A NEW EXOCRINE GLAND IN *NOVOMESSOR* (HYMENOPTERA: FORMICIDAE) AND ITS POSSIBLE SIGNIFICANCE AS A TAXONOMIC CHARACTER

BY BERT HÖLLDOBLER, ROBERT STANTON, AND HILTRUD ENGEL Department of Biology, Harvard University, MCZ Laboratories, Cambridge, Mass. 02138

INTRODUCTION

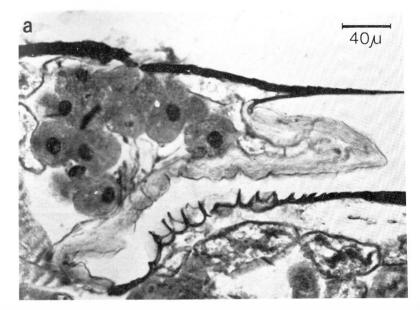
The genus *Novomessor* is comprised of only three species: *N. albisetosus*, *N. cockerelli* and *N. manni*. The first two species are rather common in the Southwestern United Staes and Northern Mexico (CREIGHTON 1950, 1955), and the latter has been collected along the Pacific coast of Mexico (KANNOWSKI 1954).

The forms of *Novomessor* were originally described as *Aphaenogaster*, and recently W. L. Brown (1974) suggested that they should be placed back in that genus. He pointed out that "the characters supposed to distinguish the two genera are not very strong when one considers the whole world fauna of this complex". Brown's arguments were especially supported by his reexamination of *Novomessor manni* Wheeler and Creighton (1934) and *Aphaenogaster ensifera* Forel (1899), which he found to be synonymous. He concluded his reasoning by stating "...the example of *A. ensifera* and *N. manni* may help to alert myrmecologists to the kind of change to be expected of a worldwide reclassification. One of the changes in status resulting from this study is of course the return of *cockerelli* and *albisetosus* to their original generic assignment in *Aphaenogaster*".

In the course of a comparative study of communication mechanisims in *Novomessor*, we discovered a new complex exocrine gland. Since this gland is a very distinct character, it should be given considerable weight in the future taxonomic assessment of the species possessing it.

MATERIAL AND METHODS

Live specimens of *N. albisetosus* and *N. cockerelli* were collected in southern Arizona near Portal. For histological investigations the



b

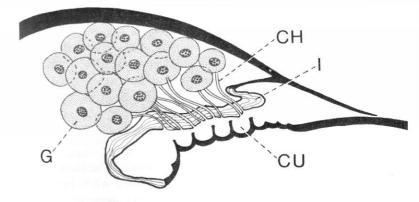


Figure 1

a) Sagittal section through the third and fourth tergite of a *N. albisetosus* worker. b) Schematic drawing of the histological section, showing the glandular cells (G), the glandular channels (CH), the cuticular cup structure (CU), and the intersegmental membrane (I) between the third and fourth segment.

^{*}Manuscript received by the editor June 15, 1976.

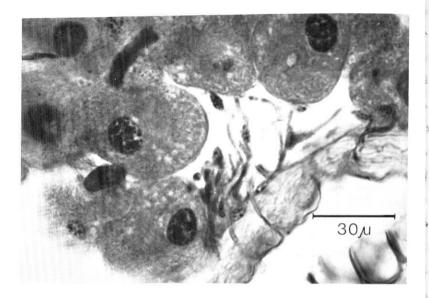


Figure 2. Sagittal section through the tergal gland complex, showing the channels that open through the intersegmental membrane.

ants were fixed in alcoholic Bouin (Dubosq Brasil), embedded in Methyl Methacrylate and sectioned 8 μ with a Jung Tetrander I microtome (RATHMAYER 1962). The staining was Azan (Heidenhain). The SEM pictures were taken with an AMR 1000 A Scanning Electron Microscope. For comparative morphological studies of cuticular surface structures we used dry specimens of the ant collection of the Museum of Comparative Zoology of Harvard University.

RESULTS

Whenever we dug up a nest of *N. albisetosus* we noticed a very repugnant odor. The same odor can be released when the gaster of a *Novomessor* worker is crushed. First we assumed that the substance originates either from the poison gland or the Dufour's gland or the hindgut, yet after all these organs were removed from the gaster the abdominal residue still exuded the odor strongly. Next we dissected segment by segment. In this way we finally determined that the odor was emanating from the third and fourth

Table 1. Species of ants which have been checked for the presence or absence of the cuticular cup structure. Except where noted, all ants that were looked at were workers.

With Structure:

Novomessor albisetosus Mayr (workers, males, and females) Novomessor cockerelli Andre (workers, males, and females) Ocymyrmex picardi Forel

Without Structure:

Aphaenogaster crocea

subsp. sicula Emery A ensifera Forel*

A. famelica F. Smith

A. flemingi M. R. Smith

A. fulva Roger

A. gibbosa Latreille

A. laevior Emery

A. lamellidens Mayr

A. longiceps F. Smith

A. loriae Emery

A. mariae Forel

A. miamiana Wheeler

A. obsidiana var. epirotes Emery

A. osimensis

Aphaenogaster pallida subsp. finzii Muller

A. phalangium Emery

A. poultoni Crawley

A. praedo Emery

A. pythia Forel

A. rudis Emery

A. sagei Forel

A. sardoa Mayr

A. spinosa Emery

A. splendida Roger

A. subterranea Latreille

A. swammerdami Forel

A. texana Emery

A. tennesseensis Mayr

A. testaceopilosa Lucas

Aphaenogaster tipuna Foral

A. treatae Forel

A. uinta Wheeler

A. weigoldi Viehmeyer

Stenamma brevicorne Mayr

S. diecki Emery

S. manni Wheeler

S. schmittii Wheeler Pheidole dentata Mayr

P. (Ischnomyrmex) longipes F. Smith

Tetramorium sericeiventre Emery

Ocymyrmex weitzeckeri Emery

O. weitzeckeri var. arnoldi Forel

Cataglyphis albicans var. cubica Forel

Cataglyphis bicolor Fabricius

C. viatica Fabricius

Messor aciculatus Smith

M. aegyptiacus Emery

M. barbarus Linne

M. capitata Latreille
M. luebberti Forel

M. meridionalis André

M. sanctus Forel

M. striaticeps André

M. barbarus structor Latreille

Veromessor andrei Mayr

V. lariversi M. R. Smith

V. pergandei Mayr

^{*}Brown (1974) has shown that *Novomessor manni* Wheeler & Creighton is a synonym of this species.

tergal segment. From these results we hypothesized that a gland might exist between the third and fourth tergite, and which anparently cannot be spotted under a dissecting microscope. We therefore conducted a series of histological investigations which finally confirmed our suspicion. Workers of N. albisetosus and N. cockerelli possess two large glandular complexes, located bilaterally under the third tergite (Fig. 1). One complex consists of approximately 50 single glandular cells, each of which sends an individual channel through the intersegmental membrane between the third and fourth tergite (Fig. 2). The external openings of these channels are closely associated with a series of cuticular "cups", which are located at the apical end of the dorsal surface of the fourth segment. Under the dissecting microscope the arrangement of the series of cups looks like a netlike structure, but the SEM pictures clearly reveal the hexagonal shape of the individual cups which are arranged like the cells of a honeybee comb (Fig. 3). Normally this part of the fourth tergite is tightly overlapped by the third tergite, and only by pulling the segments apart is the structure exposed. We assume that the cups serve as repositories for the glandular secretions. When the substance is needed the ant exposes this area and the chemical evaporates. Indeed, the odor can be released simply by pulling the third and fourth tergite slightly apart. These tergal glands with the associated cuticular cup structure are found not only in the worker caste but also in queens and males (Fig. 4). In addition males of N. albisetosus and N. cockerelli were found to possess a similar glandular complex located bilaterally under the fourth tergite. The glandular channels open through the intersegmental membrane between the fourth and fifth segment. The cuticular cup structure at the fifth segment is, however, much less conspicuous than that at the fourth segment.*

In general, there appear to be no distinct differences in the tergal glands and the cup structures of N. albisetosus as opposed to N. cockerelli. Although we did not have fixed specimens of A. ensifera (=N. manni), the investigation of dried specimens in the systematic collection of the Museum of Comparative Zoology revealed that the

cup structure is missing in this species. Furthermore we surveyed 32 species of *Aphaenogaster* and 4 species of *Stenamma*, and in none of them could we find the cup structure (Tab. 1). An additional histological study of two *Aphaenogaster* species (*A. texana, A. rudis*) confirmed the absence of the tergal glands. It thus seems reasonable to suppose that the absence of the cup structure also indicates the absence of the tergal glands.

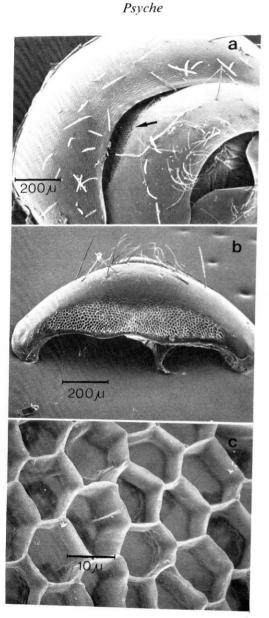
Although none of the investigated forms of Aphaenogaster and Stenamma possess the cup structure, we found a very similar cuticular structure in Ocymyrmex picardi (tribe Ocymyrmecini). This came as a surprise, because the species is taxonomically not at all close to Novomessor. In Ocymyrmex the structure is also located on the dorsal surface of the fourth tergite (Fig. 5).

The "cups" do not have the same approximate hexagonal shape and they appear to be not as deep as those of *Novomessor*. Since we could not obtain fixed specimens, we are unable to say if the structure is also associated with tergal glands.

DISCUSSION

With the possible exception of Ocymyrmex picardi, where a similar net-like structure was found at the fourth tergite, the newly discovered exocrine tergal glands seem to be restricted to the two species Novomessor albisetosus and N. cockerelli. They are absent in A. ensifera (= N. manni) and in all other investigated species of Aphaenogaster. Our findings seem therefore to support Brown's contention that N. manni should be reclassified as a species of Aphaenogaster. On the other hand, the existence of a large and rather complex exocrine gland associated with a particular cuticular structure in N. albisetosus and N. cockerelli (the type species of Novomessor) may argue against the assignment of the genus Novomessor to the synonymy of Aphaenogaster. It is clear that the repugnant odor, released by disturbed ants of N. albisetosus, originates from these tergal glands. We believe that the secretion's function is defense, although our experiments have not yet identified the kind of enemies against which the substance is directed. Only little is known about the natural product chemistry of Novomessor. Vick et al. (1969) found a series of hydrocarbons in Novomessor cockerelli, but they did not attempt to identify the glandular source of these substances. However, they discuss rather vaguely the discovery of new abdominal glands: "A very large

^{*}Another, previously undescribed exocrine glandular complex was found in workers and queens of N. albisetosus and N. cockerelli ventrally at the fourth segment. The glandular channels open through the membrane near the cloaca. We are currently investigating the function of this gland.



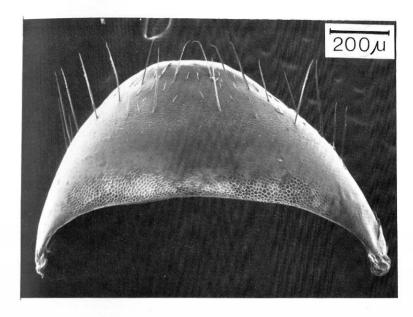


Figure 4. The SEM picture of the fourth tergite of a male of N. albisetosus.

glandlike structure, which we call the 'dorsal gland', occupied the dorsal part of the gaster above the digestive tract. It varied in size, but often it extended from the posterior to the anterior end of the gaster and from side to side. It was composed of countless small round yellow globules apparently connected by what may be glandular tissue". But then they write: "It is possible that what appeared to be glandular tissue was not that and the dorsal gland might be some type of fat body arrangement". Our histological investigation did not reveal any glandular type which would fit the description of the 'dorsal glands'. We believe that Vick *et al.* have indeed described the fat body tissue, but then it is hard to understand how the fat body can be mistaken for a new 'dorsal gland'.

Figure 3 (opposite)

a) SEM picture of the gaster of a *N. albisetosus* worker. The third tergite is slightly lifted and the net-like cup structure can be seen on the surface of the fourth tergite.

b) Separated fourth tergite with the cup structure fully exposed.

c) The SEM close up picture shows clearly the hexagonal cups.

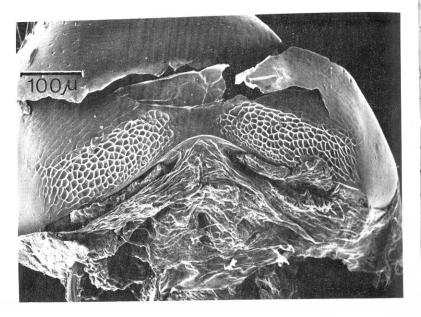


Figure 5. SEM picture of a dried specimen of a Ocymyrmex picardi worker showing the net-like cup structure.

Even more confusing is the description of additional 'anal glands'. Vick et al. write: "In addition, there were several glands or reservoirs which we call the 'anal glands', that opened dorsally near or into the cloacal opening. Each of these glands was composed of a few linearly arranged globules that became progressively smaller distally from their attachment near the anus. No other glandular tissue was seen attached to them and distally they seemed to float free in the haemolyph". This description does not at all fit the glandular complex we discovered ventrally at the last abdominal segment, but it is a rather accurate description of the ovaries.

ACKNOWLEDGEMENTS

We would like to thank Mr. Ed Seling for his superb assistance during the SEM work. Dr. Barry Bolton (British Museum of Natural History, London) offered very valuable advice and suggested that we check *Ocymyrmex picardi*. This work was supported by the NSF grants BMS 75-06447 and BMS-7412494.

REFERENCES

BROWN, W. L.

1974. Novomessor manni a synonym of Aphaenogaster ensifera (Hymenoptera: Formicidae). Ent. News, 85: 45-53.

CREIGHTON, W. S.

1950. The ants of North America. Bull. Mus. Comp. Zool. Harv. 104:1-585, 57 pl.

1955. Studies on the distribution of the genus *Novomessor* (Hymenoptera: Formicidae). Psyche, Cambridge, Mass. **62**: 89-97.

FOREL, A.

1899. Insecta. Hymenoptera (Formicidae). Biologia Centrali-Americana 3: 1-160, 4 pl.

KANNOWSKI, P. B.

1954. Notes on the ant *Novomessor manni* (Wheeler and Creighton). Occas. Pap. Mus. Zool. Univ. Michigan 556: 1-6.

RATHMAYER, W.

1962. Methylmethacrylat als Einbettungsmedium für Insekten. Experientia 18: 47.

VICK, K., DREW, W. A., McGurk, D. J., EISENBRAUN, E. J. AND WALLER, G. R. 1969. Identification of Hydrocarbons from *Novomessor cockerelli*. Ann. of

1969. Identification of Hydrocarbons from *Novomessor cockeretti*. Ann. o the Entomol. Soc. of America **62**(4); 723-725.

WHEELER, W. M. AND CREIGHTON, W. S.

1934. A study of the ant genera Novomessor and Veromessor. Proc. Amer. Acad. Arts. Sci., Boston, 69: 341-387.