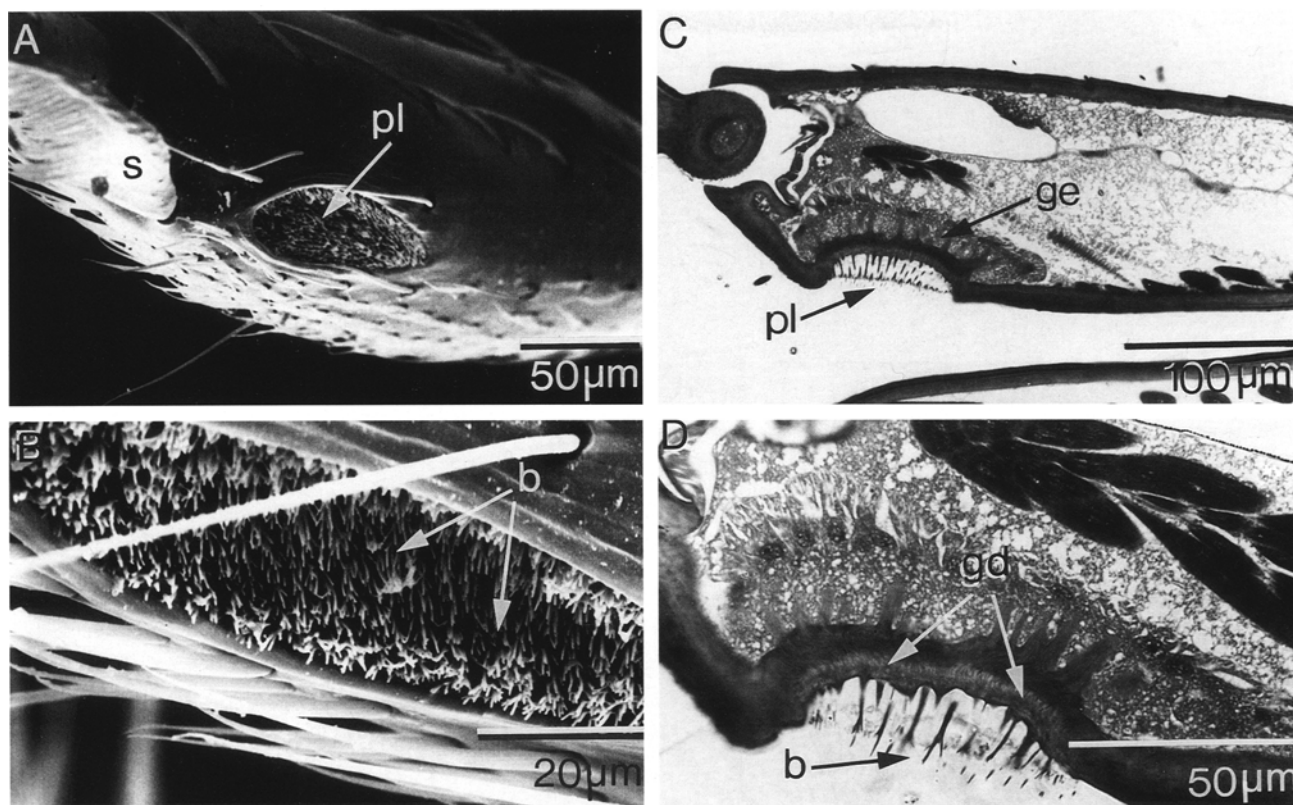
long) the glandular ducts converge in especially densely spaced pores, however, smaller ducts penetrate the cuticle over the entire pore plate (Fig. 4).

The appearance of the metatibial gland in the investigated *Cerapachys* species is quite different. The pore plate in *C. turneri* has an oval shape, measuring about 55 $\times$ 30  $\mu$ m, and is densely covered with forked bristles. Cuticular ducts connecting with the glandular cells of the epithelium open at the base of these bristles. The external structure of the metatibial gland in *C. turneri* has the appearance of a brush (Fig. 5). In *C. biroi*, the pore plate is not, as in *C. turneri*, covered with bristles, but instead consists of a spongiform structure perforated by many pores. The oval measures approximately 15 $\times$ 10  $\mu$ m (Fig. 6). In *Sphinctomyrmex steinheili*, the oval pore plate (50 $\times$ 20  $\mu$ m) is devoid of bristles, has a slightly spongiform surface, and is covered with many pores. The pronounced cylindrical epithelial cells are connected with the pores by densely packed cuticular ducts (Fig. 7).

## II. Metatibial glands in the Ponerini

Our SEM and histological investigations show that the differences in the metatibial gland structures between the Ponerini and doryline section are no more pronounced than the differences among species within the doryline section. We investigated three *Diacamma* species, which all possess well-developed metatibial glands. In *D. va-*





**Fig. 5A–D** Metatibial gland of *Cerapachys turneri* worker. **A** SEM of the oval-shaped pore plate (*pl*); spur (*s*). **B** Close-up of the pore plate showing the dense layer of forked bristles (*b*). **C** Sagittal section through the metatibia showing the glandular epithelium (*ge*) and the glandular opening (*go*) which is a depression in the cuticle. **D** Close-up of the section through the metatibial gland, showing the glandular ducts (*gd*) through the cuticle and the forked bristles (*b*)

*gans*, the glandular epithelium extends about one quarter of the tibial length (Fig. 1). The width of the glandular tissue is approximately 130  $\mu\text{m}$ . The external pore plate is partly associated with spatula-shaped bristles (Fig. 8). This area is only slightly lateral and close to the articulation of the main spur. A similar situation was found in *Diacamma* sp. from Malaysia where the gland extends only one-seventh of the length of the tibia (Fig. 1), the epithelium has a width of approximately 95  $\mu\text{m}$ , and the pore plate is also partly covered by spatula-shaped bristles (Fig. 9). In *Diacamma* sp. from Japan, the glandular

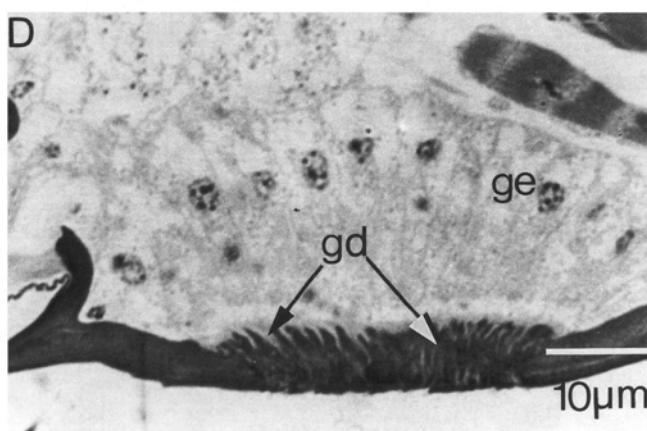
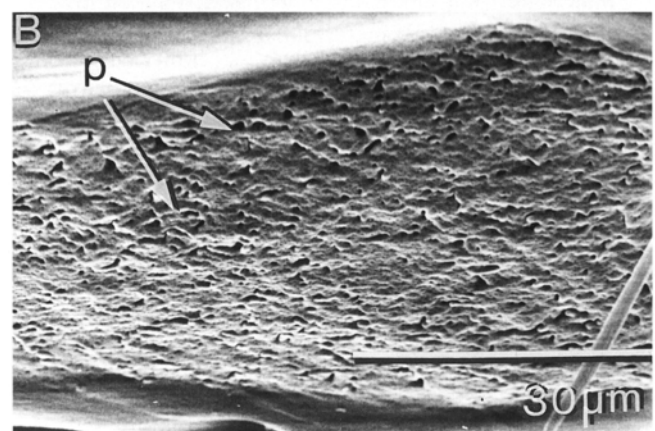
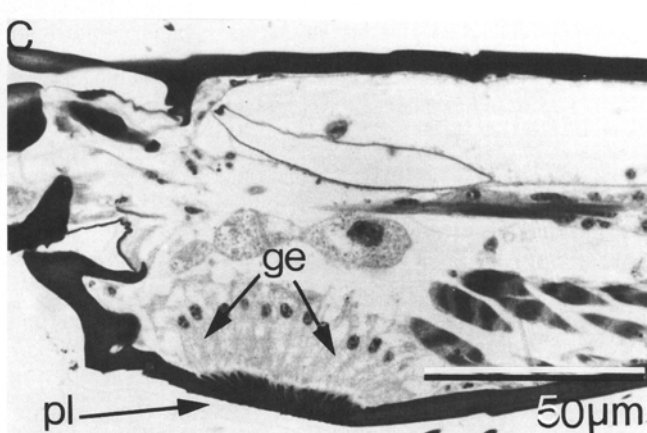
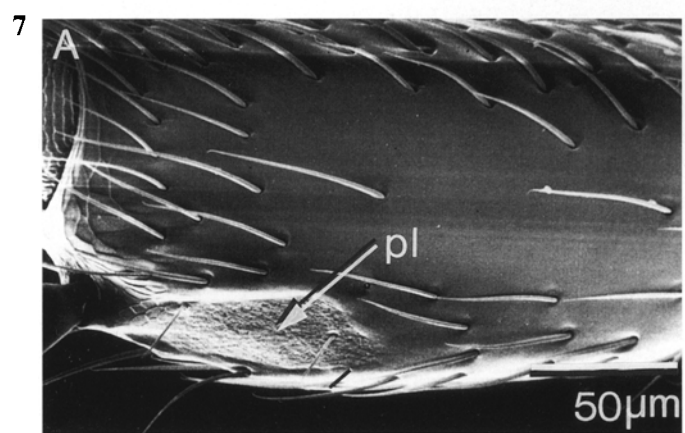
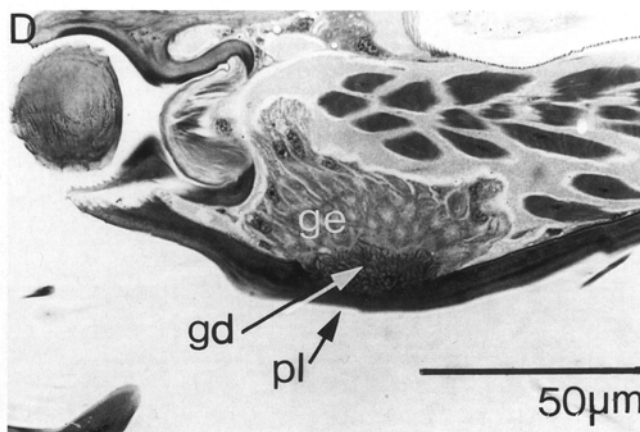
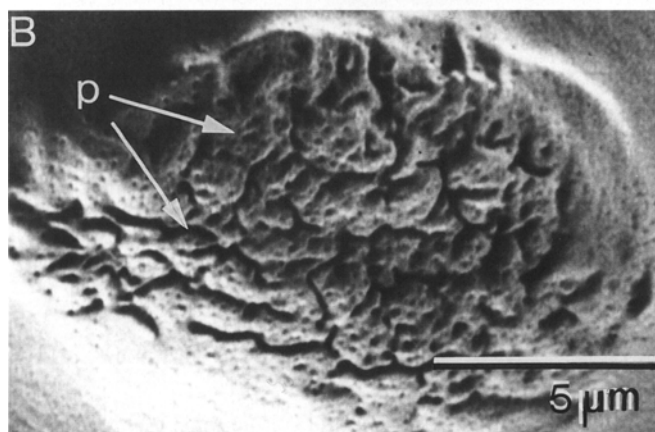
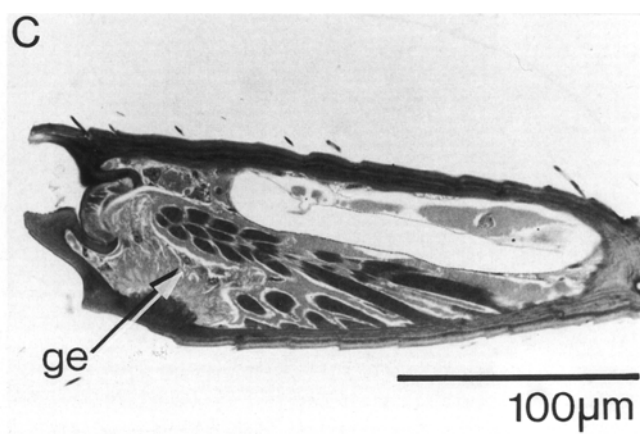
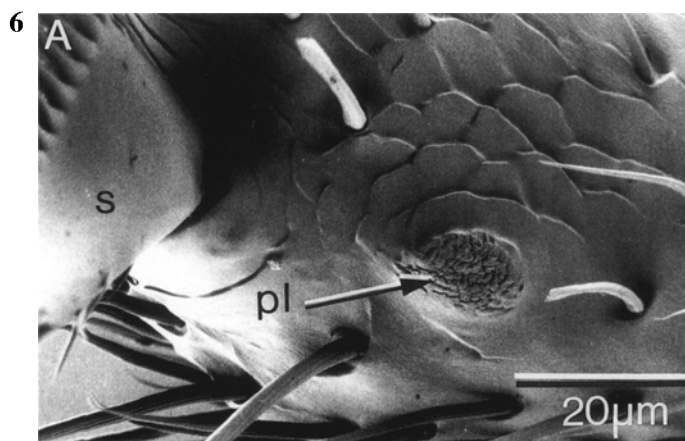
structure extends approximately one-fifth of the length of the tibia (Fig. 1), and width of the epithelium measures about 75  $\mu\text{m}$ . Externally the pore plate can be entirely covered by thick bristles, some of them spatula-shaped, whereas in other specimens a small bald patch of the pore plate can be seen (Fig. 10).

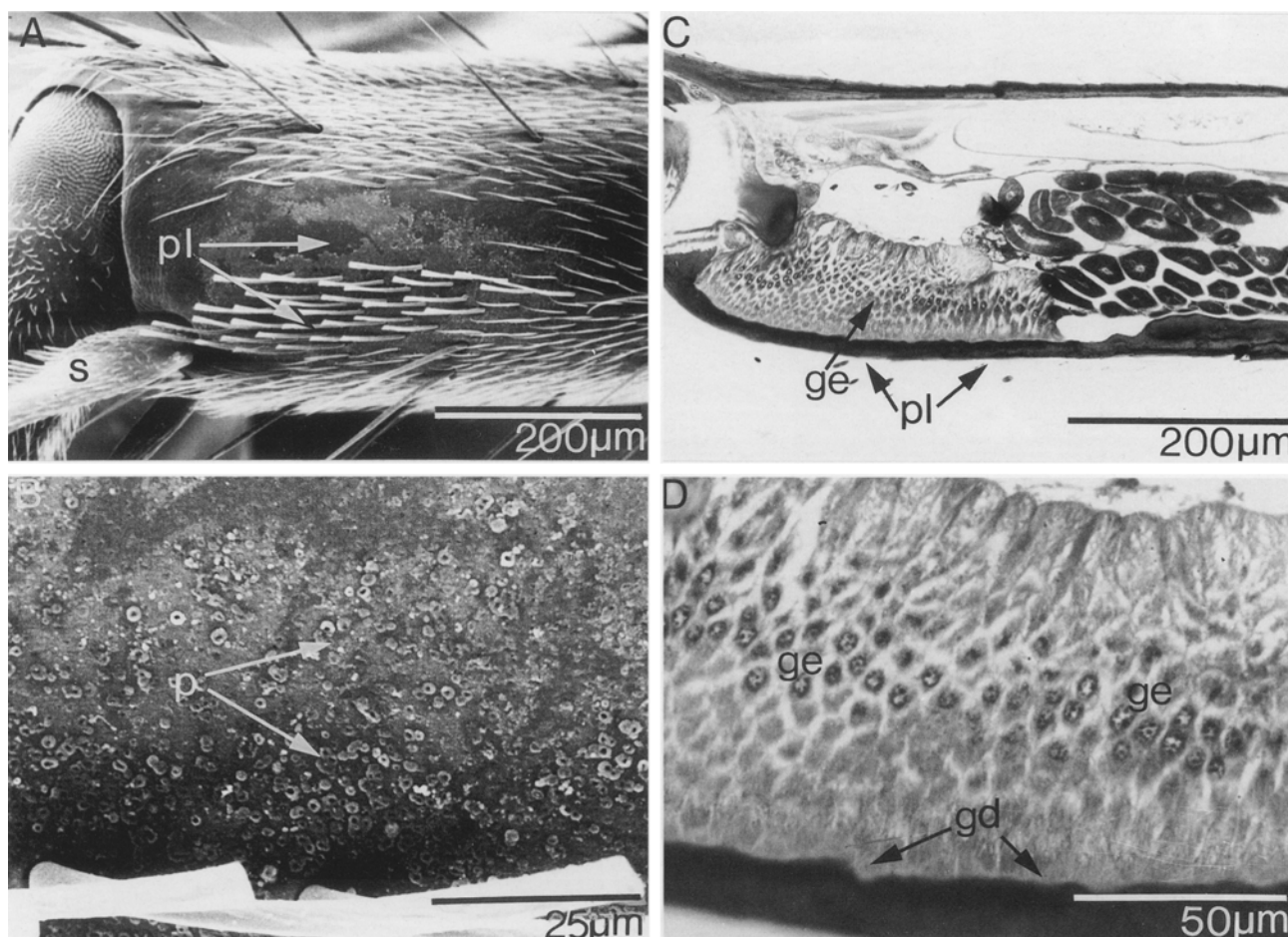
In the genus *Pachycondyla*, the appearance of the metatibial glands varies. In *P. rufipes*, the glandular epithelium is approximately one-quarter of the tibial length (Fig. 1). The bald pore plate area is located more lateral to the inner face of the tibia, but the patch of spatula-shaped bristles extends to the ventral side and close to the articulation of the main spur (Fig. 11). The surface of the pore plate has a honeycombed structure and each hexagonal structure continues inside the tibia. The glandular ducts of the epithelial cells are bundled in hexagonal units and connect, as such, with the outside surface of the pore plate. We also found metatibial glands in *P. crenata*, *P. tessierinoda*, *P. tridentata*, and *P. villosa*, though the structures of the pore plates and associated bristles varied among the species. For example, in *P. villosa* and *P. marginata* the glandular epithelium is very flat and measures less than one-fifteenth of the tibial length. A very small epithelial metatibial gland can be seen in *Pachycondyla* [= *Paltothyreus*] *tarsata*. It consists of a short, flat layer of epithelial cells (approximately one-ninth of the tibial length). The small pore plate is covered with bristles and the pores are slit-shaped (Fig. 12). In addition to the epithelial gland, *P. tarsata* possess another type of metatibial gland which has paired clusters of

**Fig. 3A–D** Metatibial gland of *Neivamyrmex nigrescens* worker. **A** SEM showing pore plate (*pl*); spur (*s*). **B** SEM close-up showing pores (*p*) in pore plate. **C** Sagittal section through metatibia showing the glandular epithelium of the metatibial gland. **D** Close-up of glandular epithelium and cuticle with glandular ducts (*gd*)

**Fig. 4A–D** Metatibial gland of *Aenictus turneri* worker. **A** SEM showing area of pore plate (*pl*). **B** SEM close-up of pore plate. **C** Sagittal section through metatibia, showing glandular epithelium (*ge*). **D** Close-up of section showing glandular epithelium (*ge*) and the densely packed glandular ducts (*gd*)







**Fig. 8A–D** Metatibial gland of *Diacamma vagans* worker (from India). **A** SEM of pore plate (*pl*) which is partly covered by spatula-shaped bristles; spur (*s*). **B** Close-up of pore plate showing pores (*p*) which are partly covered by coagulated secretion. **C** Sagittal section through metatibia, showing glandular epithelium (*ge*). **D** Close-up of glandular epithelium with glandular ducts (*gd*)

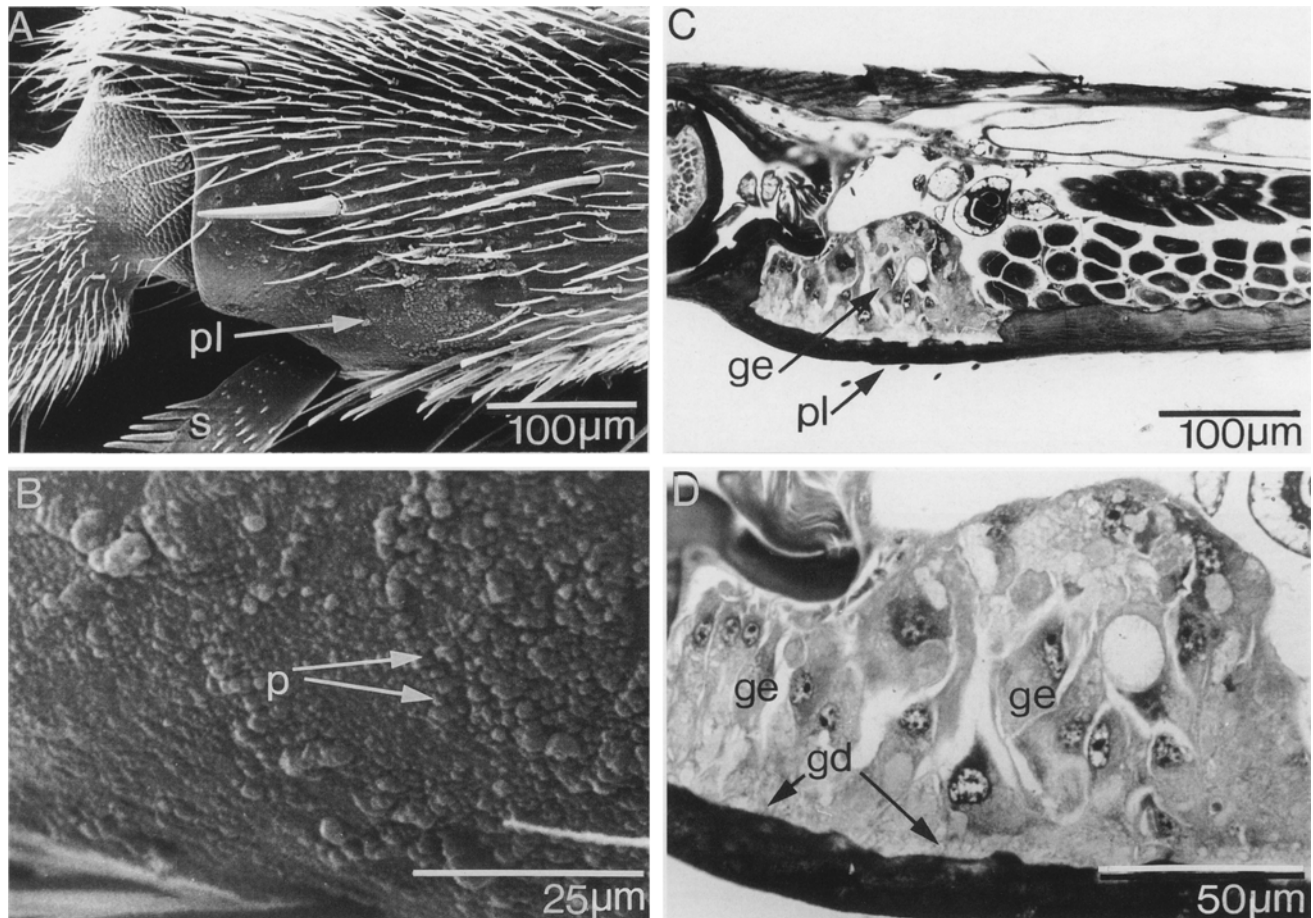
glandular cells (approximately 15 cells in each cluster) located laterally in the tibia near the main spur. Each cell measures approximately 25 µm in diameter and is endowed with a glandular duct that opens through the intersegmental membrane laterally between the tibia and basitarsus. Similar cell clusters, however, each consisting only of 4–8 cells, exist in the middle and front legs.

**Fig. 6A–D** Metatibial gland of *Cerapachys biroi* worker. **A** SEM of the oval pore plate (*pl*). **B** Close-up of the spongiform pore plate with pores (*p*); spur (*s*). **C** Sagittal section through metatibia showing area of glandular epithelium (*ge*). **D** Close-up of section through metatibial gland showing glandular ducts (*gd*)

**Fig. 7A–D** Metatibial gland of *Sphinctomyrmex steinheili* worker. **A** SEM of pore plate (*pl*). **B** Close-up of pore plate showing pores (*p*). **C** Sagittal section through metatibia showing glandular epithelium (*ge*). **D** Close-up of section showing glandular ducts (*gd*)

### III. Application of metatibial gland secretions

Almost nothing is known about the function of the metatibial gland, however, two observations in species of the genera *Diacamma* and *Cerapachys* indicate how its secretion are employed by the ants. In the queenless *Diacamma vagans*, the metatibial gland appears to be involved in the regulation of mating. The dominant worker in a colony frequently patrols through the nest and directs antennal boxing or mandibular threats toward nest-mates. The dissection of ovaries confirmed that only the dominant individual laid eggs (Peeters et al. 1992). The dominant ant is distinguished by another behavior: she frequently rubs both hindlegs against her posterior gaster tergites (Fig. 13). High-speed video recordings of this behavior suggest that the ant applies secretions from the metatibial gland to the surface of the gaster. This secretion might serve as a sexual attractant, since the dominant worker needs to copulate with a foreign male (Peeters et al. 1992). This has now been confirmed in *Diacamma* sp. from Japan (K. Tsuji personal communication). *Cerapachys biroi* is queenless and workers reproduce by parthenogenesis (Tsuji and Yamauchi 1995). Various *C. biroi* workers frequently rub the opening of the metatibial gland against the ventro-lateral area of their gasters. Nothing is yet known about the function of the secretion.



**Fig. 9A–D** Metatibial gland of *Diacamma* sp. worker (from Malaysia). **A** SEM showing pore plate (pl) near the spur (s). **B** Close-up of pore plate showing pores (p) covered with granular material, presumably coagulated secretion. **C** Sagittal section of metatibia showing glandular epithelium (ge). **D** Close-up of glandular epithelial cells and ducts (gd)

## D. Discussion

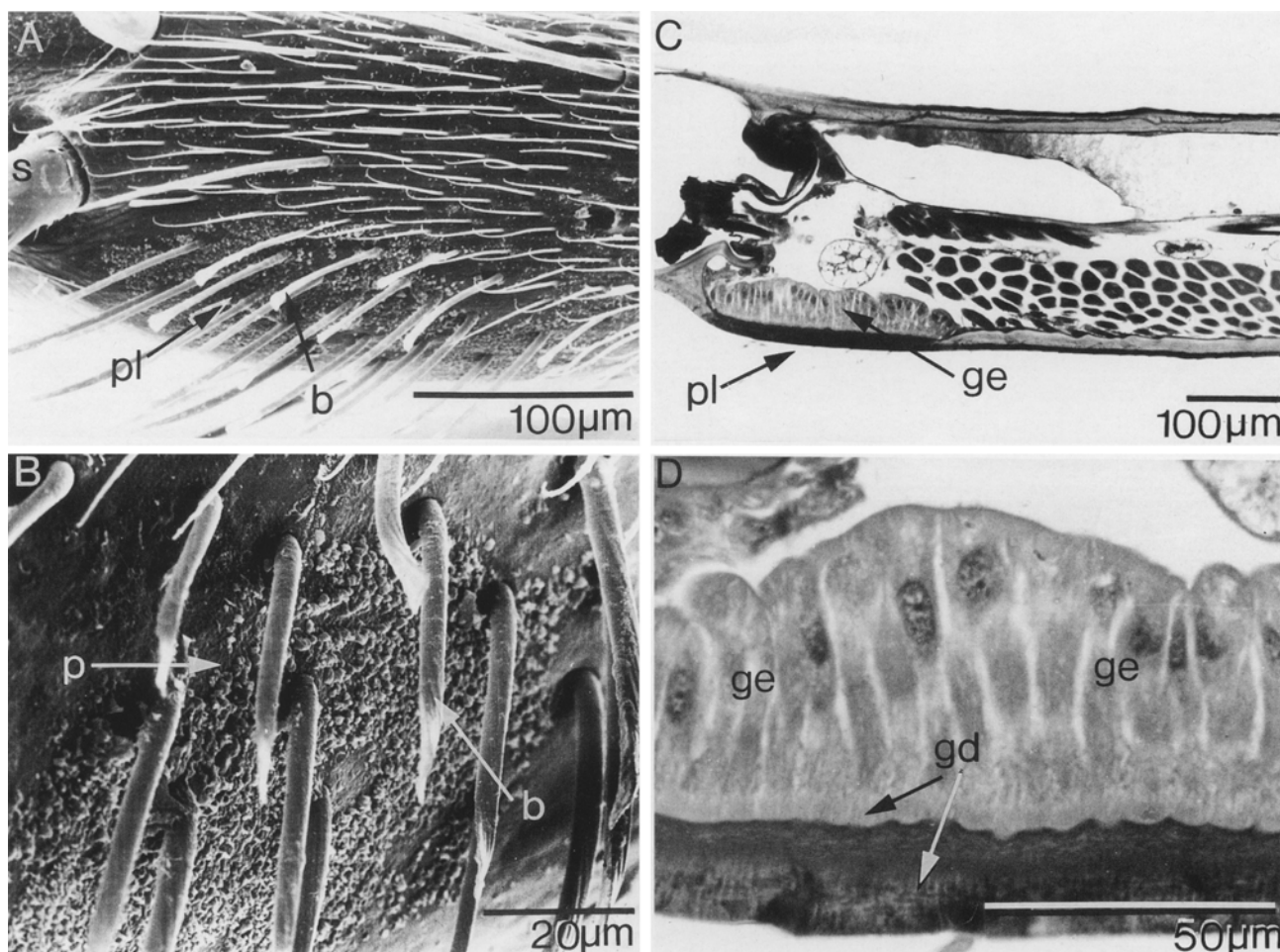
The existence of a metatibial gland was first noted by Bolton (1990) who considered this structure to be a synapomorphy of the doryline section subfamilies. He found it in at least 12 genera belonging to these subfamilies. A similar structure was detected within the tribe *Ponerini* (Ponerinae) in 29 species of *Pachycondyla* and in most species of the genus *Diacamma*. Bolton's characterization of the metatibial gland is based on inspection with a stereomicroscope of the external features of the putative glandular area. A histological verification of the glandular nature of the associated internal tissue was thus needed. These histological investigations combined with SEM studies of the external morphology revealed many new details of the metatibial structures.

In representative species of the army ant genera *Ecton*, *Neivamyrmex*, *Dorylus*, and *Aenictus*, the pore plate is convex and elongates more than half of the length of the entire tibia. It is perforated by numerous pores which

are the openings of cuticular ducts each originating from a glandular cell. No special bristles are associated with the pore plates. The morphologies of the metatibial gland are distinctly different in the Cerapachyinae. The glandular epithelium consists of slender cylindrical cells which are concentrated in a relatively small area on the inner lateroventral side of the tibia close to the main spur. In *Sphinctomyrmex steinheili*, the pore plate sits in a slight depression and has an inconspicuous spongiform surface without any associated bristles. In *Cerapachys biroi*, the pore plate consists of an elaborate spongiform surface located in a small oval depression in the cuticle. In *C. turneri*, the opening of the metatibial gland is a pronounced pit-like depression in the cuticle which is filled with forked bristles, resembling a brush. In some African *Cerapachys* (e.g., *C. nkomoensis*), on the other hand, the metatibial gland is enormous, extending about one-third of the length of the tibia in external view (B. Bolton, personal communication).

The internal morphology of the metatibial gland of the Cerapachyinae is very similar to that of the metatibial gland of the Ponerini. Bolton (1990) does not consider this gland of the Ponerini to be homologous to that found in species of the doryline section. He states that in the Ponerini "the glandular patch is lateral, on the inner face of the metatibia basally and away from the articulation of the main spur." However, as can be seen in the SEM





**Fig. 10A–D** Metatibial gland of *Diacamma* sp. worker (from Japan). **A** SEM showing pore plate near spur (*s*). **B** Close-up of pore plate with granular material covering pores (*p*). The pore plate is associated with thick, spatular-shaped bristles (*b*). **C** Sagittal section through metatibia showing glandular epithelium (*ge*). **D** Close-up of epithelium with glandular ducts (*gd*)

micrographs (Figs. 8–12), the lateral position of the external glandular patch varies in the Ponerini, being more obvious in *P. rufipes* (Fig. 11) and hardly noticeable in *Diacamma* sp. from Malaysia (Fig. 9). Furthermore, the bristle fields are part of the external glandular structure and they extend close to the articulation of the spur. In the investigated species of the genus *Cerapachys*, the glandular patch can have a slightly lateral position, but the internal arrangement of the glandular tissue of the metatibial glands in the Cerapachyinae and Ponerini is very similar. From these comparative findings we doubt whether it is justified to conclude that the metatibial glands of the Ponerini are not homologous to those of the doryline section subfamilies.

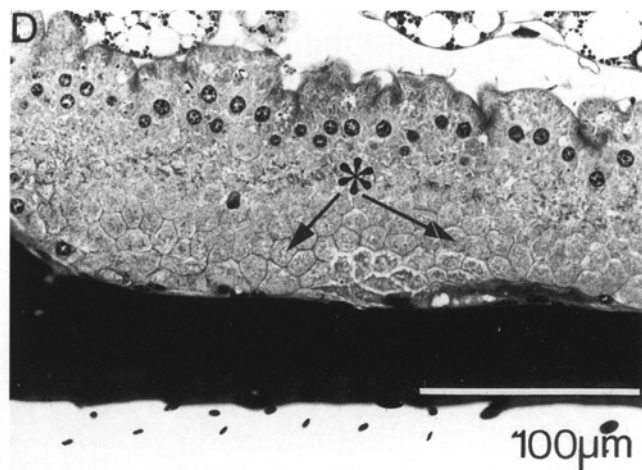
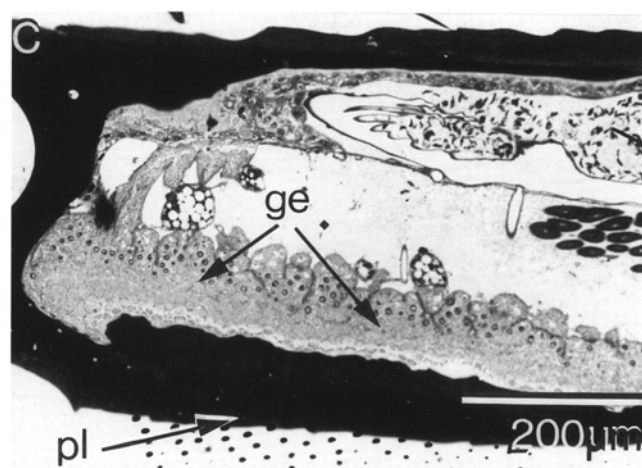
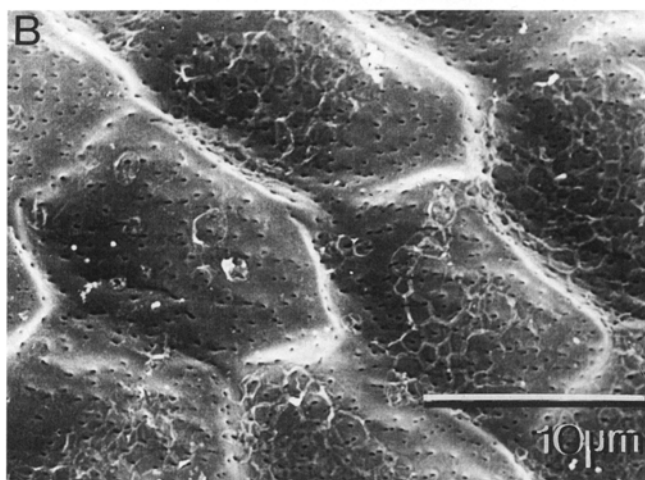
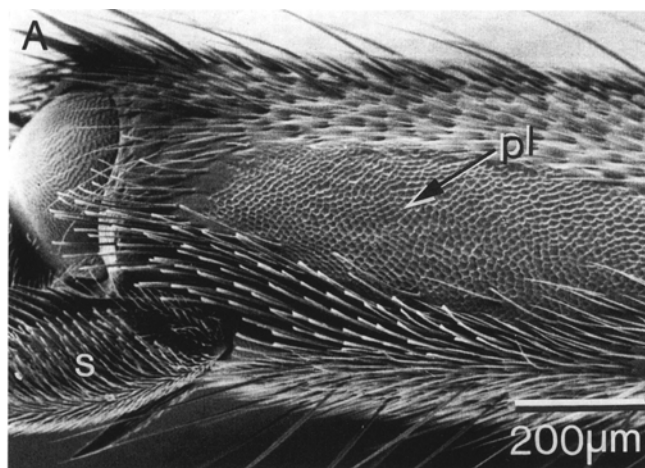
The fact that this type of metatibial glands appears to be lacking in other species of the Ponerinae, Leptanillinae, and elsewhere throughout the Formicidae (Bolton 1990), suggests that, within the poneroid group, the metatibial gland independently evolved twice, once in the

common ancestors of the subfamilies of the doryline section and once in the ancestors of the Ponerini. One could thus argue that the absence of the structure is the plesiomorphic state. This appears to be the most parsimonious explanation and the conclusion Bolton draws from his extensive morphological survey in which he considered seven additional synapomorphies of the doryline section subfamilies.

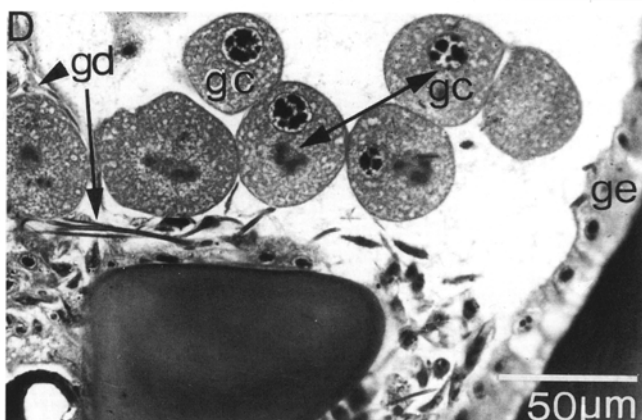
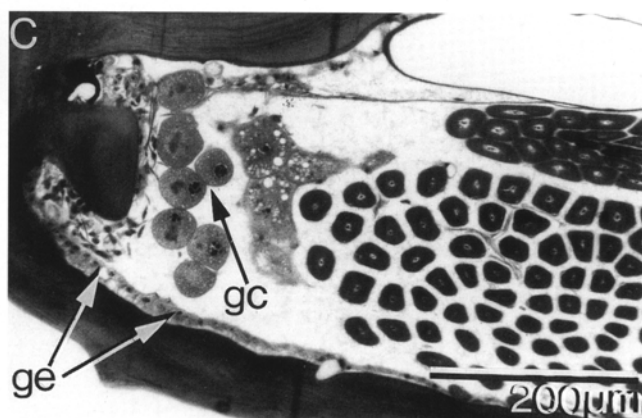
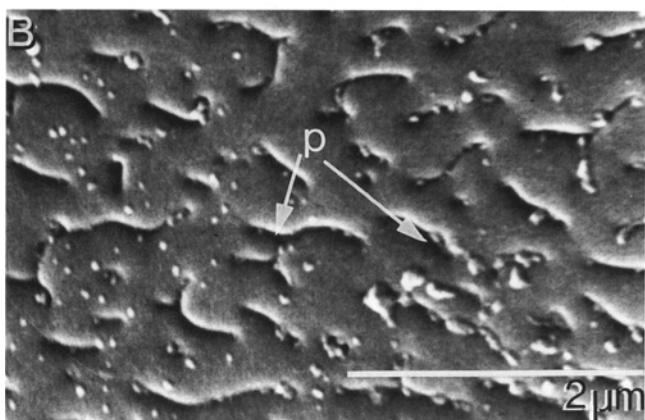
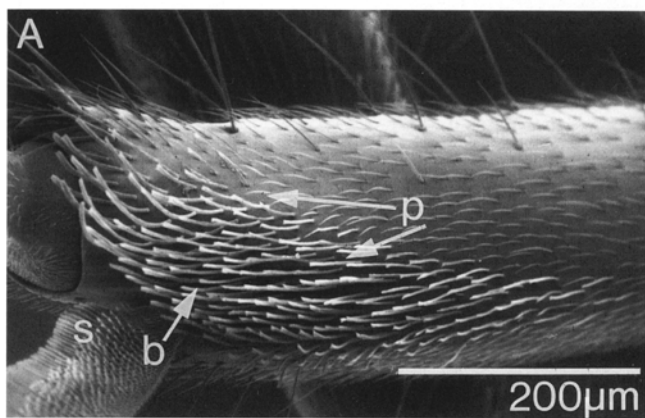
As an alternative, focusing solely on the metatibial gland, one could also argue that the presence of the metatibial gland in the Ponerini and in the doryline section subfamilies is a symplesiomorphy and the absence in other Ponerinae and Leptanillinae is a derived state. To decide between these alternatives, we would need to know more about the internal morphology of the metatibia in species of other tribes of the Ponerinae. Did we find epithelial structures that indicate a vestigial form of a metatibial gland? Indeed, we found such an epithelium in *Prionopelta amabilis*, a representative of the Amblyoponini (Ponerinae). Based on the morphological features known to us, it is, in our judgement, not yet possible to decide between these two alternatives. We also would need to know more about the function of the metatibial glands.

In *Pachycondyla* [= *Paltothyreus*] *tarsata*, the epithelial metatibial gland is hard to recognize, but there is also

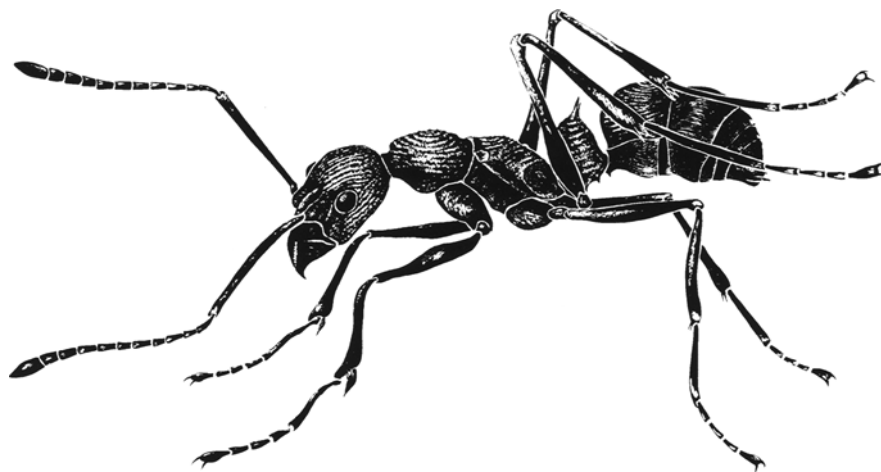
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**Fig. 13** Dominant worker of *Diacamma* sp. (from India) rubbing metatibial glands over gaster targites. Drawing based on video recordings



another kind of gland consisting of paired clusters of glandular cells. This latter structure appears to be an autapomorphy of this species. In fact, *P. tarsatus* has several glandular features not found in any other species of the genus *Pachycondyla* investigated. Workers possess large unpaired intersegmental glandular cell clusters on the medial line between the seventh and sixth, sixth, and fifth, and fifth and fourth abdominal sternites (Hölldobler and Engel 1978). These glands are employed in trail communication (Hölldobler 1984).

Recently, Bolton (personal communication) found that metatibial glands are extensively present in genera of the *Strumigenys* group of the Dacetoniini. Bolton suggests that these glands have evolved independently of those seen in the Ponerinae and the doryline section subfamilies, because they are present on all legs and are located on the dorsal (outer) surface.

Thus, the metatibial gland is remarkably complex and well developed in various ants, but its function remains to be discovered. Recently we found that this gland is involved in sexual calling in several *Diacamma* species. It is present in all the workers in a colony, but only the dominant individual behaves in a characteristic manner which leads to the release of metatibial gland secretions.

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**Fig. 11A–D** Metatibial gland of *Pachycondyla rufipes* worker. **A** SEM of pore plate (*pl*). Some of the pore plate area near spur (*s*) is associated with spatula-shaped bristles. **B** Close-up of naked pore plate showing hexagonal structure and pores. **C** Sagittal section of metatibia showing glandular epithelium (*ge*). **D** Close-up of glandular epithelium with hexagonal bundles of glandular ducts marked by an asterisk

**Fig. 12A–D** Metatibial gland of *Pachycondyla* [= *Paltothyreus*] *tarsata*. **A** SEM of pore plate which is mostly covered by thick bristles (*b*). **B** Close-up of naked spot of the pore plate showing very small slit-shaped pores (*p*). **C** Sagittal section through metatibia showing the thin layer of glandular epithelium (*ge*) and the glandular cells (*gc*) of a second gland. **D** Close-up of the glandular cells (*gc*) with long glandular ducts (*gd*)

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