

Insectes Sociaux, Paris.
1975, Tome 22, n° 4, pp. 405-414.

**FEMALES OF *FORMICA RUF*A L. (HYM., FORMICIDAE)
WITH ENLARGED LABIAL GLANDS (*)**

By E. T. G. ELTON

*Research Institute for Nature Management, Kemperbergerweg 11,
Arnhem, The Netherlands.*

Reçu le 7 avril 1975.

Accepté le 26 septembre 1975.

SUMMARY

Females with enlarged labial glands were found in two colonies of the polygynous form of *Formica rufa* L. They were distinguishable from normal females by more or less extensive brown patches on otherwise black scutums, and by slightly enlarged pronotums. They mated in the ordinary way; afterwards they were found to have their spermathecas full of living sperm and later produced normal workers and workers with enlarged labial glands (Wasmann's « pseudogynes », Novak's « secretergates »). There were indications that the power of flight, if any, was poorer than that of normal females.

ZUSAMMENFASSUNG

**Weibchen von *Formica rufa* L. (Hym., Formicidae)
mit vergrößerten Labialdrüsen.**

In zwei Kolonien der polygynen Form von *Formica rufa* L. wurden Weibchen mit vergrößerten Labialdrüsen gefunden. Sie unterschieden sich von normalen Weibchen durch braune Flecken auf dem schwarzen Scutum und ein etwas vergrößertes und abnormal gewölbtes Pronotum. Die Paarung dieser Weibchen verlief normal, danach wurde festgestellt daß die Spermatheca mit lebendem Sperma gefüllt war. Ihre Nachkommenschaft bestand aus normalen Arbeiterinnen und Arbeiterinnen mit vergrößerten Labialdrüsen (Wasmanns « Pseudogynen », Novaks « Secretergaten »). Es gab Hinweise daß, wenn sie überhaupt über Flugvermögen verfügen, dieses geringer ist als das der normalen Weibchen.

(*) R.I.N. Communication 133.

INTRODUCTION

The existence of females with enlarged labial glands was first presumed by NOVAK (1948) after he had actually found this disorder in certain worker-like ants, hitherto known as « pseudogynes ». The latter term was coined by WASMANN (1895) and reflects their resemblance to females because of the enlarged thoraces. Pseudogynes have been found in several *Formica* species. In those belonging to the *Formica rufa* group their resemblance to females is often enhanced by the pigmentation of parts of the thorax and a slight depression in the enlarged mesonotum, suggesting a division into scutum and scutellum (WASMANN, 1895; RONCHETTI, 1961). WASMANN later made an extensive study of the pseudogynes of *Formica (Raptiformica) sanguinea* Latr. and distinguished several varieties (1909). It is clear from his writings (1895, 1909; 1915) that he regarded them all as intercastes between workers and females.

NOVAK (1948), however, showed that the most common varieties of pseudogynes of *F. sanguinea* are in any case true worker ants, but with the thoraces distended as a result of the swelling of the labial glands. The labial glands swell in the pupal stage, before the cuticle hardens. He thought that males and females might have the same disorder. A study of the detailed descriptions by WASMANN not only of the less common kinds of his pseudogynes, but also of other aberrations, led Novak to believe that Wasmann's « gynecoid macropseudogynes » and « macronote brachypterogynes » were females with hypertrophied labial glands. As the names indicate the former was included under the heading « pseudogynes » whereas the latter was not. If Novak's presumptions were true, this would be inconsistent, also because the « gynecoid macropseudogynes » would be real « gynes », not « pseudogynes ». He therefore proposed a new set of names, « secretogynes », « secretaners » and « secretergates » for females, males and workers with enlarged labial glands, and the general term « secretoforms ». These terms are analogous to Wheeler's (1926) « mermithergates », « phthisogynes », etc., and are used in this paper. NOVAK also gave names to the known and presumed varieties within the main categories of secretergates and secretogynes. We are not concerned with the varieties of secretergates and those of the secretogynes are only mentioned in passing in section I.

Novak's presumptions regarding the existence of secretogynes and secretaners were confirmed by BAUSENWEIN (1960), who found them in polygynous « wood ants », probably either *Formica polyctena* Foerst. or the polygynous form of *F. rufa* L. BAUSENWEIN, however, stated that the thoraces had not undergone any external change. It is now safe to state that secretogynes occur in the polygynous form of *Formica rufa* L. 1761 nec 1758 (YARROW, 1954, 1955; see also BETREM, 1960) and that they may be distinguished from normal females by certain external thoracic peculiarities, at all events in the specimens so far examined. I first saw aberrant females, later shown to be secretogynes of this

species, on the single nest of an artificially founded colony (No. U 111 in the records of this Institute) during the swarming period in 1971. The proportion to normal females was about 1 to 2. No further attention could be paid to the matter at the time.

The colony had become much smaller by 1974 and only a few winged sexuals were seen during the swarming period. One of the 3 or 4 females was of the aberrant type. Another colony (No. U 119), however, also of the polygynous form of *F. rufa* and, like U 111 founded artificially in 1960, produced greater numbers of females having the same aberrations. This study is mainly based on specimens from and observations at this colony.

It was frequently visited in May and June 1974. The swarming period appeared to last from 9 May or possibly a few days earlier, till 6 June, when the last winged specimen, a male, was seen on the nest. Both sexes were present during the entire period but the proportion of females increased in the course of time. Males and females were only seen on the surface of the nest in the morning. They were more numerous when the weather was fine, but the numbers always started to decrease between 9 a.m. and 10 a.m. All of them had disappeared by about 10.30 a.m. There was no difference between aberrant and normal females in this respect. All the winged females seen on the surface during the first 8 days of the swarming period, 157 in all, were collected; 70 of them, or nearly 45 %, were of the aberrant type, i.e. secretogynes. Some more aberrant and normal females were taken later, but not all the ones that appeared on the surface.

I. — EXTERNAL CHARACTERISTICS AND STATE OF THE LABIAL GLANDS

The aberrant females had cloudy brown patches of varying sizes on their otherwise black scutums (compare fig. 1 *a* with fig. 1 *b*). In 75 specimens the extent of these lighter areas ranged from two small faint spots to the whole surface of the scutum, except for a few darker marks here and there. Another respect in which they differed from normal females was that they had slightly but distinctly enlarged and bulging pronotums, which, when viewed in profile, were seen to have a sharp bend in the upper part, near the suture with the scutum (compare fig. 1 *c* with fig. 1 *d*). Occasionally, the pronotum, too, had a somewhat mottled appearance instead of the usual darker zone along the edge bordering the scutum.

The wings were not smaller or otherwise different from those of normal females, so these secretogynes do not come under either of the two varieties distinguished by Novak : the brachypteroid and micropteroid secretogynes (i.e. Wasmann's macronote brachypterogynes and gynecoid macropseudogynes, see Introduction). It remains to be seen, however, whether we now have three varieties, for it has not yet been proved that the short-winged forms meant by Novak actually have swollen labial glands. If they do not, they cannot be

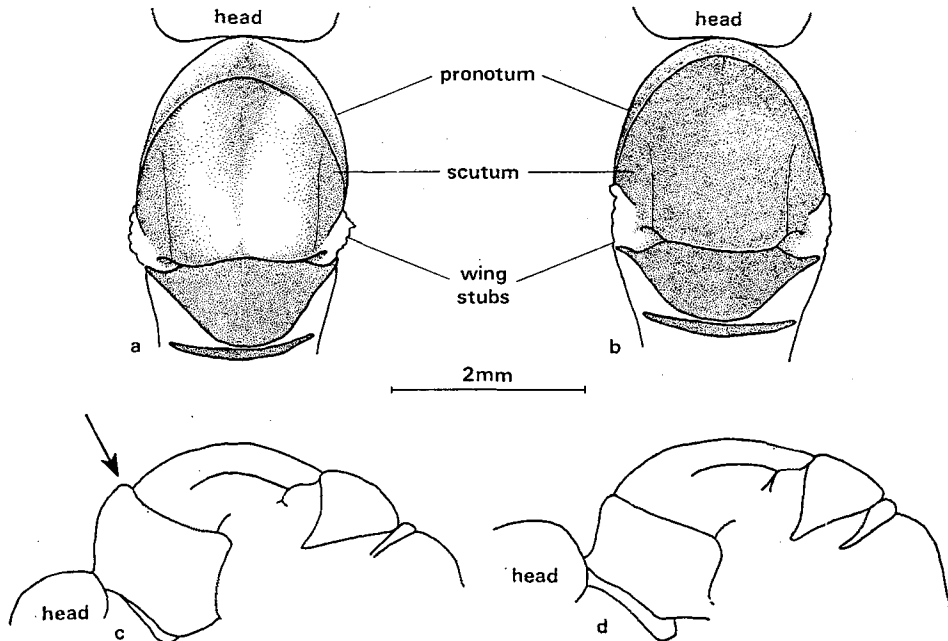


FIG. 1. — *a*) Dorsal view of thorax of secretogyne, showing lighter patches on scutum. *b*) Dorsal view of thorax of normal female. *c*) Profile of thorax of same secretogyne as in *a*. Note sharp bend in upper part of pronotum. *d*) Profile of thorax of same normal female as in *b*.

All drawings were made to the same scale with a Camera Lucida.

FIG. 1. — *a*) Dorsalansicht des Thorax einer Secretogyne, mit den helleren Flecken auf dem Scutum. *b*) Dorsalansicht des Thorax eines normalen Weibchens. *c*) Thorax der Secretogyne unter *a* im Profil. Man beachte das starke Hervortreten des oberen Teiles des Pronotums. *d*) Thorax des normalen Weibchens unter *b* im Profil.

Alle Zeichnungen wurden mittels einer Camera Lucida in demselben Maßstab hergestellt.

regarded as secretogynes and the form with the normal wings would be the only one in the category known as secretogynes. (It is not known whether Bausenwein's secretogynes had normal wings, for he did not comment on the wings of his specimens.)

The state of the labial glands was ascertained by dissecting freshly killed specimens. They were all winged and had been taken from the surface of the nest. 13 aberrant females from colony U 119, taken between 9 and 27 May 1974, had extremely swollen labial glands; especially the reservoirs were greatly enlarged (fig. 2 *a*). These glands were also greatly enlarged in the only aberrant specimen from colony U 111, taken 5 June 1974. On the other hand, 16 externally normal females from U 119, also taken between 9 and 27 May, had normal labial glands (fig. 2 *b*). It is therefore assumed that all the females with black and brown mottled scutums and enlarged pronotums were secretogynes, but that all the externally normal females were not.

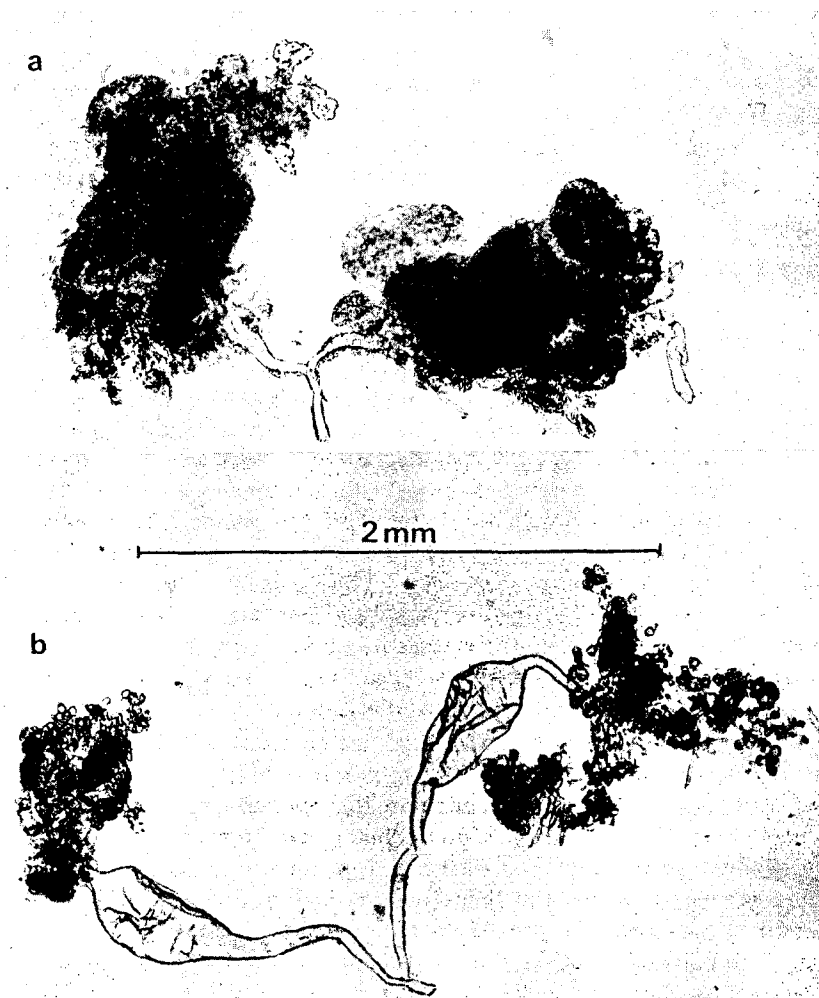


FIG. 2. — Labial glands of *a)* secretogyne, *b)* normal female, magnification identical. In *b*, the tubuli of the glands proper, to the extreme left and right, are obscured by pieces of other tissue.

FIG. 2. — Labialdrüsen *a)* einer Secretogyne, *b)* eines normalen Weibchens, bei gleicher Vergrößerung wie *a*. In *b* sind die Tubuli der eigentlichen Drüsen ganz links und ganz rechts von anderen Geweben verdeckt.

It should be noted that colony U 111 was known to have contained secretergates (Wasmann's « pseudogynes »), i.e. workers with the same disorder as the secretogynes, ever since 1968 and possibly earlier. In U 119 they were first noticed in March 1974, but may have been present in previous years. That they were not only secretergates according to their external characteristics, but actually had swollen labial glands was proved by dissecting an individual from

each colony. A certain proportion of the males may also have had diseased labial glands, but this was not verified.

The glands or rather the reservoirs of the glands of all the secretogynes examined, were enlarged to approximately the same extreme degree, forming white opaque masses which occupied much of the thoraces. They were easy to find among the internal organs of the thorax; whereas the normal glands with their small, membranous, transparent reservoirs were not. No transitions were observed between extremely swollen and normal glands. Transitions do exist, however. They were found by RONCHETTI (1961), though not in secretogynes but in secretergates, and in one of the other species of the *F. rufa* group. He published a series of drawings in which the slightly diseased glands shown only have small, irregular swollen patches on the reservoirs. The patches are larger in each successive drawing and in the last drawing the reservoirs as a whole are greatly enlarged and deformed. In all the drawings the glands proper — bundles of small tubes — have retained their normal size and shape, but in the last one the tubes connecting them with the reservoirs are also affected and form a single swollen mass with the latter. All the glands I examined were in this state, with the possible exception of the tubuli of the glands proper. I could not identify the latter with any certainty. They may have been torn off during dissection and lost sight of. Or they may have become swollen themselves and become partly embodied in a single irregular mass with the other parts of the glands. The latter seems more likely. In the latter event the more slender projections in figure 2a could be the swollen tubuli.

The 13 aberrant females from U 119 whose labial glands were examined, were selected from 75 such specimens and they included two with the smallest and faintest brown spots on the scutum that could be found. When examined superficially, the latter might be mistaken for normal females; in fact secretogynes might exist in which the lighter marks are entirely absent. Moreover, a female which on dissection proved to be quite normal also had an extremely small and faint brown spot on the right-hand side of the scutum. The colour of the scutum is, therefore, not an entirely reliable touchstone for secretogynes. This might also be true of the size and consequently the shape of the pronotum, although in the material available there was a distinct gap between the size ranges of the pronotums of secretogynes and those of normal females. Among 89 apparently normal females only 2 were found with a faint suggestion of pronotal enlargement — one of them on the right-hand side only. They both indeed turned out to have normal labial glands. (They were not among the 16 referred to above.)

A clear distinction could be made throughout the material available between secretogynes and normal females with the aid of the two external characteristics. If, on the other hand, individuals were to be encountered with black or nearly black scutums, and pronotums intermediate in size between the ranges mentioned above, it might be impossible to decide one way or another without examining the glands themselves.

II. — MATING, DEALATION AND REPRODUCTION

Most of the males on the surface of the nest did not take any notice of the females they met, not even when walking over them. Some, however, tried to mate with any female they encountered, though *not* with workers or other males, as those of the closely allied species *Formica polyctena* Foerst. frequently try to do. Most of the females refused to mate, turning the tips of their gasters away from those of the males and running about frantically until the males let go. In a few cases, however, copulation actually took place, with both normal females and secretogynes. Most of the females known to have mated were captured for examination of the spermathecas.

Among them were 8 secretogynes, 5 with the spermatheca full of living sperm, 3 with the spermatheca empty (7 of the 8 specimens belonged to the 13 aberrant females of U 119 seen on dissection to have hypertrophied labial glands). Of the 10 normal females known to have mated, 5 had full spermathecas; in 3 they were only partly filled and in the remaining 2 they were empty. (3 of the specimens with full spermathecas were from the group of 16 externally normal females seen on dissection to have normal labial glands.)

The instances of empty or only partly filled spermathecas may have been due to disturbance during the process of mating, for the mating females, with the males attached, were lifted from the nest with a pair of tweezers and put in a wide collecting tube. Although this was done as carefully as possible and copulation continued in the tube for from 1/2 to 2 minutes, it was later thought better to leave them undisturbed on the nest until they separated. Some of the females were lost sight of after separating because they mingled with the unmated females, but 2 secretogynes and 1 normal female were captured. All three had full spermathecas, and are included in the figures for full spermathecas given above. Undisturbed copulation with one of the secretogynes lasted a little over 3 minutes; with the normal female it lasted a little over 5 minutes.

Four mated secretogynes were kept with workers in separate artificial nests in which the ants had the choice of compartments with different constant temperatures, ranging from 24-27 °C. Two died, one after 53 and one after 54 days, without having laid any eggs. One of them had an unmistakably diseased ileum and rectum, for both were hard and swollen and there was a brown spot on the wall of the ileum; but the spermatheca contained living sperm. The other was too decayed to allow any conclusions to be reached regarding the state of the internal organs; the spermatheca, however, was much less affected and contained spermatozoa which still made weak undulating movements. In these two specimens, therefore, failure to lay eggs was not due to absence of sperm. The two remaining secretogynes produced normal workers and secretergates, which implies that they had laid fertilized eggs and that their offspring were viable.

Two dealated secretogynes found on the surface of the nest in the swarming period were also kept with workers in artificial nests. One did not lay any

eggs in the following 5 months, and the experiment was discontinued. (The presence of sperm was not ascertained in this case.) The other produced normal workers and secretergates, which implies that she had mated, had laid fertilized eggs and produced viable offspring.

All these observations show that the sexual functions of at least some, and probably all secretogynes are not impaired by the labial gland disorder.

The presence of secretergates among the offspring of secretogynes poses several questions. Those involved in the transmission of the disorder will be dealt with in a subsequent paper; in anticipation of the latter it may be stated that transmission is not genetic, but in many respects resembles that of infectious diseases. Other relevant questions are being studied and I hope to report on them in due course.

Two of the four secretogynes kept in artificial nests from the day they mated lost their wings, one after 11 and one after 15 days; one retained 3 of its wings until it died 53 days later, and the fourth retained its wings throughout the experiment, which lasted 161 days. In the two latter cases the tips of the wings had worn down within the first few weeks after mating. All these specimens had sperm in their spermathecas, as was evident either from direct observation after dissection, or from the fact that they produced worker ants.

The retention of wings for more than a few hours or days after mating is unusual, and the question arises as to whether in these cases it was due to the swelling of the labial glands, or alternatively to the conditions of captivity. It should be noted that I found several queens with one or more wings in winter in field nests of polygynous *F. rufa*, and that at least 3 of them had sperm in their spermathecas, which implies that they had mated and had retained their wings since the swarming period of the previous spring or earlier. These 3 specimens also came from a colony which was found (although 10 years later) to be free of the labial gland disorder. COLLINGWOOD (personal communication, 1958), too, found females with worn down wings in *F. rufa* nests outside the swarming season in England. Had the females in all such cases been of the aberrant type, this would almost certainly have been noticed. The evidence available, therefore, seems to indicate that the tendency to retain wings after mating is already present to some extent in normal females of polygynous *F. rufa*. On the other hand, the tendency may be enhanced either by the swelling of the labial glands, or by the conditions of captivity.

III. — POWER OF FLIGHT

Neither normal females nor secretogynes were ever seen taking off from the surface of the nest (U 119), whereas males were frequently seen to do so.

Normal females and secretogynes did occasionally walk off the nest and were seen wandering around the base of the mound. Whether any of them left

the nest permanently is not known. They were not seen climbing about in the vegetation near the nest and attempting to take off from there, as other wood ant species are seen to do. Yet the wings, not only of the normal females, but also of the secretogynes, seemed quite normal, and the normal females, when placed under a source of radiant heat in the laboratory were seen to make short flights.

An experiment was therefore set up in which an artificial nest containing 41 secretogynes, 23 normal females, a few males and many workers was connected with a circular arena. The latter had a diameter of 40 cm and a wall 7 cm high, which, having been treated with « Fluon » (HOLLEMAN and ELTON, 1965) was an impassable barrier to non-flying ants. A lamp emitting a high proportion of heat rays (a 250 watt Philips « Infra Red Reflector Lamp ») was hung over the arena. In the following few days the lamp was switched on occasionally for periods of 10 to 30 minutes and the ants observed. After a short while most of the males and females were running about in the arena and some made short flights. Eight females were captured immediately after landing, i.e. before being lost sight of among the others. Six of them had flown 10 to 30 cm within the arena, 2 had flown over the wall and for distances of about 80 cm, towards the window. None of them were secretogynes; they were normal, according to their external characteristics, and on dissection were seen to have normal labial glands. (They belonged to the group of 16 normal females referred to in section I). This evidence is not conclusive, but it strongly suggests that the power of flight of the secretogynes, if any, was poorer than that of the normal females.

Whether the flight muscles were affected by the swelling of the labial glands was not investigated. BAUSENWEIN (1960) states that the flight muscles of secretogynes were pushed away dorsally and showed « fatty degeneration ». It may be inferred from his text, however, that the specimens concerned were in an « advanced imaginal stage » (p. 46) so that it is not certain that this state of the flight muscles already existed in the young, swarming females.

The ability to walk was not affected by the condition of the labial glands, for secretogynes ran about as quickly and energetically as normal females.

ACKNOWLEDGEMENTS. — I am indebted to Mr. G. J. S. M. HEIJMANS for showing me useful dissection techniques, to Mr. J. H. de GUNST for making the photographs of figure 2, and to Mr. J. BROTHERHOOD for checking the text.

REFERENCES

- BAUSENWEIN (F.), 1960. — Untersuchungen über sekretorische Drüsen des Kopf- und Brustabschnittes in der *Formica rufa*-Gruppe. *Cas. čsl. Spol. ent.* (Acta soc. ent. čsl.), 57, 31-57.
- BETREM (J. G.), 1960. — Ueber die Systematik der *Formica rufa*-Gruppe. *Tijdschr. Ent.*, 103, 51-81.
- HOLLEMAN (H. C.) and ELTON (E. T. G.), 1965. — Fluon barriers for confining non-flying insects in open containers. *Ent. Ber.*, 25, 178-180.

- NOVÁK (V.), 1948. — Příspěvek k otázce vzniku patologických jedinců (pseudogyn) u mravenců z rodu *Formica* (Předběžné sdělení). On the question of the origin of pathological creatures (pseudogynes) in ants of the genus *Formica* (preliminary communication). *Věst. čsl. zool. Spol.* (Acta Soc. Zool. Cech.), 12, 97-131.
- RONCHETTI (G.), 1961. — Secretergati in Popolazioni di Formiche del gruppo *Formica rufa*. *Collana Verde*, 7, 61-74.
- WASMANN (E.), 1895. — Die ergatogynen Formen bei den Ameisen und ihre Erklärung. *Biol. Zbl.*, 15, 606-622, 625-646. — 1909. Zur Kenntnis der Ameisen und Ameisengäste von Luxemburg. III Teil, *Archs Inst. gr.-duc. Luxemb.*, 4, 1-114. — 1915. Neue Beiträge zur Biologie von *Lomechusa* und *Atemeles*. *Z. wiss. Zool.*, 114, 233-402.
- WHEELER (W. M.), 1926. — Ants. Their structure, development and behaviour. *Columbia Univ. Press*, New York, xxv+663 p.
- YARROW (I. H. H.), 1954. — Application for the re-examination and re-phrasing of the decision taken by the International Commission regarding the name of the type species of « *Formica* » Linnaeus, 1758 (Class Insecta, Order Hymenoptera). *Bull. Zool. Nom.*, 9, 313-317. — 1955. The British ants allied to *Formica rufa* L. (Hym., Formicidae). *Trans. Soc. Br. Ent.*, 12, 1-48.
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