Insectes Sociaux, Paris
1986, Volume 33, n° 3, pp 278-295

MORPHOLOGY AND ULTRASTRUCTURE OF THE ABDOMINAL GLANDS IN DOLICHODERINE ANTS (HYMENOPTERA, FORMICIDAE)

J. BILLEN *

Limburgs Universitair Centrum, Department SBM, B-3610 Diepenbeek (Belgium) and Laboratorium voor Systematiek en Ecologie, K.U. Leuven Naamsestraat 59, B-3000 Leuven (Belgium)

Reçu le 12 juin 1985 Accepté le 9 mai 1986

SUMMARY

Ants of the subfamily Dolichoderinae possess four major abdominal glands. The lack of a functional sting probably explains the rather moderate development of the sting associated poison and Dufour's glands. The extremely large pygidial gland has become the main source of the dolichoderine defensive secretions, while the Pavan's gland, when present, produces the trail substances.

The large tergal gland between tergites 6 and 7, formerly called the anal gland, due to its anatomical position and general morphological characteristics, is homologous to the pygidial gland, which is found in all other ant subfamilies. Pavan's gland, on the other hand, is apparently a peculiarity to the Dolichoderinae and Aneuretinae. The sac-like appearence of the Pavan's gland only represents the reservoir part, while the real secretory component of the gland is to be located in the thickened epithelium of the seventh abdominal sternite.

Ultrastructural examination reveals a well-developed smooth endoplasmic reticulum along with numerous mitochondria as the major cytoplasmic constituents in the pygidial, Dufour's and Pavan's gland. Both characters can be related to the lipophilic secretion of these glands, while the moderately developed granular endoplasmic reticulum of the poison gland secretory cells may point to some protein synthesis. Both the pygidial and poison gland are comprised of individual secretory units with a glandular cell and its own duct cell, while the Dufour's and Pavan's gland correspond to the glandular epithelium type.

* Senior Research Assistant of the Belgian National Fund for Scientific Research.

RESUME

Morphologie et ultrastructure des glandes abdominales des fourmis Dolichodérines (Hymenoptera, Formicidae)

Les fourmis appartenant à la sous-famille des Dolichoderinae possèdent quatre glandes abdominales principales. La taille plutôt médiocre de la glande de Dufour et de la glande à venin est probablement liée à l'absence d'un aiguillon fonctionnel. La glande pygidiale très grande est chez ces fourmis la source des substances défensives la plus importante, tandis que les phéromones de piste sont sécrétées par la glande de Pavan.

Sa dénomination comme glande pygidiale est justifiée par la position anatomique et les caractères morphologiques en général, ce qui réfute l'hypothèse d'une glande anale qui serait propre aux espèces dolichodérines. La glande de Pavan par contre semble être une structure unique parmi les Dolichoderinae et Aneuretinae. Le sac comme on l'a décrit auparavant ne constitue que le réservoir de la glande de Pavan, alors que la partie sécrétrice correspond à l'épithélium épaissi du septième sternite.

Des recherches ultrastructurales révèlent un réticulum endoplasmique lisse bien développé et de nombreuses mitochondries dans la glande pygidiale, la glande de Dufour et la glande de Pavan. Ces caractères s'accordent avec la sécrétion lipophile dans ces glandes, tandis que l'ergastoplasme plutôt médiocre dans les cellules sécrétrices de la glande à venin indique une production de protéines. La glande pygidiale et la glande à venin sont composées d'unités sécrétrices individuelles comprenant une cellule glandulaire et une cellule du canalicule. La glande de Dufour et la glande de Pavan sont formées par des épithéliums glandulaires.

INTRODUCTION

The Dolichoderinae are generally considered as one of the highly evolved ant subfamilies. They have ceased to use the sting as a defensive or offensive weapon and therefore, display a reduced or atrophied venom apparatus. The well-developed pygidial gland in this subfamily compensates for sting reduction, and produces the alarm-defense substances (PAVAN and RONCHETTI, 1955 ; TRAVE and PAVAN, 1956). This gland was formerly called the " anal gland ", although its general anatomy and opening between the sixth and seventh tergite provide evidence of its homology with the pygidial gland in other subfamilies (HÖLLDOBLER, 1982).

Trail pheromones in most Dolichoderinae emanate from the " organo ventrale " (PAVAN, 1955 ; WILSON and PAVAN, 1959), that became well known as Pavan's gland. The gland is regarded as a neoformation that only occurs in the *Dolichoderinae* and the closely related *Aneuretus simoni*, where it is equally the source of the trail subtances (TRANIELLO and JAYASURIYA, 1981). It opens between the 6th and 7th abdominal sternite, though the real glandular part was recently ascribed to the modified 7th sternal epidermis (FANFANI and DAZZINI VALCURONE, 1984 ; BILLEN, 1985 b).

Notwithstanding the largely reduced condition of the sting, the poison and Dufour's gland remain associated with it. Due to the function of alarm and trail pheromone production being performed by the pygidial and Pavan's gland, respectively, the actual function of the two sting glands in the *Dolichoderinae* is rather indistinct. Both glands, in fact, are fairly small in comparison with their appearance in other subfamilies.

Apart from the recent histological description of the Pavan's gland in *Dolichoderus doriae* (DAZZINI VALCURONE and FANFANI, 1982) and *Iridomyrmex humilis* (FANFANI and DAZZINI VALCURONE, 1984), and its ultrastructural investigation in *D. quadripunctatus* (BILLEN, 1985 b), the actual information dealing with the morphology of *dolichoderine* glands refers to rather old anatomical papers (PAVAN, 1955 ; PAVAN and RONCHETTI, 1955 ; MIRADOLI ZATTI and PAVAN, 1957). The present study reports on the morphology and ultrastructure of the abdominal glands in the workers of some *Dolichoderinae.*

MATERIAL AND METHODS

Our morphological data deal with foraging worker individuals of *Azteca* sp. (collected at Barlovento, Venezuela), *Bothriomyrmex decapitans* (Oukaimeden, Morocco), *Dolichoderus quadripunctatus* (Würzburg, FRG), *Iridomyrmex humilis* (Barcelona, Spain) and *Tapinoma nigerrimum* (Calvi, Corsica).

Both dissected glands and abdominal halves were fixed in 2 % cold glutaraldehyde, buffered at pH 7.3 and 490 mosm with 0.05 M sodium cacodylate and 0.15 M saccharose. Postfixation in 2 % osmium tetroxide preceded dehydration in a graded acetone series and embedding in Araldite. Double stained thin sections were viewed in a Philips EM 400 electron microscope. Semi-thin sections, stained with methylene blue and thionin, were used for light microscopy.

RESULTS

The dolichoderine abdomen generally contains four distinct exocrine glands (*fig. 1*). Most conspicuous in all species investigated are the more or less paired pygidial glands, that open between the 6th and 7th abdominal tergites through a common slit-like orifice. Due to the ventral position of the seventh tergites in most Dolichoderinae, the pygidial gland opening is located at the extreme tip of the abdomen. The real anal opening in consequence has shifted to a more anterior position along with the sting remnants and its associated poison and Dufour's glands. The most anterior position is occupied by Pavan's gland, which consists of a distinct secretory epithelium on the 7th abdominal sternite, and a separate reservoir sac that is located between the 6th and 7th sternites.

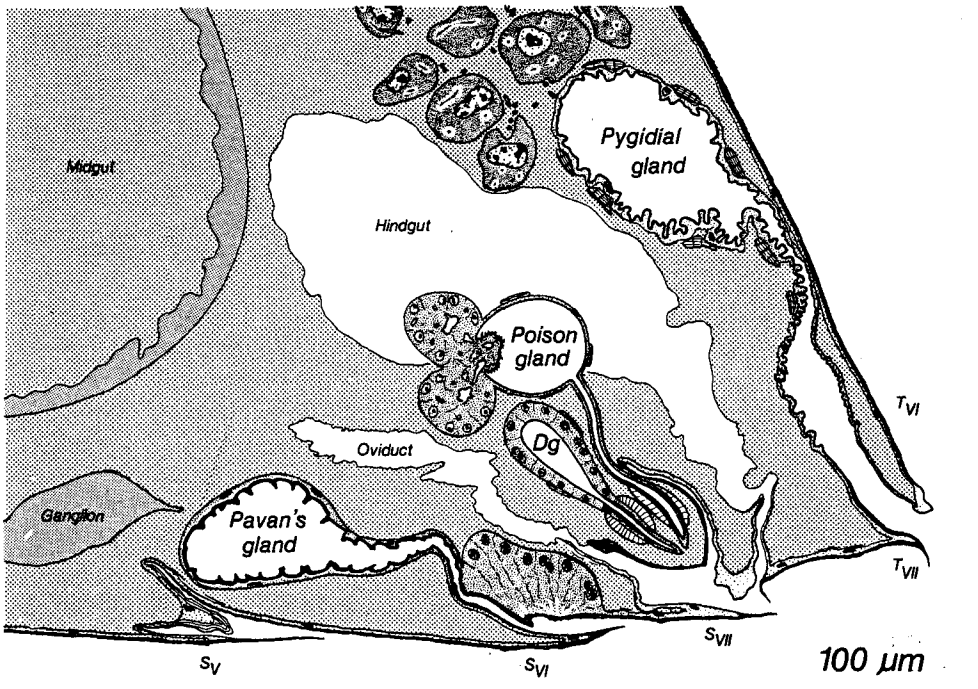


Fig. 1. — Longitudinal section through the dolichoderine abdominal tip showing the four major glands (drawing according to histological sections of an *Iridomyrmex humilis* worker). Dg: Dufour's gland.

Fig. 1. — Section sagittale à travers la partie abdominale postérieure montrant les quatre glandes principales des Dolichoderinae (selon des sections histologiques d'une ouvrière d'*Iridomyrmex humilis*). Dg: glande de Dufour.

1. Pygidial gland morphology

The pygidial gland is composed of a large, bilobed reservoir and two clusters of several tens of big secretory cells overlying the reservoir in a dorsolateral position (*fig. 1*). Each cell is provided with a narrow efferent ductule which, after fusion with the other ductules, continues in a common duct prior to opening in the posterolateral region of the reservoir (*fig. 4*).

The secretory cells have a diameter ranging between 20 and 40 µm. The rounded nuclei, with a diameter of approximately 15 µm, occupy a more or less central position in the cell and contain one or two distinct nucleoles. The most obvious characteristic of the cytoplasm is the considerably twisted intracellular end apparatus which may be encountered several times in a plane section (*fig. 2*). Ultrastructurally, this intracellular ductule shows a relatively thick and fibrillar endocuticular lining, which sometimes may be

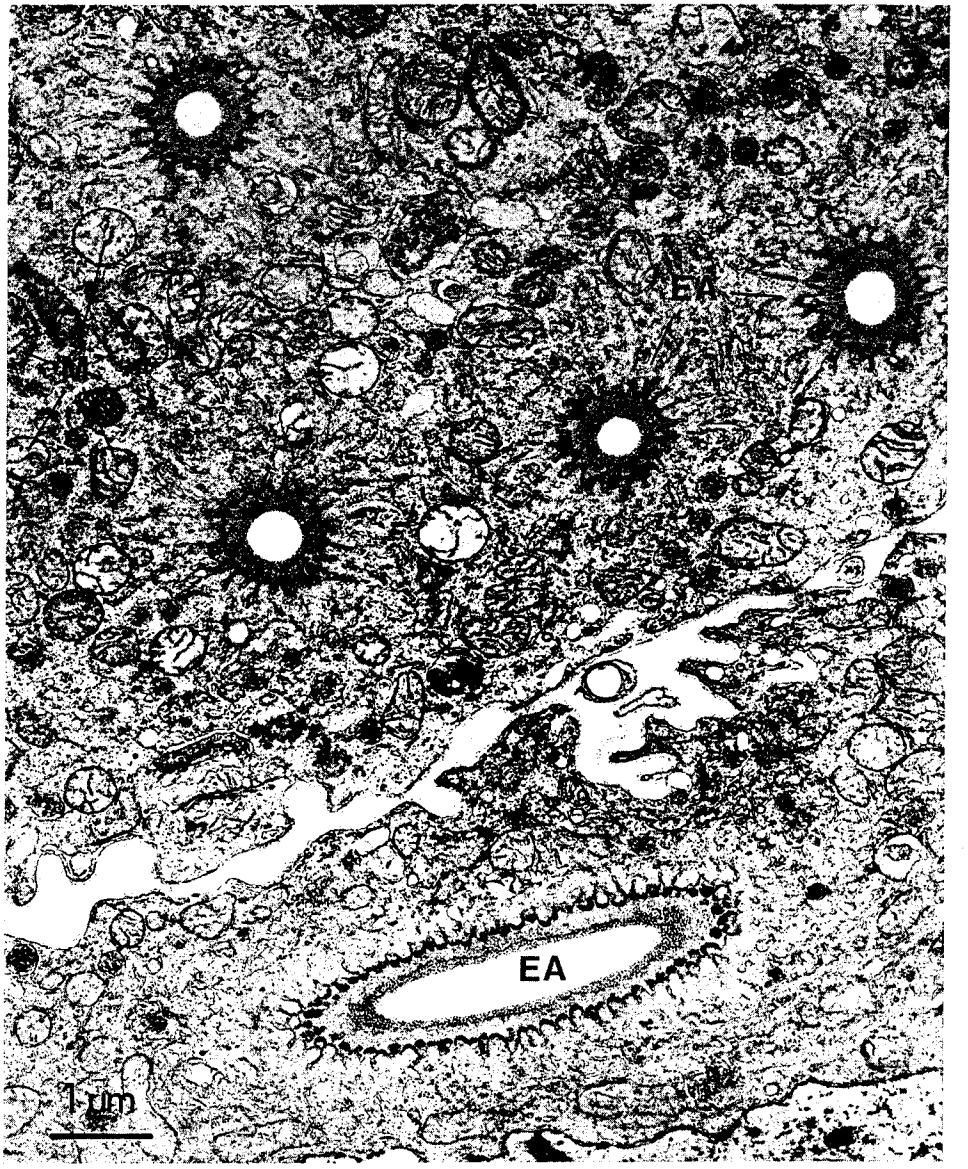


Fig. 2. — Detail of adjacent pygidial gland secretory cells in *B. decapitans*, showing sections through the twisted intracellular end apparatus (EA) and numerous mitochondria (M).

Fig. 2. — Détail des cellules sécrétrices de la glande pygidiale chez *B. decapitans*. Notez l'appareil terminal intracellulaire assez sinueux (EA) et les mitochondries très abondantes (M).

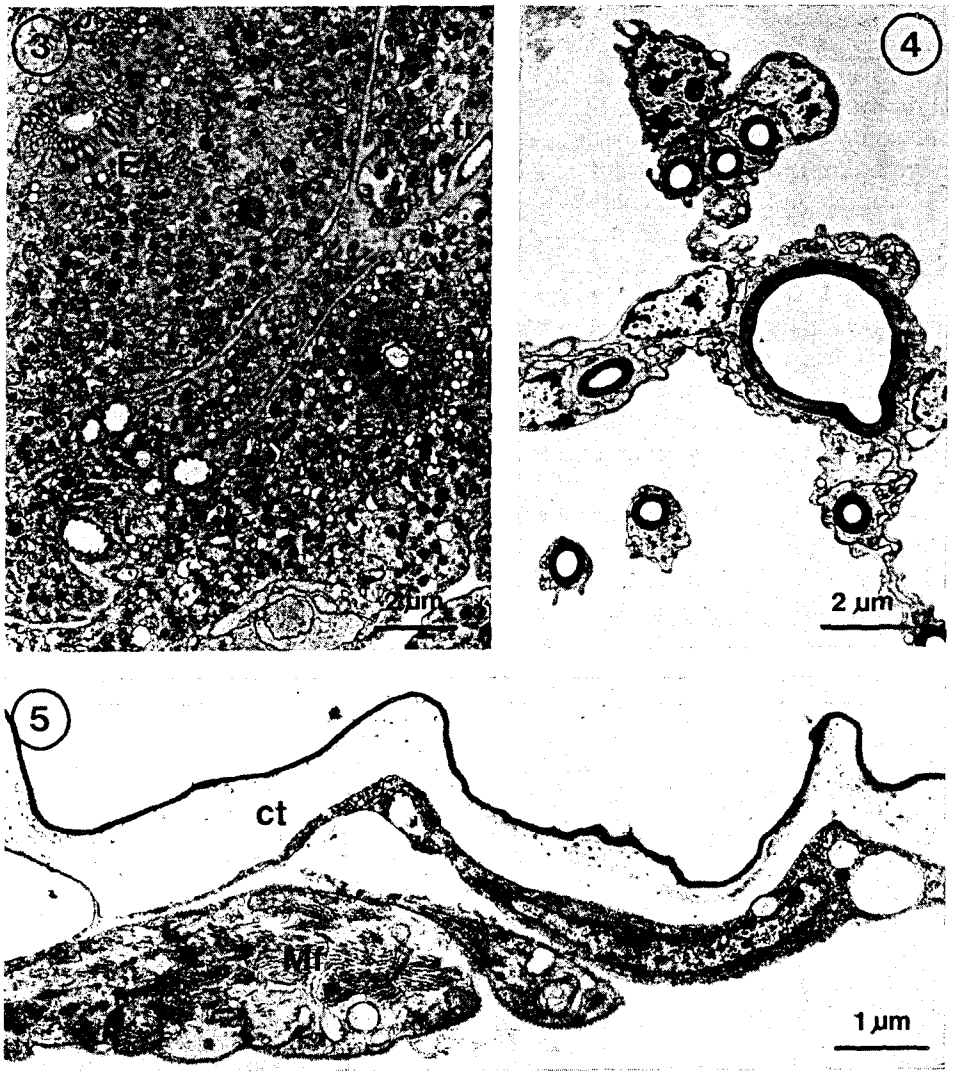


Fig. 3. — Pygidial gland cell cytoplasm in *T. nigerrimum*. EA : end apparatus, tr : tracheoles.

Fig. 4. — Detail showing pygidial gland individual ductules and common duct in *B. decapitans*.

Fig. 5. — Pygidial gland reservoir wall in *I. humilis*. ct : cuticle, Mf : muscle fibres.

Fig. 3. — Cytoplasme des cellules de la glande pygidiale chez *T. nigerrimum*. EA : appareil terminal, tr : trachéoles.

Fig. 4. — Détail des ductules individuelles et le conduit commun de la glande pygidiale chez *B. decapitans*.

Fig. 5. — Réservoir de la glande pygidiale chez *I. humilis*. ct : cuticule, Mf : fibres musculaires.

covered by a thin and discontinuous epicuticle. The cell membrane surrounding the ductule has a dinstinct microvillar appearance with electron-dense condensations on top of the microvilli (*fig. 2*). The cytoplasm contains an abundance of nearly spherical mitochondria, numerous free ribosomes and some cisternae of smooth endoplasmic reticulum. An amorphous basement membrane with a thickness of approximately 50 nm forms the outer cell lining. A tracheolar network extends between the secretory cells, with local penetration of tracheoles in the cytoplasm, which were occasionally observed (*fig. 3*).

Upon leaving the cell, the cuticular ductule lining becomes a continuous and electron-dense layer with a thickness of 0.3 µm. Its inner diameter of 0.5 µm within the duct cell remains the same as it had within the secretory cell. Except for the region of the nucleus, the duct cell cytoplasm is reduced to a very narrow strand surrounding the ductule. The individual ductules finally join with each other to become a 5 µm wide common duct that opens in the reservoir (*fig. 4*).

The pygidial gland reservoir wall comprises a much folded epithelium of nearly squamous cells that is covered with a cuticular layer of 0.5 to 1 µm thickness (*fig. 5*). The cells contain a very flattened nucleus and a cytoplasm with some vacuoles and free ribosomes. A distinct muscular supply sur-

---

Fig. 6. — Semi-thin section showing the poison gland components in *I. humilis*. CG : convoluted gland, FF : free filaments, R : reservoir.

Fig. 7. — Free filament lumen and surrounding secretory cells of the poison gland in *I. humilis*. ed : extracellular ductule, mlb : multilamellar body, N : nucleus, RER : vesiculate granular endoplasmic reticulum.

Fig. 8. — Detail of contact between intracellular end apparatus (EA) and extracellular ductule (ed) in *Azteca* sp. ; note the twisted aspect of the microvilli (mv).

Fig. 9. — Convoluted gland ultrastructure in *I. humilis*. EA : end apparatus, N : nucleus.

Fig. 10. — Poison gland reservoir wall in *I. humilis*. ct : cuticle.

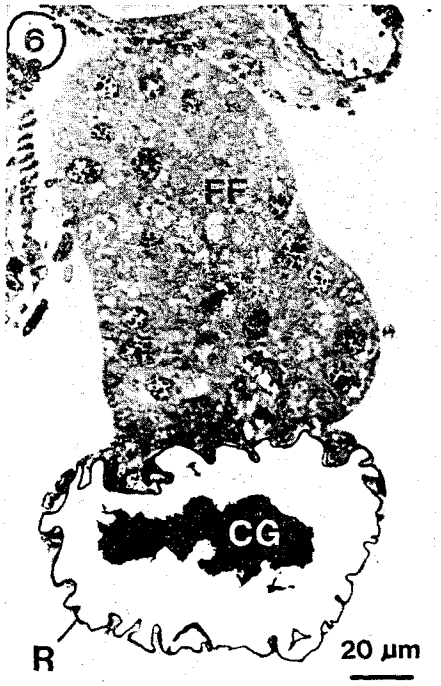
Fig. 6. — Section semi-fine chez *I. humilis* montrant les éléments de la glande à venin. CG : glande convolutée, FF : filament libre, R : réservoir.

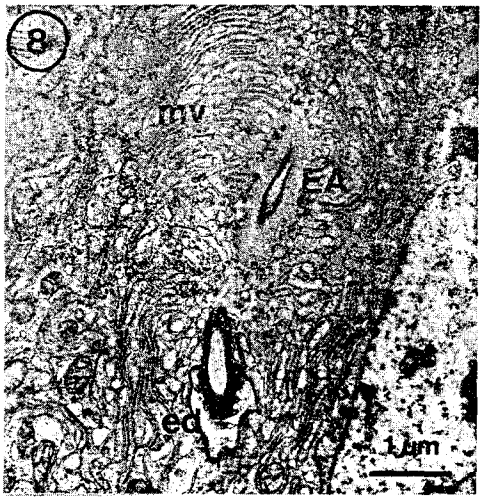
Fig. 7. — Lumen du filament libre et cellules sécrétrices de la glande à venin chez *I. humilis*. ed : ductule extracellulaire, mlb : corpuscules multilamellaires, N : noyau. RER : ergastoplasme vésiculaire.

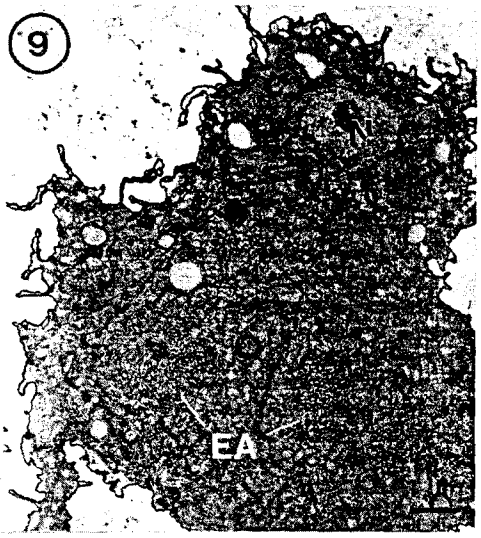
Fig. 8. — Jonction entre l'appareil terminal intracellulaire (EA) et le ductule extracellulaire (ed) chez *Azteca* sp. ; mv : microvillosités assez sinueuses.

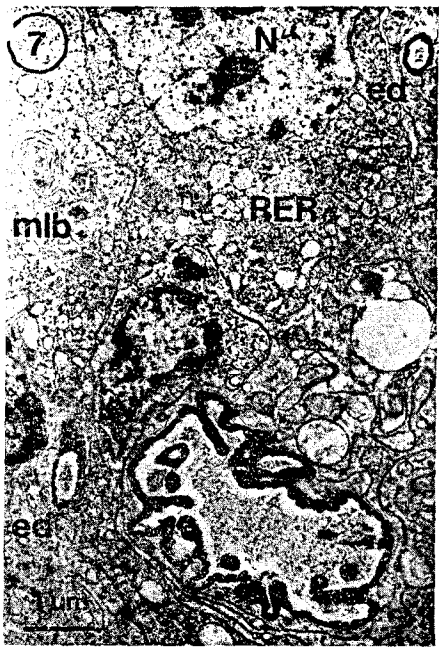
Fig. 9. — Ultrastructure de la glande convolutée chez *I. humilis*. EA : appareil terminal. N : noyau.

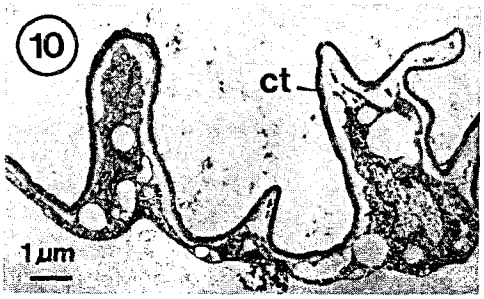
Fig. 10. — Paroi du réservoir de la glande à venin chez *I. humilis*. ct : cuticule.


6
FF
CG
R
20 µm


8
mv
EA
ed
1 µm


9
EA


7
N
ed
mlb
RER
ed
1 µm


10
ct
1 µm

rounds the gland reservoir. The single duct, which is not associated with any particular muscles, opens through a slit-like orifice between the 6th and 7th tergites.

2. Poison gland morphology

The ant poison gland is comprised of a thin-walled reservoir that opens in the sting base through a narrow duct, and two free filaments that carry the secretion of the glandular cells to the reservoir. A peculiarity to all Dolichoderine species is the globular shape of the free filaments in comparison with their long and slender appearance in other ant subfamilies. The entrance of the secretory filaments occurs through the so-called convoluted gland, which is to be considered as an invaginated secretory tissue bulb into the reservoir (*figs. 1 and 6*).

The polygonal secretory cells are arranged around the central filament lumen towards which they each send a narrow collecting ductule with an internal diameter between 0.2 and 0.3 µm (*figs. 7 and 8*). Their cytoplasm shows a moderately developed vesiculate granular endoplasmic reticulum and numerous ribosomes. A few mitochondria and multilamellar inclusions are randomly scattered in the cell. The secretory apparatus consists of a straight or slightly curved intracellular ductule with cuticular lining and

---

Fig. 11. — Transverse section of Dufour's gland in *I. humilis*.

Fig. 12. — Dufour's gland epithelium in *T. nigerrimum*. bm : basement membrane, ct : cuticle, N : nucleus.

Fig. 13. — Detail of cuticle (ct) and apical Dufour's gland cytoplasm in *B. decapitans* showing Golgi apparatus (ga) and granular endoplasmic reticulum (RER).

Fig. 14. — Basal half of Dufour's gland cell in *I. humilis*. bm : basement membrane, mlb : multilamellar bodies.

Fig. 15. — Transverse section through the Dufour's gland duct in *T. nigerrimum*. Note heavily sclerotized cuticle (ct), muscle fibres (Mf) and bundles of microtubules (MT). hd : hemidesmosomes.

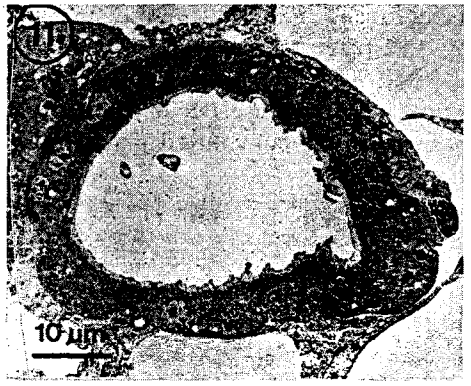
Fig. 11. — Section transversale à travers la glande de Dufour chez *I. humilis*.

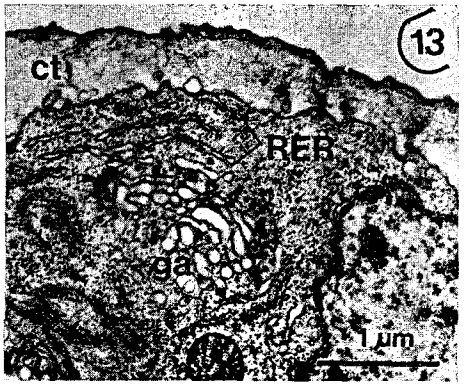
Fig. 12. — L'épithélium de la glande de Dufour chez *T. nigerrimum*. bm : membrane basale, ct : cuticule, N : noyau.

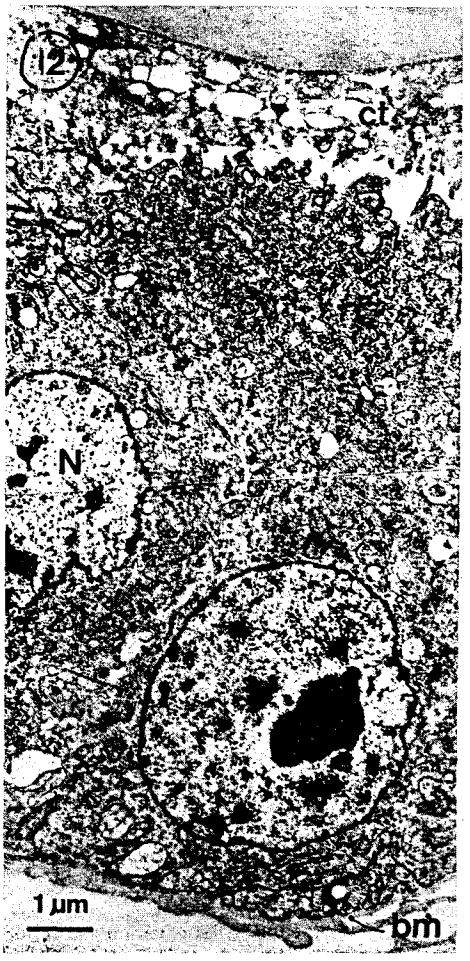
Fig. 13. — Région apicale du cytoplasme et cuticule (ct) de la glande de Dufour chez *B. decapitans*. ga : appareil de Golgi, RER : ergastoplasme.

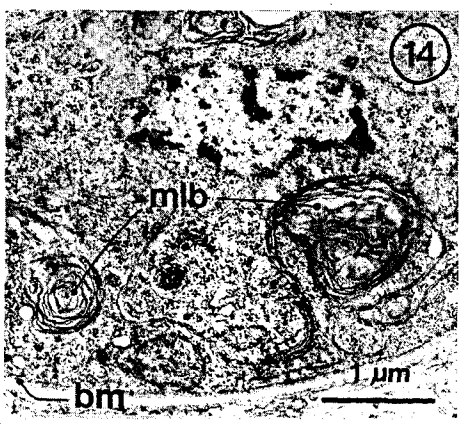
Fig. 14. — Région basale du cytoplasme de la glande de Dufour chez *I. humilis*. bm : membrane basale, mlb : corpuscules multilamellaires.

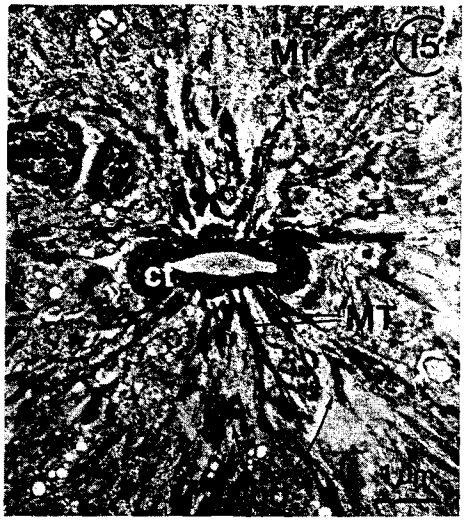
Fig. 15. — Section transversale à travers le conduit de la glande de Dufour chez *T. nigerrimum*. ct : cuticule, hd : hémidesmosomes, Mf : fibres musculaires. MT : microtubules.


11
10 µm


13
ct
RER
ga
1 µm


12
ct
N
1 µm
bm


14
mlb
1 µm
bm


15
MT
cr
MT

surrounding microvillar sheath, ultrastructurally similar to the pygidial gland end apparatus. Exceptionally long and often much twisted microvilli were only observed in the *Azteca* individuals (*fig. 8*).

The same morphological characteristics, including the occurrence of the intracellular secretory apparatus are retained in the convoluted gland, apart

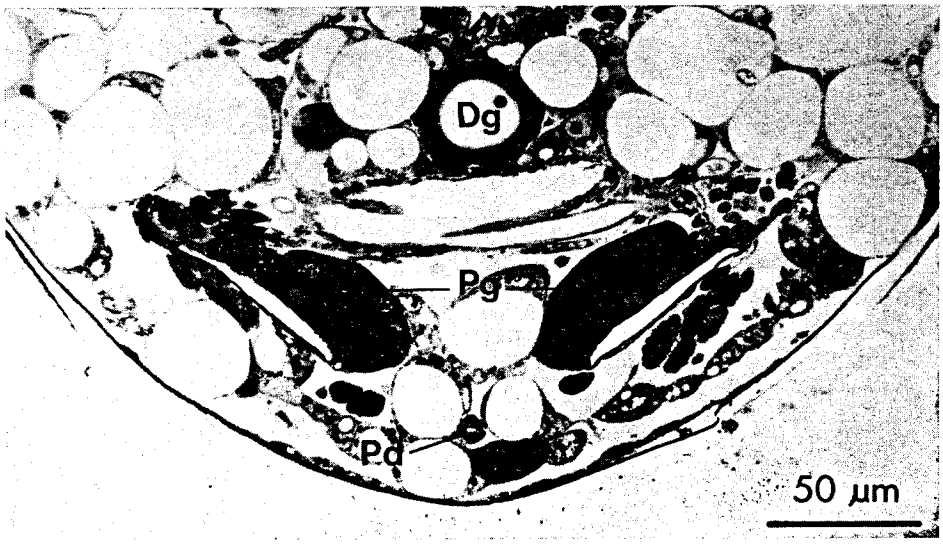


Fig. 16. — Transverse section near the abdominal tip in *I. humilis* showing the Dufour's gland (Dg), and the Pavan's gland duct (Pd) and secretory epithelium (Pg).

Fig. 16. — Section transversale auprès de l'extrémité abdominale chez *I. humilis*, montrant la glande de Dufour (Dg) ainsi que l'épithélium glandulaire (Pg) et le conduit (Pd) de la glande de Pavan.

Fig. 17. — Pavan's gland reservoir wall in *D. quadripunctatus*. ct : cuticle, N : nucleus.

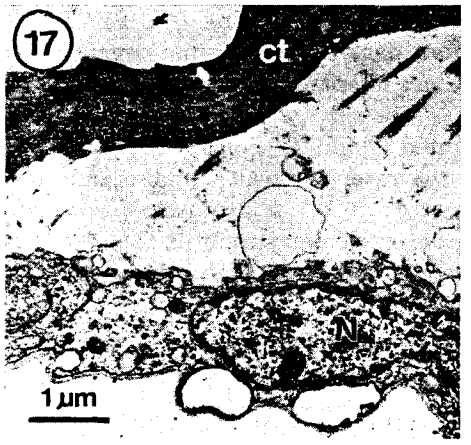
Fig. 18. — Illustration of the secretory epithelium of the dolichoderine Pavan's gland.

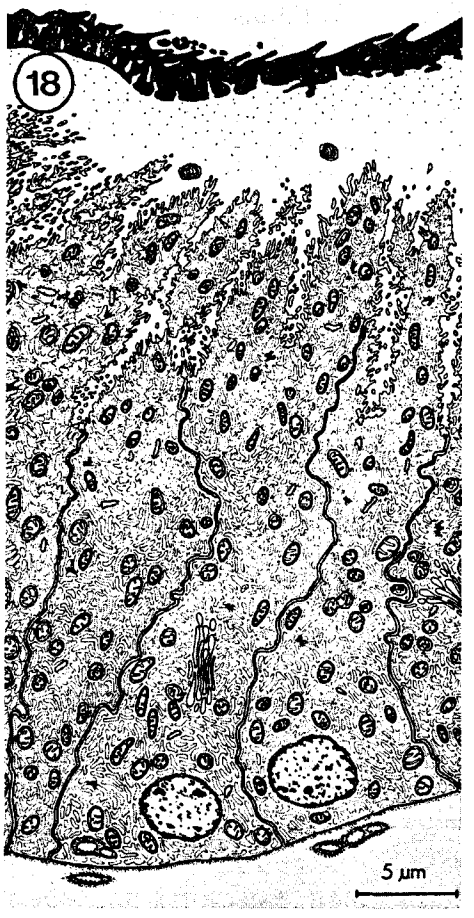
Figs. 19 to 21. — Apical (19), central (20) and basal (21) cytoplasm of the secretory epithelium of Pavan's gland in *D. quadripunctatus*. M : mitochondria, mlb : multilamellar bodies, mv : microvilli, N : nucleus, SER : smooth endoplasmic reticulum, tr : tracheoles.

Fig. 17. — Réservoir de la glande de Pavan chez *D. quadripunctatus*. ct : cuticule, N : noyau.

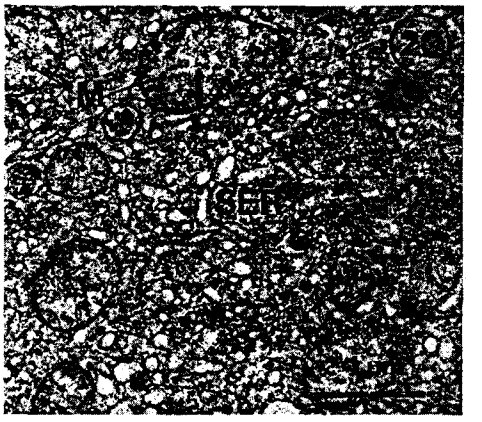
Fig. 18. — Schéma de l'épithélium sécréteur de la glande de Pavan des Dolichoderinae.

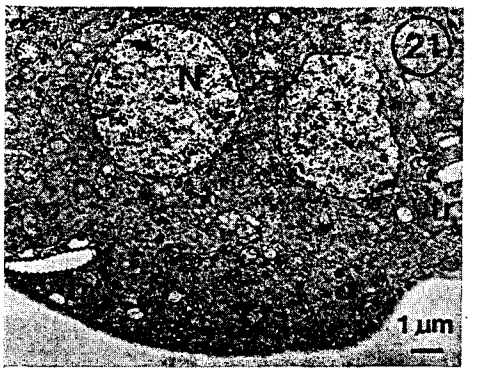
Figs. 19 à 21. — Région apicale (19), centrale (20) et basale (21) des cellules sécrétrices de la glande de Pavan chez *D. quadripunctatus*. M. : mitochondries, mlb : corpuscules multilamellaires, mv : microvillosités, N : noyau, SER : réticulum endoplasmique lisse, tr : trachéoles.


17
ct
N
1 µm


18
5 µm


19
plb
m


20
SER


21
N
1 µm

from the endoplasmic reticulum that is apparently lacking (*fig. 9*). Tissue in this part of the gland has a much more packed cytoplasmic organization than that in the free filaments, and hence displays a very electron-dense aspect (*fig. 6*).

The cuticular lining of the convoluted gland is continuous with the reservoir lining. The thin epithelium of the reservoir wall contains only few organelles but quite numerous vacuoles (*fig. 10*). A few muscle fibres surround the reservoir, while a more extensive muscular supply is found at the ventral side of the most posterior region of the poison gland duct.

3. Dufour's gland morphology

The dolichoderine Dufour gland is a rather small piriform sac that opens through a slit-like duct ventral of the poison gland duct. It is comprised of a simple layer of epithelial cells with a thickness between 5 and 15 μm, and a cuticular lining of 0.15 to 1.5 μm (*fig. 11*).

The rounded nuclei display a dispersed chromatin and occupy a slightly basal position in the cells (*fig. 12*). A well-developed smooth endoplasmic reticulum and an abundance of free ribosomes constitute the main cytoplasmic components. Mitochondria are fairly numerous and Golgi apparatus (*fig. 13*) and multilamellar bodies (*fig. 14*) were often observed. Granular endoplasmic reticulum is very rare in *Azteca, Iridomyrmex* and *Tapinoma,* whereas it occurs as a distinct cytoplasmic element in *Dolichoderus* and to a lesser extent in *Bothriomyrmex* (*fig. 13*). Irregularly arranged slender microvilli are found in *Iridomyrmex* and *Tapinoma* (*fig. 12*), they may occur in *Azteca* and *Bothriomyrmex,* but are lacking in *Dolichoderus.* The basal cell membrane shows a few shallow invaginations and is lined with an amorphous basement membrane of approximately 60 nm (*figs 12 and 14*).

Muscle fibres surrounding the Dufour's gland occur, though their number is very limited. The duct, however, is surrounded by a very extensive supply of muscle fibres that attach to the duct epithelium by means of hemidesmosomes (*fig. 15*). Bundles of microtubules within the duct cell have a parallel orientation to the underlying myofilaments and transmit the muscular pulling force to the heavily sclerotized cuticle of the slit-like duct.

4. Pavan's gland morphology

Since its first description (PAVAN, 1955), the Pavan's gland has been regarded as an unpaired median sac that opens between the 6th and 7th abdominal sternites in many dolichoderine species. Ultrastructural examination of the sac wall reveals a very thin epithelium with a thickness of hardly 2 μm and an irregularly folded cuticular layer of approximately 1 μm (*fig. 17*). The cells contain a flattened nucleus and a cytoplasm in which only some free ribosomes and a few mitochondria are found. In between the cuticle and epithelium, a distinct and electron- lucid subcuticular space occurs (*fig. 17*).

In close structural (and functional) relation to this thin-walled sac is a conspicuous glandular epithelium with a thickness between 25 and 30 μm. It corresponds with the considerably thickened epidermis of the anterior part of the 7th sternite (*fig. 1*). Due to the slight V-shape of the anterior border of this sternite, the glandular epithelium in cross section may appear as two lateroventral units (*fig. 16*), though these will approach and eventually join each other more posteriorly.

Between the cuticular lining and the epithelium, a considerable subcuticular space is observed. The cuticle itself is penetrated by numerous irregular pore canals with a diameter around 0.5 μm. The cytological organization of the columnar cells is illustrated in *figure 18*. The apical cell membrane is differentiated into a distinct microvillar border all along its numerous invaginations (*fig. 19*). An abundance of mitochondria and a very well-developed smooth endoplasmic reticulum are the most characteristic elements in the glandular cells (*figs. 19 and 20*). A distinct Golgi apparatus is also evident, while some microtubules and free ribosomes are scattered throughout the cytoplasm. A few multilamellar bodies may be found, either within the glandular cells or in the subcuticular space (*fig. 19*). Nuclei are relatively small and are invariably basally located. Tracheoles occur adjacent to the basement membrane and are often seen to penetrate between the gland cells (*fig. 21*).

The occurrence of such a glandular epithelium in addition to the thin-walled reservoir sac was a common character in all species investigated, except for *Tapinoma nigerrimum*. Workers of this species apparently lack the reservoir sac, while their 7th abdominal sternite only shows a slightly thickened epithelium.

DISCUSSION

According to their cellular organization, insect exocrine glands can conveniently be classified into two groups. Glandular epithelia constitute the morphologically most simple type, and are found e.g. in the Dufour's and Pavan's glands. The other type glands are composed of bi-cellular functional units, each comprising a secretory cell and its accompanying duct cell, as in the pygidial gland. Also the poison gland belongs to this group, though it is somewhat aberrant due to the epithelial arrangement of the secretory cells in two free filaments. The duct cells consequently are rather short, because of the nearby filament lumen into which they release the secretion of the corresponding glandular cells.

The poison gland free filaments in the Dolichoderinae typically have a globular appearance which clearly discerns them from the other sub-

families. The occurrence of granular endoplasmic reticulum in the secretory cells is a general feature for the poison gland in ants (BILLEN, 1985a, 1986b), bees (OWEN and BRIDGES, 1976) and wasps (KANWAR and KANWAR, 1975 ; EDSON *et al.*, 1982 ; DELFINO *et al.*, 1983), and corresponds with the proteinaceous venom composition. Although information on the chemical composition of the dolichoderine venom is lacking (BLUM and HERMANN, 1978), the rather moderate development of granular endoplasmic reticulum in their poison gland may reflect a rather small proteinaceous fraction in the venom. A similar situation was observed in *Myrmica rubra* (BILLEN, 1986b), whereas species with a strong proteinaceous venom, irrespective of the presence of a functional sting, all display a well-organized granular endoplasmic reticulum (BILLEN, 1985a). The venom is collected by the intracellular end apparatus and efferent ductules and reaches the reservoir after passage through the convoluted gland. The latter probably acts as an additional secretory compartment, as is suggested by the occurrence of the end apparatus.

Venom ejection is affected by the contracting reservoir muscles and the more extensive muscular supply inserted onto the ventral duct region. The Dufour's gland duct is also provided with a considerable muscular attachment. Therefore, both the poison and Dufour's gland possess an independent discharging mechanism. The ultrastructural organization, with straight bundles of duct cell microtubules that transmit the muscular forces to the thickened duct cuticle, correspond with the myoepidermal junction in insects generally (AUBER, 1963 ; LAI-FOOK, 1967) and the muscular insertion on the ant Dufour's gland in particular (BILLEN, 1982 ; 1986a).

The epithelial cells of the Dufour's gland hardly display characters that are typical for the Dolichoderinae. General features shared with other subfamilies are the numerous mitochondria and the multilamellar bodies, that may represent secretory vesicles (HEFETZ and ORION, 1982). Notwithstanding the existence of a morphological Dufour's gland pattern for most ant subfamilies (BILLEN, 1986a), the dolichoderine gland does not seem too constant. Irregular apical microvilli are often found, but not in *D. quadripunctatus*. Moreover, the aberrant position of *Dolichoderus* is confirmed by its fairly well-developed granular endoplasmic reticulum, whereas the other species (with *Bothriomyrmex* to a lesser extent) are characterized by a smooth endoplasmic reticulum. The latter cytoplasmic element, at least, is in accordance with the chemical information of the dolichoderine Dufour's gland as a source of hydrocarbons (CAVILL and HOUGHTON, 1973 ; BLUM and HERMANN, 1978). Extensive smooth endoplasmic reticulum is reported as a common cytoplasmic constituent in insect epidermal glands that produce small-sized nonproteinaceous molecules (NOIROT and QUENNEDEY 1974 ; PERCY, 1974). Chemical data on the Dufour's gland in *Dolichoderus*, unfortunately, are not available hitherto.

What role the Dufour's and poison gland play in dolichoderine biology, remains unknown. Their relatively small size most probably goes along with

sting reduction, which would considerably limit the offensive or defensive role these glands play in other subfamilies. As a rule, the alarm-defence substances in Dolichoderinae are produced in the extremely enlarged pygidial gland. They correspond chemically with a variety of ketones and cyclopentanoid monoterpenes (TRAVE and PAVAN, 1956 ; BLUM and HERMANN, 1978).

The pygidial gland ultrastructure with cisternae of smooth endoplasmic reticulum and an abundance of mitochondria can be related to the synthesis of these lipophilic molecules. Secretion from the glandular cells is collected by the well-developed end apparatus from where the extracellular ductules carry it to the big reservoir sac. Extensive muscles surrounding the reservoir control the discharge of secretion.

The anatomical position of the dolichoderine " anal gland " opening between the 6th and 7 th abdominal tergites, justifies its homology with the pygidial gland, which is found in all ant subfamilies (JANET, 1898 ; KUGLER, 1978 ; HÖLLDOBLER, 1982, 1984 ; HÖLLDOBLER and ENGEL, 1978). Ultrastructural evidence for homology is provided by observations of the pygidial gland in some doryline and ponerine species (own unpublished data). The distinct appearance of the gland in the Dolichoderinae most probably is one of the reasons for sting reduction in this subfamily.

The Pavan's gland, on the other hand, seems restricted to Dolichoderinae and the related aneuretine species *Aneuretus simoni* (MIRADOLI ZATTI and PAVAN, 1955 ; TRANIELLO and JAYASURIYA, 1981). The initial description by PAVAN (1955) of a thin-walled sac, opening between the 6th and 7th abdominal sternites, after nearly 30 years, has to be revised with the new reports of a considerable and well-defined glandular epithelium on the 7th sternite (DAZZINI VALCURONE and FANFANI, 1982 ; FANFANI and DAZZINI VALCURONE, 1984 ; BILLEN, 1985b). The new concept of Pavan's gland, therefore comprises a secretory epithelium and a thin-walled reservoir sac. Functional evidence for this is provided by the similar positive trail-following results obtained by separate extracts of the two parts (FANFANI and DAZZINI VALCURONE, 1984). The biologically active constituent for *I. humilis* was identified as (Z)-9-hexadecenal (CAVILL *et al.*, 1979).

Ultrastructural examination reveals a highly active glandular tissue (BILLEN, 1985b). The well-developed smooth endoplasmic reticulum along with the numerous mitochondria and Golgi apparatus, are in agreement with the production of a nonproteinaceous secretion. The microvillar border and cuticular pores facilitate the transport of secretion from the glandular part to the reservoir. The latter process, according to FANFANI and DAZZINI VALCURONE (1984), should merely be affected by gravity, regarding the more ventral position of the reservoir.

Sternal glands in ants have been reported in several ponerine species, but consist of individual glandular cells that send their narrow ducts through

the intersegmental membrane (HÖLLDOBLER and ENGEL, 1978 ; JESSEN *et al.*, 1979 ; JESSEN and MASCHWITZ, 1983). A glandular epithelium on the 7th abdominal sternite has been observed in a few species of Ecitoninae, Myrmicinae and Ponerinae (HÖLLDOBLER and ENGEL, 1978), but never shows the anatomically well-defined aspect of the dolichoderine glandular epithelium. A separate reservoir sac, as described in the Dolichoderinae, is always lacking. For these reasons, the real Pavan's gland (i.e. the glandular epithelium and its reservoir), is to be considered as a peculiarity in the Dolichoderinae and the phylogenetically very related *Aneuretus*. On the other hand, the occurrence of the Pavan's gland is not an absolute condition for all Dolichoderinae. Its absence in *Tapinoma nigerrimum* and *Liometopum microcephalum* was noticed yet by MIRADOLI ZATTI and PAVAN (1957). Since the gland apparently does not occur out of the Dolichoderinae - Aneuretinae complex, however, it remains a valuable diagnostic character for both closely related groups.

ACKNOWLEDGMENTS. — I am very grateful to Prof. A. BUSCHINGER, Dr. X. ESPADALER, Dr. K. JAFFE and Dr. H. VELTHUIS for their generosity in collecting specimens for this study. Special thanks are due to E. PLAUM for the superb technical assistance and to Dr. E. EVESHAM for reading the manuscript.

References

AUBER J., 1963. — Ultrastructure de la Jonction Myo-épidermique chez les Diptères. *J. Microscopie, 2,* 325-336.

BILLEN J., 1982. — The Dufour Gland Closing Apparatus in *Formica sanguinea* Latreille (Hymenoptera, Formicidae). *Zoomorphology, 99,* 235-244.

BILLEN J., 1985a. — Comparative Ultrastructure of the Poison and Dufour Glands in Old and New World Army Ants (Hymenoptera, Formicidae). *Actes Coll. Insectes Soc., 2,* 17-26

BILLEN J., 1985b. — Ultrastructure de la Glande de Pavan chez *Dolichoderus quadripunctatus* (L.) (Hymenoptera, Formicidae). *Actes Coll. Insectes Soc., 2,* 87-95.

BILLEN J., 1986a. — Comparative Morphology and Ultrastructure of the Dufour Gland in Ants (Hymenoptera, Formicidae). *Entomol. Gener., 11,* 165-181.

BILLEN J., 1986b. — Morphology and Ultrastructure of the Dufour's and venom Gland in the Ant, *Myrmica rubra* (L.) (Hymenoptera : Formicidae). *Int. J. Ins. Morphol. Embryol., 15,* 13-25.

BLUM M.S., HERMANN H.R., 1978. — Venoms and Venom Apparatuses of the Formicidae: Dolichoderinae and Aneuretinae. In : S. Bettini (editor) : *Arthropod Venoms.* Springer, Berlin — Heidelberg — New York, p. 871-894.

CAVILL G.W.K., HOUGHTON E., 1973. — Hydrocarbon Constituents of the Argentine Ant, *Iridomyrmex humilis. Aust. J. Chem., 26,* 1131-1135.

CAVILL G.W.K., ROBERTSON P.L., DAVIES N.W., 1979. — An Argentine ant aggregation factor. *Experientia, 35,* 989-990.

DAZZINI VALCURONE M., FANFANI A., 1982. — Nuove Formazioni Glandolari del Gastro in *Dolichoderus* (*Hypoclinea*) *doriae* Em. (Formicidae, Dolichoderinae). *Pubbl. Ist. Entomol. Agr. Univ. Pavia, 19,* 1-18.

DELFINO G., MARINO PICCIOLI M.T., CALLONI C., 1983. — Ultrastructure of the Venom Glands in *Polistes gallicus* (L.) (Hymenoptera Vespidae). *Monitore zool ital. (N.S.), 17,* 263-277.

EDSON K.M., BARLIN M.R., VINSON S.B., 1982. — Venom Apparatus of Braconid Wasps : Comparative Ultrastructure of Reservoirs and Gland Filaments. *Toxicon, 20,* 553-562.

FANFANI A., DAZZINI VALCURONE M., 1984. — Nuovi Dati Relativi alla " Glandola di Pavan " in *Iridomyrmex humilis* Mayr. (Formicidae Dolichoderinae). *Pubbl. Ist. Entom. Univ. Pavia, 28,* 1-9.

HEFETZ A., ORION T., 1982. — Pheromones of Ants of Israel : I. The Alarm-Defense System of some Larger Formicinae. *Isr. J. Entomol., 16,* 87-97.

HÖLLDOBLER B., 1982. — Chemical Communication in Ants : New Exocrine Glands and Their Behavioral Function. In : M.D. Breed, C.D. Michener and H.E. Evans (Editors) : *The Biology of Social Insects.* Westview Press, Boulder Colorado, 312-317.

HÖLLDOBLER B., 1984. — A New Exocrine Gland in the Slave Raiding Ant Genus *Polyergus. Psyche, 91,* 225-235.

HÖLLDOBLER B., ENGEL H., 1978. — Tergal and Sternal Glands in Ants. *Psyche, 85,* 285-329.

JANET C., 1898. — Etudes sur les Fourmis, les Guêpes et les Abeilles. Note 17 : Système glandulaire tégumentaire de la *Myrmica rubra.* Observations diverses sur les Fourmis. Carré & Naud, Paris, 1-30.

JESSEN K., MASCHWITZ U., 1983. — Abdominaldrüsen bei *Pachycondyla tridentata* (Smith) : Formicidae, Ponerinae. *Ins. Soc., 30,* 123-133.

JESSEN K., MASCHWITZ U., HAHN M.. 1979. — Neue Abdominaldrüsen bei Ameisen. I. Ponerini (Formicidae : Ponerinae). *Zoomorphologie, 94,* 49-66.

KANWAR K.C., KANWAR U., 1975. — Fine Structure of the Venom Gland of *Vespa orientalis. Toxicon, 13,* 102-103.

KUGLER C., 1978. — Pygidial Glands in the Myrmicine Ants (Hymenoptera, Formicidae). *Ins. Soc., 25,* 267-274.

LAI-FOOK J., 1967. — The Structure of Developing Muscle Insertions in Insects. *J. Morph., 123,* 503-528.

MIRADOLI ZATTI M.A., PAVAN M., 1957. — Studi sui Formicidae. III. Nuovi Reperti dell' Organo Ventrale nei Dolichoderinae. *Boll. Soc. Ent. Ital., 87,* 84-87.

NOIROT C., QUENNEDEY A., 1974. — Fine Structure of Insect Epidermal Glands. *Ann. Rev. Entomol., 19,* 61-80.

OWEN M.D., BRIDGES A.R., 1976. — Aging in the Venom Glands of Queen and Worker Honey Bees (*Apis mellifera* L.) : Some Morphological and Chemical Observations. *Toxicon, 14,* 1-5.

PAVAN M., 1955. — Studi sui Formicidae. I. Contributo alla conoscenza degli organi gastrali dei Dolichoderinae. *Natura (Milano), 46,* 135-145.

PAVAN M., RONCHETTI G., 1955. — Studi sulla morfologia esterna e anatomia interna dell'operaia di *Iridomyrmex humilis* Mayr e ricerche chimiche e biologiche sulla iridomirmecina. *Atti Soc. It. Sc. Nat.. 94,* 379-477.

PERCY J.E., 1974. — Ultrastructure of sex-pheromone gland cells and cuticle before and during release of pheromone in female eastern spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera : Tortricidae). *Can. J. Zool., 52,* 695-705.

TRANIELLO J.F.A., JAYASURIYA A.K., 1981. — Chemical Communication in the Primitive Ant *Aneuretus simoni :* The Role of the Sternal and Pygidial Glands. *J. Chem. Ecol., 7,* 1023-1033.

TRAVE R., PAVAN M., 1956. — Veleni degli insetti. Principi estratti dalla formica *Tapinoma nigerrimum* Nyl. *La Chimica e l'Industria, 38,* 1015-1019.

WILSON E.O., PAVAN M., 1959. — Glandular Sources and Specificity of some Chemical Releasers of Social Behavior in Dolichoderine Ants. *Psyche, 66,* 70-76.