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PYGIDIAL GLANDS IN THE MYRMICINE ANTS (HYMENOPTERA, FORMICIDAE)

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SUMMARY

Fifty-two species, representing 39 genera of the ant subfamily Myrmicinae were surveyed for the presence of « pygidial glands » between the 6th and 7th abdominal terga. In 7 genera the actual glandular reservoirs were seen intact after dissection. In an additional 7 genera, reservoirs were not preserved, but pygidial sculpture suggests their presence in the living animal.

Depending on the species, the reservoirs and their orifices are paired or single. The gland cells were preserved in 2 species, and it seems to be that in both species the cells connect independently to the reservoir. Also in these 2 species, no muscle layer could be seen on the reservoir. Apparently associated with the pygidial glands is an emargination and/or sculpturation of the anterior margin of the pygidium.

There is evidence of pygidial glands scattered throughout the Myrmicinae, however they seem to be most concentrated and more likely to be especially well developed in one branch of the subfamily. Within that branch they seem most likely to occur in genera with reduced stings. Possible homology of the pygidial glands with the dolichoderine anal glands is discussed.

ZUSAMMENFASSUNG

Pygidialdrüsen myrmiciner Ameisen (Hymenoptera, Formicidae).

Einundfünzig Ameisenarten aus 39 Gattungen der Unterfamilie Myrmicinae wurden auf das Vorhandensein oder Fehlen von Pygidialdrüsen zwischen dem 6ten und 7ten abdominalen Tergit überprüft. Bei sieben Gattungen wurden nach der Präparation noch intakte Sekretbehälter gefunden, in sieben weiteren waren diese Behälter zwar nicht mehr erhalten, aber die Form des Pygidiums liess auf ihr Vorhandensein beim lebenden Tier schliessen.

Von Art zu Art verschieden finden sich paarige oder einfache Sekretbehälter, paarige Behälter besitzen paarige Mündungen. Die das Sekret abscheidenden Drüsenzellen zweier Arten waren erhalten geblieben. Soweit erkennbar, mündet jede mit einem von den anderen Zellen unabhängigen Ausführgang in den Sekretbehälter. Diese Behälter

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sind, soweit erkennbar war, nicht von einer Muskelschicht umgeben. Offenbar im Zusammenhang mit den Pygidialdrüsen stehen die beobachteten Ausbuchtungen und/oder die Skulpturen am vorderen Rand des Pygidiums.

Offenbar sind Pygidialdrüsen bei den Myrmicinae weit verbreitet. Besonders gut entwickelt sind sie jedoch in einem Zweig dieser Unterfamilie und dort bei den Gattungen, die einen reduzierten Stachel aufweisen. Die Frage nach der Homologie dieser Pygidialdrüsen mit den Analdrüsen der Dolichoderinae wird diskutiert.

INTRODUCTION

In the course of a survey of the sting apparatus morphology of the ant subfamily Myrmicinae (KUGLER, 1977), I also prepared slides of the pygidium and hypopygium of many species. My initial interest was in the potential taxonomic value of the sclerites, but late in the survey I discovered large glandular reservoirs attached to the anterior edge of the pygidium in several species. Reviewing my preparations, I found indications of the same kind of gland in other species.

Similarly situated glands, the « anal glands » described by FOREL (1878), are apparently ubiquitous in the Dolichoderinae. Within the Myrmicinae, small glandular clusters have been reported attached to the intersegmental membrane between the 6th and 7th abdominal terga in *Myrmica rubra* (JANET, 1902) and in 2 species of *Novomessor* (HÖLLDOBLER *et al.*, 1976); but in none of these species was a reservoir seen. Here, several of these « pygidial glands » that feature a reservoir are described, and a survey of the occurance of the glands within the subfamily is presented, supplementing that of HÖLLDOBLER *et al.* (1976). In addition their intra- and intersubfamilial taxonomic significance is discussed.

METHODS

Except for *Cyphomyrmex salvini*, only worker ants were examined. Nearly all specimens had previously been dried or preserved in 70 % ethanol. The dry specimens were first soaked in Barber's fluid for a day previous to dissection in order to soften the sclerites. Under 70 % ethanol each pygidium was separated from the surrounding sclerites. Then they were transferred to a 30 % lactophenol solution, heated to boiling, cooled, rinsed in 70 % ethanol, and placed in a spot of warm glycerin jelly on a microscope slide. The dissections were positioned dorsal surface up as the jelly cooled and congealed. After cooling was complete, a coverslip, its lower surface coated with warm glycerin jelly, was positioned on top of each preparation. The slides were examined with a Wild M21 phasecontrast microscope at 400X. Dissections of live individuals of *Pheidole sp.* A were not cleared with lactophenol, and some were stained with methylene blue, but otherwise were treated in the same way. Some of the preserved specimens of *Ocymyrmex* cf. *arnoldi* likewise were not treated with lactophenol in order to preserve non-chitinous tissue.

For most species, only one or two specimens were available for study, but 5 specimens of *O.* cf. *arnoldi* and many individuals of *Pheidole sp.* A were examined. For the poorly represented species, the glycerin jelly mounting technique permitted maximum examination by allowing rapid repositioning to any view.

RESULTS

Table I lists the species examined for pygidial glands in the context of the classificatory scheme of WHEELER (1922). They are divided into 3 categories; those with glands, those in which glands are indicated but not seen, and those with no indication of pygidial glands. A discussion of each category follows.

The species definitely with pygidial glands have distinct reservoirs, produced by invagination of the intersegmental membrane between abdominal tergum 6 and tergum 7 (pygidium). In addition, there is always some modification of the anterior border of the pygidium. The reservoirs are most enlarged in *Ocymyrmex* cf. *arnoldi* and *Pheidole sp.* A (*biconstricta* group).

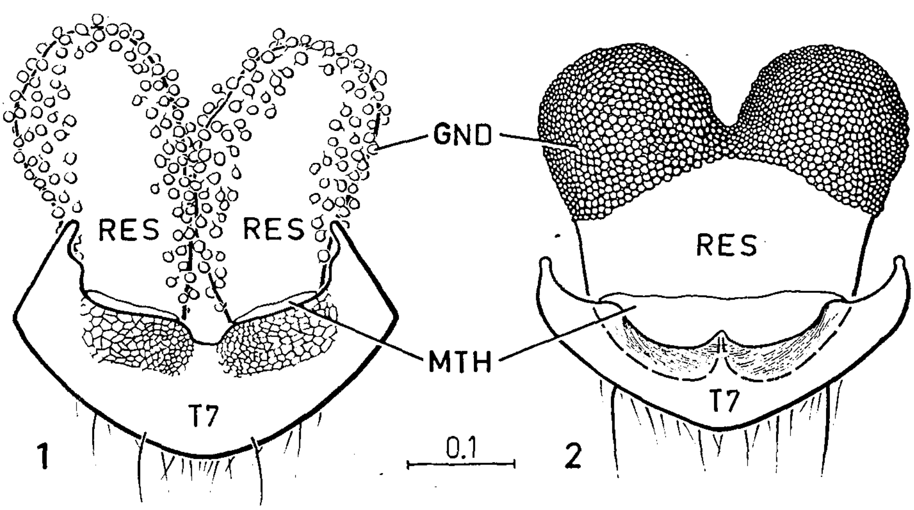

FIG. 1 and 2. — Dorsal view of the pygidium and pygidial glands of two myrmicine ants. *Fig. 1 : Ocymyrmex* cf. *arnoldi*, worker. *Fig. 2 : Pheidole sp.* A, soldier. Abbreviations : *gnd*, gland cell; *mth*, mouth of reservoir; *res*, reservoir; *T7*, tergum 7 (pygidium).

ABB. 1 und 2. — Dorsalansicht des Pygidiums und der Pygidialdrüse zweier myrmiciner Ameisen. *Abb. 1 : Ocymyrmex* cf. *arnoldi*, Arbeiterin. *Abb. 2 : Pheidole sp.* A, Soldat. Abkürzungen : *gnd*, Drüsenzelle; *mth*, Mündung des Sekretbehälters; *res*, Sekretbehälter; *T7*, Tergit 7 (Pygidium).

In *O.* cf. *arnoldi* (fig. 1) there are 2 reservoirs that empty independently onto 2 distinct, slightly concave, reticulate patches on the anterior margin of the pygidium (that part normally covered by the 6th tergum). Covering all but the upper surface of the reservoirs are many unicellular glands, each with its own ductule to the reservoir. No muscle layer was seen in any of the 3 uncleared preparations.

In *Pheidole sp.* A (fig. 2) the pygidium has a pair of notches in its anterior edge near the midline. Behind the notches is an area of fine, transverse lunate, and faintly reticulate striation. The reservoir is single, but bilobed. Its lower wall attaches to the pygidium in such a way as to make a pair of pockets underneath the notches. The mouth of the reservoir is wide, covering the distance between the lateral extremities of the pockets. I see no evidence of musculature on the reservoir. What appear to be unicellular glands densely cover the lobes of the reservoir, but no tubules could be seen between the cells and the reservoir.

Lordomyrma caledonica, Prodicroaspis sarasini, Promeranoplus sp. 2 and *Cyphoidris spinosus* all have paired reservoirs about the length of the pygidium. They attach to shallow concavities in the anterior margin of the pygidium. These depressions are lined with reticulate sculpture similar to, but weaker than, that of *O.* cf. *arnoldi* (fig. 1). In *L. caledonica* the depressions are most marked. In *C. spinosus* they are closer to the midline, and the sculpture, which is stronger than in the others, is continuous along the very anterior edge of the tergum.

Myrmecina graminicola has 2 small reservoirs, shorter than the length of the pygidium. The anterior border of the pygidium is neither notched nor concave, but it does have a single band of fine transversely lunate and faintly reticulate striae extending between the outer edges of the reservoirs. This striation is much like that of *Pheidole sp.* A (fig. 2), but stronger and continuous.

The second group of species in table I are those in which reservoirs were not definitely seen, but in which pygidial glands are indicated by the presence of the characteristic striation or reticulation at the anterior end of the pygidium (the reservoirs themselves could have been removed while separating the 6th and 7th terga). The presence of sculpture, however, does not necessarily mean the glands are present.

Promeranoplus rouxi and *Lordomyrma tortuosa* have the same kind of paired reticulate patches as described for *Promeranoplus sp.* 2 and *Lordomyrma caledonica*. *Rogeria inermis* has a similar, but smaller pair of patches, and what may be a pair of small crumpled reservoirs in my single preparation. The existence of pygidial glands in these 3 species is quite likely.

In all other species of the second category there is a single band of weak, fine sculpture. In *Veromesor andrei* it is transversely reticulate, blending into transversely striate caudad. In the rest, the striation is transversely lunate and faintly striate as in *M. graminicola*, but weaker. Additionally in *Aphaenogaster phalangium*, the anterior edge of the tergum has a pair of weak emarginations. The pygidial glands may or may not be found in these 9 species.

The final category in table I consists of those species (32) in which neither reservoirs nor any modification of the pygidium could be seen. The anterior edges of these pygidia are neither emarginate nor concave, and their dorsal surfaces are smooth. Of course the absence of pygidial modifications does not necessarily mean the glands are also absent, but it seems likely, given the descriptions above.

TABLE I. — The myrmicine ants surveyed for pygidial glands. The genera are arranged according to the here somewhat expanded classification of WHEELER (1922). Species in which the reservoirs were visible are marked ++. Those in which they were not found, but in which their presence was indicated are marked +. Those with no indication of glands are left unmarked (1).

TABELLE I. — Die auf Pygidialdrüsen hin untersuchten Ameisenarten (Myrmicinae). Die Gattungen sind nach der hier etwas erweiterten Klassifikation von WHEELER (1922) geordnet. Die Arten, bei denen Sekretbehälter sichtbar waren sind mit ++ gezeichnet. Arten, bei denen diese Behälter nicht gefunden wurden, aber verschiedene Anzeichen auf ihr Vorhandensein beim lebenden Tier deuteten, mit +. Bei Arten ohne Zeichen wurden weder Behälter, noch Hinweise darauf gefunden (1).

MYRMICINI :

Pogonomyrmex badius.
Myrmica emeryana (2).
Manica bradleyi.

PHEIDOLINI :

Stenamma diecki.
+*Aphaenogaster phalangium.*
+*Veromessor andrei.*
+*Pheidole morrisi* (major).
++*Ph.* sp. A (major, minor).

MYRMICARIINI :

+*Myrmicaria arachnoides.*
+*M. eumenoides.*
+*M. carinata.*

CREMATOGASTRINI :

Crematogaster atkinsoni.

SOLENOPSIDINI :

Vollenhovia sp. 1.
Liomyrmex cf. *aurianus.*
Megalomyrmex near incisus.
Oxyepoecus rastratus.
Chelaner sp. 1.
+*Huberia striata.*

MYRMECININI :

Podomyrma abdominalis.
+*Lordomyrma tortuosa.*
++*L. caledonica.*
++*Myrmecina graminicola.*
Acanthomyrmex cf. *notabilis.*
Pristomyrmex brevispinosus.

MERANOPLINI :

+*Promeranoplus rouxi.*
++*P.* sp. 2.
++*Prodicroaspis sarasini.*
Meranoplus sp. 1.
M. sp. 2.
Calyptomyrmex sp. 1.

LEPTOTHORACINI :

Macromischa sallei.
Leptothorax longispinosus.
L. pergandei.
« *Rogeria* » spp. (stigmatica group).
+*Rogeria inermis.*
+*Lachnomyrmex* cf. *scrobiculatus.*
Adelomyrmex near tristani.
A. sp. 2.

OCYMYRMICINI :

++*Ocymyrmex* cf. *arnoldi.*

TETRAMORIINI :

Tetramorium grassii.
Triglyphothrix lanuginosa.

CATAULACINI :

+*Cataulacus tardus.*

CEPHALOTINI :

Cephalotes atratus.
Zacryptocerus haemorrhoidalis.
Z. multispinosus biguttatus.

DACETINI :

Daceton armigerum.
Neostruma metopia.

BASICEROTINI :

Eurhopalothrix speciosa.

ATTINI :

Cyphomyrmex salvini (♀).
Mycetophylax emeryi.

UNPLACED SPECIES :

++*Cyphoidris spinosus.*

(1) Voucher specimens have been placed in the Harvard Museum of Comparative Zoology and the Cornell University Insect Collection. They bear the label « Kugler study, 1976 ».

(2) Dr. André FRANCŒUR, who is revising *Myrmica*, cautions that this determination is based on the type specimen, and differs from the present concept of this species.

DISCUSSION

Within the Myrmicinae, 2 patterns emerge from the distribution of pygidial glands. First, we see that they are widespread within the subfamily, but they appear to have their greatest concentration in a group of advanced genera that, because of a previous study (KUGLER, 1977), I believe to be related. These are : *Promeranoplus, Prodicroaspis, Lordomyrma, Aphaenogaster, Veromessor, Novomessor* (see HÖLLDOBLER *et al.*, 1976), *Pheidole, Lachnomyrmex, Cyphoidris, Cataulacus, Myrmicaria,* and *Ocymyrmex.* Their appearance in the primitive genus *Myrmica* (JANET, 1902) in an undeveloped state suggests that it is a primitive organ that has been secondarily enlarged and modified in some advanced genera, possibly for a different function.

The second pattern is that the pygidial glands, which have a defensive function in at least *Pheidole sp.* A (KUGLER, in prep.), tend to be found in those genera having reduced or modified stings. Of the species definitely possessing these glands, all have weak (less so in *Promeranoplus* and *Prodicroaspis*) and foreshortened (except in *Cyphoidris*) stings and lancets. Of the other 6 genera suspected of having the glands, only *Huberia striata* and *Rogeria inermis* may have piercing stings. If is generally true that the pygidial glands are defense glands, the pattern observed is in accord with an earlier observation that the loss of a functional (*i.e.* stinging) sting tended to promote the development of chemical defenses (KUGLER, 1977). It is noteworthy that in some groups where another strong chemical defense is housed in the gaster (*e.g. Crematogaster,* the Cephalotini, and probably *Meranoplus :* see KUGLER, 1977), highly developed pygidial glands are absent.

As mentioned earlier, the myrmicine pygidial glands bear a resemblance to the anal glands of the Dolichoderinae. They both apparently serve a defensive function, and they occupy the same position in the gaster (1). Furthermore, both in the dolichoderine species studied by FOREL (1878), and in the myrmicines described here, the reservoirs vary from paired to forked. The gland cells in at least some species of each subfamily empty directly into the reservoirs.

On the other hand, several notable differences exist in the glands of the 2 subfamilies. All known anal glands have a reservoir; the pygidial glands of some myrmicine genera do not. In the Myrmicinae, paired reservoirs lead to *paired* orifices, rather than to a common mouth as in the described dolichoderines. The reservoir mouths are wide in the Myrmicinae, and very narrow in the Dolichoderinae. The muscle layer reported for the anal gland reservoirs could not be found in the 2 myrmicine species examined in this regard. In the dolichoderines examined by Forel, the gland cells are clustered, and in some species the ductules form a pair of common ducts before entering the reservoirs. In the 2 myr-

(1) Although FOREL (1878, p. 54) said that the anal gland orifice is between the anus and pygidium, my observations on several *Dolichoderus spp.* lead me to concur with PAVAN and RONCHETTI (1955) who said that the reservoir opens between the pygidium (T7) and tergum 6.

micines illustrated here, the gland cells are not clustered, nor could common ducts be seen.

Given these comparisons, what can be said about the homology of « pygidial » and « anal » glands ? Certainly, the glandular characters considered alone indicate homology. Independent appearance of similarly functioning glands, of similar general morphology, in the same place in the body would be of singular coincidence. Furthermore, the differences listed do not rule out a common origin of the glands.

However, If the glands are indeed homologous, the dolichoderines must have arisen from the myrmicines, or more likely, a common ancestor (1). This is counter to what others have deduced. After examining the proventriculus of ants and considering larval, sting apparatus, and waist characters, BROWN (1954, and personal communication) and EISNER (1957) placed the 2 subamilies on opposite sides of a split that divides the Formicidae in half. If that view is correct, the anal and pygidial glands must have convergently evolved. The following steps in independent ancestors could have led to such convergence (discussed at greater length in KUGLER, 1977) : 1) decreased dependence on live arthropod prey for food, 2) reduction of the sting after losing its primary function of subduing prey, 3) acquisition of new (often chemical) defenses to replace the lost defensive function of the sting. This sequence, however, does not explain the similarities in the position and morphology of the glands.

Brown now entertains the possibility that *Aneuretus* (ancestral to the Dolichoderinae) « ... *might* just be closer to Myrmicinae than has been thought », and suggests that a detailed examination of the relationship of the 2 subfamilies is needed (personal communication). Part of such a study will have to reveal more of the variation in the morphology of « anal » and « pygidial » glands. Until then the question of homology remains open.

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(1) It is unlikely that the dolichoderines would have arisen from the myrmicines. That scenario would require the reversal of the waist from 2-segmented to 1-segmented, and a recovery of some elements of wing venation in the sexual forms.

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