DEEL 106 AFLEVERING 9 1963

TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

INHOUD:
Titelpagina en register van deel 106

Tijdschrift voor Entomologie, deel 106, afl. 9. Gepubliceerd 2-XII-1963

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DEEL 106 1963

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UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

Tijdschrift voor Entomologie, deel 106, 1963

Aflevering	1	verscheen	1	mei	1963
Afleveringen	2—5	verschenen	15	mei	1963
Aflevering	6	verscheen	13	augustus	1963
Aflevering	7	verscheen	16	september	1963
Afleveringen	8—9	verschenen	2	december	1963

REGISTER VAN DEEL 106

* Eén sterretje duidt een naam aan nieuw voor de wetenschap
* An asterisc denotes a name new to science
** Twee sterretjes geven aan een soort of vorm nieuw voor de Nederlandse fauna
** Two asteriscs denote a species or form new to the Netherlands fauna

The names of genera and species of the following groups which are listed at the end of the respective papers, are not repeated in the present index. For these lists the reader is referred to the following pages of the present volume:
Agaonidae (Hymenoptera), p. 109
Their fig hosts (*Ficus* species, Plantae), p. 110
Myriopoda, p. 205
Bactra species, etc. (Lepidoptera, Tortricidae), p. 356.

INHOUD VAN DEEL 106

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De *Entomologische Berichten* worden eveneens door de Nederlandsche Entomologische Vereeniging uitgegeven en zijn bestemd voor de publicatie van kortere artikelen, van faunistische notities etc., alsmede van de Verslagen der Vergaderingen en van mededelingen van het Bestuur. Zij verschijnen twaalf maal per jaar in een aflevering van 16 of meer bladzijden. Deze 12 afleveringen vormen samen een deel.

TRICHOPTERORUM CATALOGUS

Ook de *Trichopterorum Catalogus* van F. C. J. Fischer wordt door de Nederlandsche Entomologische Vereeniging voor rekening van de auteur uitgegeven. De eerste vier delen verschenen in 1960, 1961, 1962 en 1963. Er zullen nog elf delen volgen, in totaal worden het er 15. Alle bekende recente en fossiele soorten van de gehele wereld met hun synoniemen worden er in behandeld. Van alle genera worden de type-soorten aangewezen en de literatuur zal van 1758 tot eind 1960 met de geografische verspreiding vermeld worden. Delen I en II kosten f 39,— per stuk, delen III en IV f 45,—. Van alle delen zijn ook éénzijdig bedrukte exemplaren beschikbaar. De prijsverhoging hiervoor bedraagt f 2,50.

Alle zakelijke correspondentie betreffende de Vereeniging te richten aan de Secretaris, W. Hellinga, Weesperzijde 23II, Amsterdam-O.

Alle correspondentie over de redactie van het Tijdschrift voor Entomologie te richten aan de Hoofdredacteur, Dr. A. Diakonoff, Rijksmuseum van Natuurlijke Historie, Leiden.

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Alle betalingen te richten aan de Penningmeester, Drs. H. Wiering, Doorntjes 29, Bergen (N.H.), postgiro 188130, ten name van de Nederlandsche Entomologische Vereeniging te Bergen (N.H.).

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Names of genera and lower systematic categories, new terms and the like are to be underlined by the author in the manuscript by a single straight line. Any other directions as to size or style of the type are given by the editors, not by the author. Italic type or spacing to stress ordinary words or sentences is to be avoided. Dates should be spelled as follows: either "10.V.1948" or "10 May, 1948". Other use of latin numerals should be avoided, as well as abbreviations in the text, save those generally accepted. Numbers from one to ten occurring in the text should be written in full, one, two, three, etc. Titles must be kept short. Footnotes should be kept at a minimum.

Authors will be charged with costs of extra corrections caused by their changing of the text in the proofs.

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Mosely, M. E., 1932. "A revision of the European species of the genus *Leuctra* (Plecoptera)". Ann. Mag. Nat. Hist., ser. 10, vol. 10, p. 1—41, pl. 1—5, figs. 1—57.

Text references to this list might be made thus:

"Mosely (1932) says...." or "(Mosely, 1932)".

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DEEL 106 AFLEVERING 1 1963

TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

INHOUD:

J. T. Wiebes. — Taxonomy and host preferences of Indo-Australian fig wasps of the genus *Ceratosolen* (Agaonidae), pp. 1—112, figs. 1—329, pl. 1.

Tijdschrift voor Entomologie, deel 106, afl. 1. Gepubliceerd 1-V-1963

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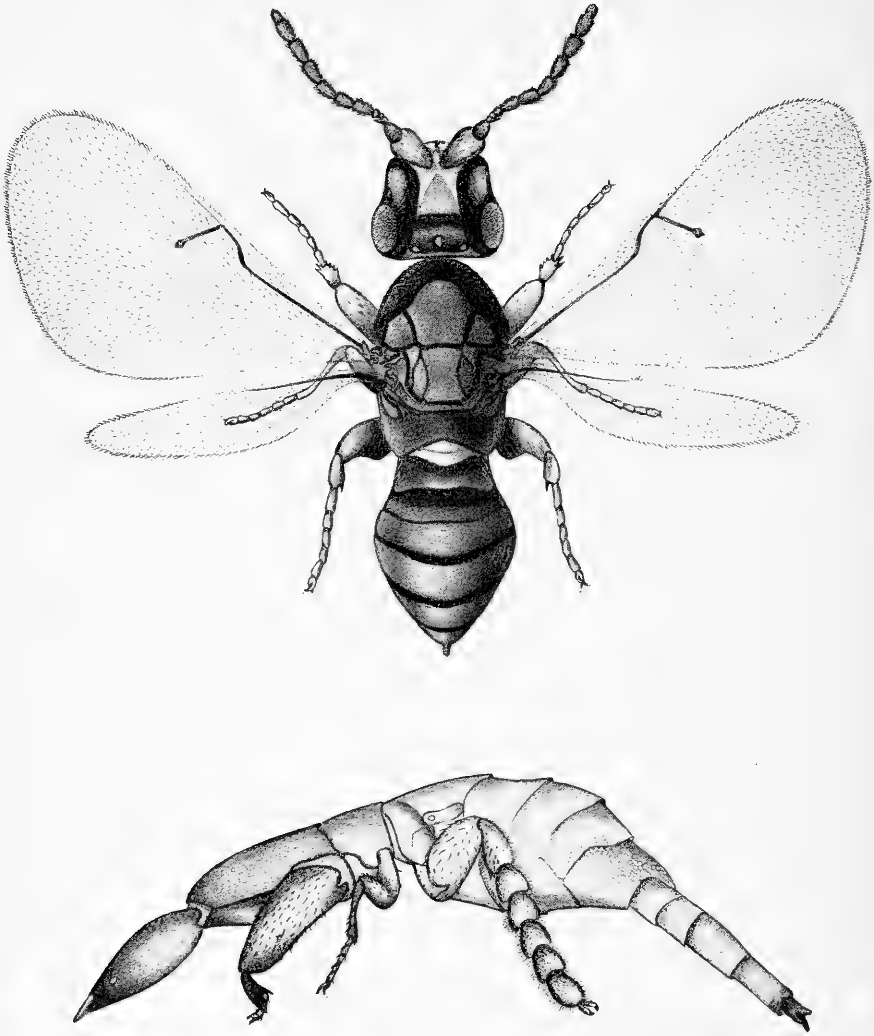

Pl. 1, *Ceratosolen vechti* Wiebes, female and male, × 30. H. HEIJN del.

TAXONOMY AND HOST PREFERENCES OF INDO-AUSTRALIAN FIG WASPS OF THE GENUS CERATOSOLEN (AGAONIDAE)

BY

J. T. WIEBES

Rijksmuseum van Natuurlijke Historie, Leiden

Contents

Introduction

The systematic position of the fig wasps has for a long time been a challenging problem to biologists. Up to about 1880, the literature on fig wasps consisted of only a few occasional papers on the curious creatures found in the receptacles of *Ficus* species, and on the function they were supposed to fulfil, or were denied to have, in the process of caprification. For a survey of the literature prior to 1880, I refer to the critical review by MAYER (1882).

SAUNDERS (from 1878 onwards) and WESTWOOD (1882, 1883) described a number of genera and species of fig wasps from India and Australia.

PAUL MAYER (1882) reported upon a collection of fig insects from several parts of the world, mainly collected by H. ZU SOLMS-LAUBACH in the Botanical Gardens at Bogor (Java), and by F. MÜLLER in Brazil.

GUSTAV MAYR (1885) described and named the species listed by MAYER and some additional material sent by SOLMS from Bogor, thus providing a firm basis for the study of the fig wasps. In 1906, MAYR contributed an additional paper, consisting of corrections to his 1885 paper and descriptions of new species and genera.

In the meantime ASHMEAD (1904) reviewed the classification of the Chalcidoidea, and assigned the fig wasps to their proper place in this large group of Hymenoptera.

From 1916 onwards, the knowledge of the fig wasps was greatly enlarged by GRANDI, who published some fifty-five papers on their taxonomy, morphology, and bionomics. A survey of GRANDI's work may be found in GRANDI (1955c, 1961). Among his outstanding contributions to the knowledge of the Agaonidae, the critical review (1928c) of the species described by MAYR, the monograph of *Blastophaga psenes* (second edition, 1929), and the world catalogue (last edition, 1955b) especially may be mentioned.

Up to a few years ago, only little attention could be given to the host relations of the Agaonidae, due to the fact that it was very difficult to have the host *Ficus* properly identified. Although MAYR (1885) cooperated with the botanist SOLMS, and WILLIAMS (1921, 1928) with MERRILL, the host preferences could in many instances not be ascertained.

It was a fortunate coincidence that at the time when Dr. J. VAN DER VECHT took up the study of fig wasps in the Botanical Gardens at Bogor, Java, Mr. E. J. H. CORNER was working on a revision of the genus *Ficus*. They cooperated in the study of the symbiosis between figs and fig wasps, and pointed out the fact that the relation between figs and fig wasps is highly specific. VAN DER VECHT (1956, p. 103; 1960) emphasized the particular importance of the study of the symbiosis, "for probably nowhere will botanists and entomologists find such an interesting opportunity to compare and check their ideas about certain problems of natural relationships and evolution".

VAN DER VECHT started his studies on fig wasps in 1954, and collected many samples in Java. In 1955, however, he returned to Holland, and soon found himself engaged in other work. In 1959 he suggested that I should proceed with the subject, and kindly gave the collection and his field notes in my care.

In the meantime CORNER enlarged the collection with many samples of wasps taken from figs preserved in botanical collections. A few years later he sent to me two collections of fig insects made on his expeditions to New Guinea, Melanesia, and Borneo. This material, together with the collections made by VAN DER VECHT, is preserved in the Rijksmuseum van Natuurlijke Historie, Leiden.

It soon became evident that the outcome of my study of the fig wasps could only gain by the incorporation of the data of collections available from other museums. Upon my request, material was sent on loan by various institutions. The material on which the present paper is based belongs to the institutions mentioned below; the names are preceded by the abbreviations used in the text of this paper.

BM — British Museum (Natural History), London;
BMH — Bernice P. Bishop Museum, Honolulu;
HSPA — Hawaiian Sugar Planters' Association, Honolulu (the collection of Dr. F. X. WILLIAMS);
ML — Rijksmuseum van Natuurlijke Historie, Leiden (in most instances, however, indicated by a collection number only);
NMB — Naturhistorisches Museum, Basel;
NMW — Naturhistorisches Museum, Wien;
OUM — Hope Department of Entomology, University Museum, Oxford;
USNM — United States National Museum, Washington.

Moreover, some typical specimens were received in exchange for specimens from the collection ML from Dr. G. GRANDI (Bologna) and Dr. K. J. JOSEPH (Dharwar, India) or in loan from Dr. E. F. RIEK (Canberra).

Because of practical reasons I restrict the work to the Indo-Malayan and Papuan areas. The bulk of the material is from Malaya, Indonesia, and New Guinea, and these are the areas in which CORNER made an extensive research on the genus *Ficus*. As Dr. E. F. RIEK informed me that he has prepared a manuscript on the Australian Chalcidoidea, I do not include the Australian species. Only some Australian records of Indo-Malayan species are mentioned.

All information on *Ficus* mentioned in the present paper was either given by CORNER (personal communication, and in litt. to VAN DER VECHT and WIEBES), or taken from his publications (CORNER, 1958, 1960—1962).

Acknowledgements.

For loan of material, and for generous help in numerous ways, I am indebted to the institutions mentioned above and to the following persons: J. H. ARDLEY (Lae), F. A. BIANCHI (Honolulu), B. D. BURKS (Washington), J. H. CALABY (Canberra), M. FISCHER (Vienna), M. DE V. GRAHAM (Oxford), G. GRANDI (Bologna), K. J. JOSEPH (Dharwar), F. KEISER (Basel), J. F. PERKINS (London), E. F. RIEK (Canberra), Miss. M. T. WIEBES (Leiden), and C. M. YOSHIMOTO (Honolulu).

The work on this paper could not have begun without the collection of VAN DER VECHT as a firm working basis, and it could not have been completed without the continuous cooperation of Mr. E. J. H. CORNER. I am grateful to Dr. J. VAN DER VECHT for entrusting me with this research, and for valuable comment and advice. To be permitted to cooperate with Mr. CORNER is a highly esteemed privilege.

A grant from the "Zoölogisch Insulinde Fonds" enabled me to travel to Cambridge, Oxford, and London, in order to discuss some problems with Mr. CORNER, and to go through the collections of the Oxford University Museum (Hope Department of Entomology) and the British Museum (Natural History).

The Nederlandsche Entomologische Vereeniging kindly accepted this paper for publication.

THE INDO-MALAYAN AND PAPUAN SPECIES OF THE GENUS CERATOSOLEN

TAXONOMIC REVISION

Ceratosolen Mayr

Sycocrypta Coquerel, 1855, pp. 367, 422 (monobasic, type: *S. coeca* Coquerel); Walker, 1871, p. 60 (in family Agaonidae s.l.); Newman, 1871, p. 400 (do.); Saunders, 1878, pp. 316—317 (in synonymy of *Blastophaga* Gravenhorst); Westwood, 1882, p. 48 (do.); Mayer, 1882, p. 586 (do.); Westwood, 1883, p. 379 (do.); Mayr, 1885, pp. 187—188 (incertae sedis); Dalla Torre, 1898, p. 321 (catalogue); Ashmead, 1904, p. 389 (in synonymy of *Blastophaga* Gravenhorst); Gahan & Fagan, 1923, p. 138 (types of Chalcid genera); Wiebes, 1961a, p. 236 (synonymous with *Ceratosolen* Mayr); 1961c, pp. 283—384 (proposed suppression).

Ceratosolen Mayr, 1885, pp. 150, 159, 160, 162, 164 (seven species; subgenus of *Blastophaga* Gravenhorst, key, description, key to species); Dalla Torre, 1898, pp. 323—325 (catalogue); Mayr, 1906, p. 153 (treated as separate genus); Schmiedeknecht, 1909, pp. 7, 9—10 (key, catalogue); Grandi, 1916a, pp. 133—153 (description, key to species); Gahan & Fagan, 1923, p. 29 (types of Chalcid genera); Aiyar, 1925, pp. 236—237 (catalogue of

Indo-Ceylonese species); Grandi, 1928c, pp. 221—225 (catalogue); 1935, pp. 225—229 (do.); Mani, 1938, pp. 29—30 (catalogue of Indian species); Grandi, 1941, pp. 13—18 (catalogue); 1952c, pp. 81—85 (do.); 1955b, pp. 120—125 (do.); Wiebes, 1961a, pp. 236, 238 (synonymous with *Sycocrypta* Coquerel, key); 1961c, pp. 383—384 (proposed validation).

Ceratosolens [!] Ashmead, 1904, pp. 233, 234 (key, type designated: *Blastophaga (Ceratosolen) appendiculata* Mayr).

Ceratosolensia Girault[1], 1915, p. 311 (monobasic, type, originally designated: *C. ficophaga* Girault); Gahan & Fagan, 1923, p. 29 (types of Chalcid genera); Grandi, 1928c, p. 229 (catalogue, incertae sedis); 1935, p. 239 (do.); 1941, p. 27 (do.); 1952c, p. 94 (do.); 1955b, p. 135 (do.).

Restriction.

As may be seen from the synonymy, the genus *Ceratosolen* was originally established as a subgenus of *Blastophaga* Gravenhorst. The most important differential characters are the situation of the male antennae in separate grooves, and the elongate shape of the spiracular peritremata of the eighth urotergite in the female. In 1906 MAYR, without explicitly stating the change, treated the group as a separate genus, an opinion adhered to by all subsequent authors.

It appears, however, that there are some species that constitute a grade between *Blastophaga* and *Ceratosolen*. Especially in the figs of the section *Sycidium* Miq., I find species of wasps that show *Blastophaga* characters in the male, whereas the female has large, elongate, instead of circular peritremata on the eighth abdominal segment; other species have females with circular peritremata, and males with a *Ceratosolen* facies. Suffice it here to mention the gradation in these few characters only.

The genus evidently needs redefinition against *Blastophaga* and against some genera named by GIRAULT. This redefinition, however, cannot be given before the other genera have been revised. In this paper, the genus *Ceratosolen* is treated in its restricted sense, excluding the species that do not show the above-mentioned differential characters in both sexes.

Description.

For an extensive diagnosis of the genus, I refer to GRANDI (1916a, pp. 133—153). The following description may serve to facilitate recognition, and to elucidate some terms and notations used in this paper.

The quotients given in parentheses with the descriptions of some body-parts — e.g., pronotum (10 : 7) — refer to the relative length and width, respectively; if given in square brackets behind a comparative remark — e.g., femur longer than tibia [10 : 7] — they refer to the comparison.

The morphological terms used in the descriptions are the English equivalents of those used by GRANDI (1929) in his monograph on *Blastophaga psenes* (L.). In

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[1]) Dr. E. F. RIEK, who studied the type specimens of GIRAULT's Australian Chalcodoidea, drew my attention to this new synonym, and kindly sent to me some female specimens of *C. ficophaga* for comparison with the other species of *Ceratosolen*. *C. ficophaga* seems to belong to the group of *C. appendiculatus* (Mayr), but the males should be studied for a definitive classification of the species.

a few cases, e.g., the venation of the wings, I use different names, which are self-evident.

Male. Head longer than wide. The head may be pubescent, or provided with small spines. In most cases, these adornments are omitted from the figures. Epistomal margin usually trilobate, bilobate in one species; always prominent and distinctly visible. Antenna — not counting the radicola — consisting of four to six segments: scape, pedicel, flagellar segments; not clubbed. Unless otherwise stated, the lengths of the segments are measured along the dorsal edges. In preparing the figures, care was taken not to press the antenna between slide and cover-glass. Contrarily, the mouthparts were flattened into one plane, so that they may look different when studied in situ. Labium and maxillae sometimes atrophied, mostly present; maxillae with or without distinct lateral expansions. Mandible bidentate, each tooth with a subapical expansion.

Thorax simple; dorsally, the following terga are visible: pronotum, mesonotum, metanotum. The metanotum is, in most species, incompletely separated from the propodeum. Propodeum, and its spiracular peritremata, variable in shape. Ventrally, the following sterna are visible: prosternum (with the propleurae indicated in the figures by a dotted line), mesosternum, and metasternum. The metasternum is hirsute in some species.

Tibia of the fore leg with a varying number of apical teeth. Tarsus consisting of two or three segments, which are sometimes incompletely separated. Tibiae of mid and hind legs with or without spines on the disks. The normal number of tarsal segments is five, although in one species there are only three tarsal segments in the mid and hind legs, and in other species oligomery or heteromery occurs. Unless otherwise stated, the length of the distal tarsal segment is measured without the claws. In many species the hind legs are hirsute, and the tarsi are greatly dilated. The figures of these parts are semi-diagrammatical, merely indicating the size of the segments and the length of the pubescence.

Gaster. The tenth urite may or may not bear cerci or parameres, or both; the aedeagus is in most instances dilated subapically.

Length. The measurements given refer to the total length of head, thorax, and propodeum. The colour is that of specimens preserved in alcohol.

Female. Head approximately as long as wide across the compound eyes. The length of the cheek, given in comparison with the longitudinal diameter of the eye, refers to the distance from the lower margin of the eye to the point of insertion of the mandible. Three ocelli. Lateral expansions of the epistomal margin more or less angular, or rounded. Antenna relatively simple, the club in most species only indicated by the shape of the loosely connected apical two or three segments, or absent; in other species the apical two or three segments completely united. Maxilla with or without a bacilliform process. Mandible, and its appendage, with a varying number of ventral ridges.

Thorax. Wings pubescent, or with glabrous parts. Venation of the fore wing complete, i.e., consisting of submarginal, marginal, stigmal, and postmarginal veins. Stigma sometimes with dark radiating striae.

Fore leg with a distinct comb on the dorso-apical edge of the tibia, which may consist of a varying number of teeth. In some cases, the ventral tooth of this comb is blunt. Ventro-apical edge with smaller teeth, and, mostly, with a long, simple spur. Tarsus usually pentamerous, in a few species consisting of only four segments. Mid leg slender; tarsus pentamerous, tetramerous in two species. Hind tibia with apical teeth, which may vary in shape and number. Hind tarsus pentamerous.

Gaster. The spiracular peritremata of the eighth urotergite elongate, gouge-like. The ovipositor projecting beyond the gaster to a varying extent.

Length. The measurements given refer to the total length of head, thorax, and gaster (without the ovipositor). Colour as seen in the alcohol samples.

Bionomics.

Two authors gave notes on the bionomics of species of *Ceratosolen,* viz., BAKER (1913) on *C. notus* (Baker), and WILLIAMS (1928) on the same species, on *C. appendiculatus* (Mayr) (not indicated by name), and on *C. bakeri* Grandi.

The following short description of the life of a species of *Ceratosolen* — nearly all species of which live in dioecious figs — is almost verbally borrowed from WILLIAMS (1928, p. 7).

The wasps issue from the gall flowers of a mature fig. The males, which are quite flightless, hatch first and immediately seek the females by biting open the occupied galls. After mating the males perish, with some exceptions within the receptacles. On the other hand the females are fully winged, and in seeking egress from the receptacle through the ostiole or by a hole drilled through the rind, inadvertently dust themselves with pollen from the ripe stamens. They take wing, and under proper conditions find and enter a young fig in the right stage of development, i.e., one whose stamens are as yet undeveloped but whose gall flowers and seed flowers are in the one instance ready and adapted to receive the egg, and in the other instance, the pollen to fertilize the seed-producing ovary. Evidently, the females are unable to distinguish between the male and the female fruits, and enter whatever sort is available. Of course, the wasp cannot reproduce in the seed or female fig because this is not modified to that end, neither does it find fig flowers to fertilize in the male or gall fig.

The young fig grows to maturity, the stamens and seeds ripen, and wasps issue from the galls.

Remarks.

Under each species I give a list of synonyms — not necessarily exhaustive, as the references to the catalogues are not included — the data on the material studied, a description or descriptive notes, if necessary, and, in most cases, general remarks.

In general, the geographical names mentioned are those now in common use (e.g., Bogor, not Buitenzorg).

Hosts identified by CORNER are indicated as such, other host names are given as I found them on the labels. Discussion of the host records may be found in the chapter on host preferences.

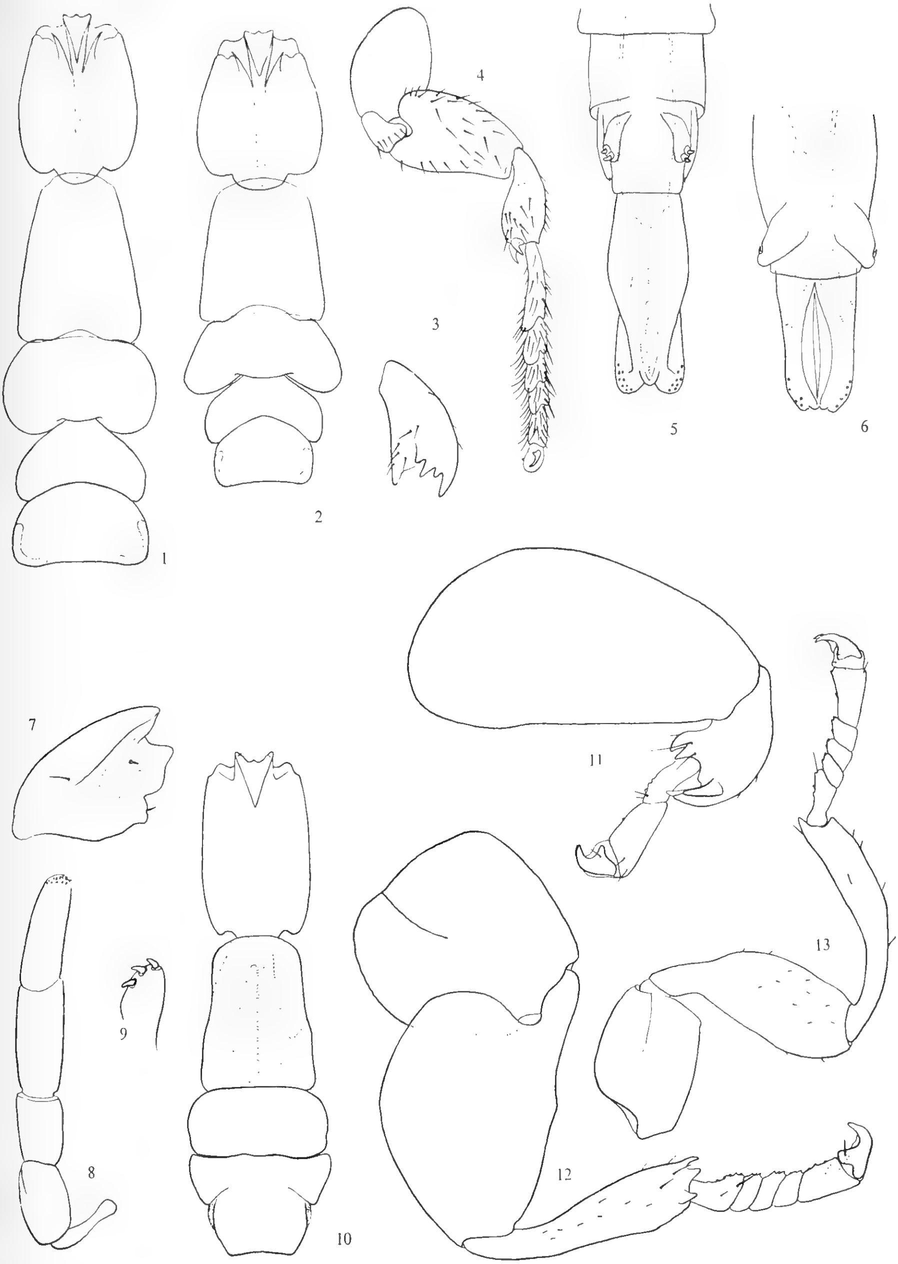

Fig. 1, *Ceratosolen hewitti,* Singapore, male, 2—5, *C. constrictus,* Java, 2, male, 3, female fore tibia, 4, female hind leg, 5, apex of male abdomen, 6, *C. pygmaeus,* Mindanao, apex of male abdomen, 7—13, *C. marshalli,* Fiji, male, 7, mandible, 8, antenna, 9, cercus of tenth urite, 10, male, 11, fore leg, 12, hind leg, 13, mid leg. Figs. 1, 2, 10, × 50; 4, × 80; 11—13, × 115; 3, 7, 8, × 155; 5, × 215; 6, 9, × 365

Figures.

If not otherwise stated, the following body-parts are figured as seen in dorsal aspect: male head and thorax, antenna; figured as seen in ventral aspect: male and female mouthparts, male genitalia; as seen in antaxial aspect: male and female legs (i.e., retrolateral aspect of fore leg, prolateral aspects of mid and hind legs), female antenna.

As there are some differences between the various samples in the state of preservation, all specimens from coll. HSPA and BMH were sent to me dry, and they had to be relaxed in alcohol, not all figures of comparable body-parts could be magnified to the same, large scale.

But for the plate, the figures are original camera lucida drawings by the author.

Ceratosolen pygmaeus Grandi (fig. 6)

Ceratosolen pygmaeus Grandi, 1927a, pp. 317—320, Pl. 4 figs. 50—65, Pl. 5 fig. 66 [descr. ♀, ♂, ex *Ficus minahassae* Miq., Mt. Maquiling (Luzon, Philippine Is.), leg. C. F. Baker].

Material.

One ♀, 1 ♂, ex *Ficus minahassae* Miq., Luzon (Philippine Is.), ex coll. GRANDI; coll. ML, no. 508.

Series ♀, 1 ♂, ex *Ficus minahassae* Miq., Los Baños (Luzon, Philippine Is.), Coll. Agric., leg. F. X. WILLIAMS, 1.VII.1921; coll. HSPA.

Series ♀, ♂, ex *Ficus minahassae* Miq., Lake Lanao (Mindanao, Philippine Is.), leg. F. X. WILLIAMS, XI.1921; coll. HSPA; coll. ML, no. 588: 5 ♀, 5 ♂.

Description — Additional note.

Male. Labium and maxillae completely atrophied. The tenth urite bears cerci, which are, due to the smallness of the specimens, and to the fact that these appendages are almost hyaline, very difficult to be observed. In the specimens from the HSPA collection, the cercus bears one claw (fig. 6).

Female. Tarsi of the fore and mid legs heteromerous.

Ceratosolen marshalli Grandi (figs. 7—13)

Ceratosolen Marshalli Grandi, 1931, pp. 8—11, figs. I—II [descr. ♀, ex *Ficus* spec., Mt. Labasa (Fiji Is.), leg. W. Greenwood, 1.VII.1923, no. W. G. 532[1])].

Material.

Series ♀, ♂, ex *Ficus* spec. near *storcki,* Fiji, leg. C. E. PEMBERTON, 1920; coll. HSPA, 1 ♂ (allotype) slide mounted; coll. ML, no. 595: 10 ♀, 2 ♂; ♂, slide 595a, ♀, 595b, c.

Description — Additional note.

Female. The specimens from the collection WILLIAMS are very similar to the

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[1]) CORNER studied W. G. 532, and identified it with *Ficus pritchardii* Seem.

species described by GRANDI as *C. Marshalli.* There are some minor differences, viz., in the specimens seen by me, the mandibular appendages bear five ventral ridges instead of four, and the sensilla of the funicular segments seem to be more numerous. As the material has been desiccated, as have GRANDI's specimens, the last mentioned character is not easily to be observed. The colour-differences between head, thorax, and gaster, mentioned by GRANDI (l.c., p. 8): "colore fondamentale isabellino-ferrugineo sfumato di umbrino, con la parte posteriore del cranio e gli urotergiti tendenti al fuligineo", are very conspicuous. I consider the sample conspecific with GRANDI's species, and describe the hitherto unknown male.

Male. Head (fig. 10) not quite twice as long as wide. Lateral lobes of the epistomal margin prominent, median lobe small. Eyes absent. Antennal grooves half closed. Antenna (fig. 8) four-segmented: scape (8 : 5) slightly longer than the pedicel (3 : 2), which is two-thirds the length of the next segment (9 : 4), Third segment nearly as long as the apical segment (3 : 1). Mandible, fig. 7; labium and maxillae atrophied.

Thorax, fig. 10. Length of the pronotum four-thirds of the posterior width, and nearly twice the anterior width. Mesonotum twice as wide as long. Metanotum incompletely separated from the propodeum, approximately as wide as the mesonotum. Propodeum wider than long [4 : 3], narrower than the mesonotum. Fore leg (fig. 11): femur more than twice as long as the tibia, which bears three dorsal and two ventro-apical teeth. Tarsus bimerous, segments in ratio 5 : 6. Mid leg (fig. 13): the coxa two-thirds the length of the clavate femur, the trochanter small. Tibia arcuate, as long as femur and trochanter combined, with acute apical edges. Tarsus pentamerous, the segments in ratio 8: 3: 3: 4: 9. Femur of the hind leg (fig. 12) slightly larger than the coxa; the tibia about as long as the femur, with three apical teeth. Tarsus pentamerous, the segments in ratio 8 : 3 : 3 : 4 : 8.

Gaster. Cerci (fig. 9) of the tenth urite with three rather robust claws.

Length, 1.1—1.3 mm. Colour light yellow-brown.

Remark.

There are several characters by which *C. marshalli* can be distinguished from *C. pygmaeus*, but it is evident from other features (e.g., the dentation of the fore legs, the constitution of the antennae) that the two are closely related.

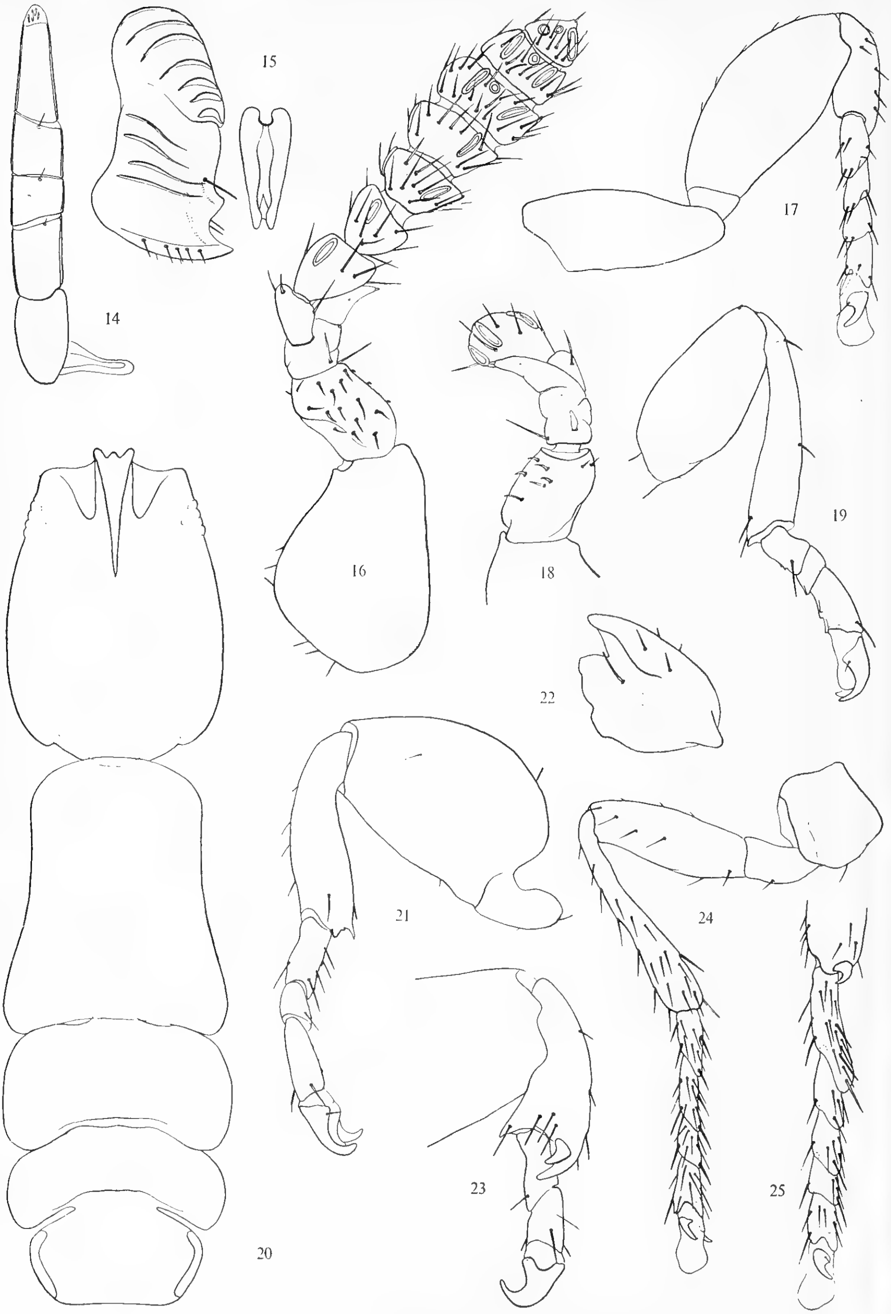
Ceratosolen nanus sp. n. (figs. 14—25)

Material.

Series ♀, ♂, ex *Ficus pungens* Reinw. (det. E. J. H. CORNER), Lae (Terr. New Guinea), leg. E. J. H. CORNER, 5.IX.1960; coll. no. 548; ♂ (holotype), slide 548a, ♀ (allotype), 548c, ♂, ♀ (paratypes), 548b, d.

Description.

Male. Head (fig. 20) slightly more than twice as long as wide anteriorly, and approximately one and a half times as long as its maximum width [13 : 9]. Dorsal surface with very small bristles. Epistomal margin obtusely trilobate, the lateral



Figs. 14—25, *Ceratosolen nanus,* New Guinea, 14, male antenna, 15—18, female, 15, mouthparts, 16, antenna, axial aspect, 17, fore leg, axial aspect, 18, antenna, detail, 19—23, male, 19, mid leg, 20, male, 21, hind leg, 22, mandible, 23, detail of fore leg, 24, female mid leg, 25, detail of female hind leg. Figs. 20, × 115; 17, 19, 21, 23—25, × 155; 14—16, 18, 22, × 215

lobes about twice as long as the median one, and without hairs. Eyes large. Antennal grooves half closed, obtuse behind. Antenna (fig. 14) five-segmented; the scape (7 : 4) slightly longer than the pedicel (3 : 2), first flagellar segment (7 : 6) half as long as the pedicel, second segment (1 : 1) somewhat longer than the first, apical segment (3 : 1) distinctly longer than the pedicel. Pedicel, first, and second flagellar segments with one apical hair. Mandible, fig. 22; labium and maxillae completely atrophied.

Thorax, fig. 20. Posterior width of the pronotum distinctly less than its length [9 : 11]. The pronotum is narrower in front than behind [7 : 9]. Length of the mesonotum one half, that of the metanotum one third of the width. Propodeum about one and a half times as wide as long [14 : 9], with rounded edges. Tibia of the fore leg (fig. 23) half as long as the femur, the tarsus (including the claws) as long as the tibia. Tibia with two large teeth at the dorso-apical edge and one small ventral tooth. Tarsal segments subequal, claws large. Mid leg (fig. 19): coxa and femur subequal, tibia a little longer, without apical teeth. Tarsus trimerous, the segments in ratio 4 : 2 : 5. Coxa of the hind leg (fig. 21) slightly longer than the femur; the tibia distinctly shorter, with ventral teeth. Tarsus trimerous, the segments in ratio 5 : 3 : 7.

Gaster. Genitalia without cerci.

Length, 0.95—1.0 mm. Colour yellowish.

Female. Head as long as wide across the eyes. Longitudinal diameter of the compound eye longer than the cheek [7 : 5]. Pubescence short. Antenna (figs. 16, 18): scape as long as fourth to seventh segments combined; pedicel not half as long as the scape, with approximately twenty spines on the axial surface. Fourth segment small. Fifth to eleventh segments gradually diminishing in length, the ninth segment the widest. Segments with few sensilla: the fifth with three, the sixth and seventh with five, the eighth with six, the ninth with seven, the tenth with five, and the eleventh with two oblong sensilla; the ninth to eleventh segments with some circular sensilla. Mouthparts, fig. 15. Mandible with four ventral ridges, longer than the appendage, which bears six ventral ridges. Labium and maxillae much like those of *C. pygmaeus*.

Thorax. Pronotum broad and bristly. Scutum nearly as long as wide; scutellum approximately as long as wide posteriorly, with a few scattered hairs. Metanotum with many hairs. Propodeum as wide as scutum and scapulae combined, with tufts of five hairs above and beneath the spiracular peritremata. Fore wing (16 : 7), 1.1 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 8: 5 : 4 : 2. Submarginal vein with three pustules, stigmal vein with four. Hind wing (6 : 1), 0.6 mm long. Wings pubescent over nearly the whole surface, marginal fringes long. Coxa and femur of the fore leg (fig. 17) subequal, the tibia half as long as the femur. Dorsal apex of the tibia with two teeth. Tarsus tetramerous, the segments in ratio 25 : 14 : 12 : 15. Coxa of the mid leg (fig. 24) semi-globular, the tibia about as long as femur and trochanter combined. Tarsus tetramerous, the segments in ratio 22 : 23 : 16 : 17. Hind leg (fig. 25): the femur a little longer than the coxa, the tibia nearly as long as the coxa. Apical tibial tooth bidentate. Tarsus pentamerous, the segments in ratio 10 : 6 : 5 : 3 : 4.

Gaster. Ovipositor barely projecting beyond the apex of the gaster.

Length, 1.2 mm. Colour light brown.

Remark.

This species is well characterized by the shape of the female antenna. The oligomery of the legs and the general facies connect it with *C. pygmaeus.*

Ceratosolen constrictus (Mayr) and **C. hewitti** Waterston (figs. 1—5; map, fig. 261)

It is possible that *C. constrictus* (Mayr) and *C. hewitti* Waterston merely represent two races of one species. *C. constrictus* is known from Java and Sumatra, *C. hewitti* from Borneo and Malaya[1]). Moreover, the specimens from Mt. Kinabalu (N. Borneo) are provisionally referred to *C. constrictus.* For distribution, see the map (fig. 261).

The males of *C. hewitti* differ from those of *C. constrictus* in the relative proportions of head, thorax, and propodeum (figs. 1 and 2), and are slightly longer. The females of *C. hewitti* have longer antennal segments than those of *C. constrictus*, longer sensilla, and more hairs near the propodeal spiracle (cf. the figures given by WATERSTON, 1921, and GRANDI, 1928c).

Although there are some characters connecting *C. constrictus* and *C. hewitti* with *C. crassitarsus* and its relatives, the general facies, the heteromery of the male mid and hind tarsi, and the absence of the tibial spur from the female fore leg, are arguments for placing them in the relationship of *C. pygmaeus.*

Ceratosolen constrictus (Mayr) (figs. 2—5)

Blastophaga spec., Mayer, 1882, p. 571 [♀, ♂, ex *Covellia subopposita* Miq.[2]), Bogor (Java), Bot. Gdn., no. 9a].

Blastophaga (Ceratosolen) constricta Mayr, 1885, pp. 154, 161, 163, 169—170, Pl. XI fig. 6 [key ♀, ♂, descr. ♀, ♂, ex *Ficus (Cystogyne) subopposita* Miq. *(fistulosa* Reinw. sec. Miq.) (det. Solms), P. Mayer, no. 9a; type: ♂].

Ceratosolen constrictus: Grandi, 1928c, pp. 184—188, figs. XXXI—XXXII [redescr. ♀, ♂, type specimens of *B. constricta* Mayr].

Material.

Series ♀, ♂, ex *Ficus fistulosa* Reinw. (det. E. J. H. CORNER), Bogor (Java), Bot. Gdn., fern garden, 1.XI.1954; coll. no. 60; ♂, slide 60a.

Series ♀, ♂, ex *Ficus fistulosa* Reinw. (det. E. J. H. CORNER), Bogor (Java), Semplak, 28.XI.1954; coll. nos. 209, 211; ♂, slide 211a, ♀, ♂, 211b, ♂, 211c, ♀, 211d.

Series ♀, ♂, ex *Ficus fistulosa* Reinw., Tjibodas (Java), 8.II.1955; coll. no. 302.

Series ♀, ♂, ex *Ficus dimorpha* King[3]) (det. E. J. H. CORNER), Pajakumbuh

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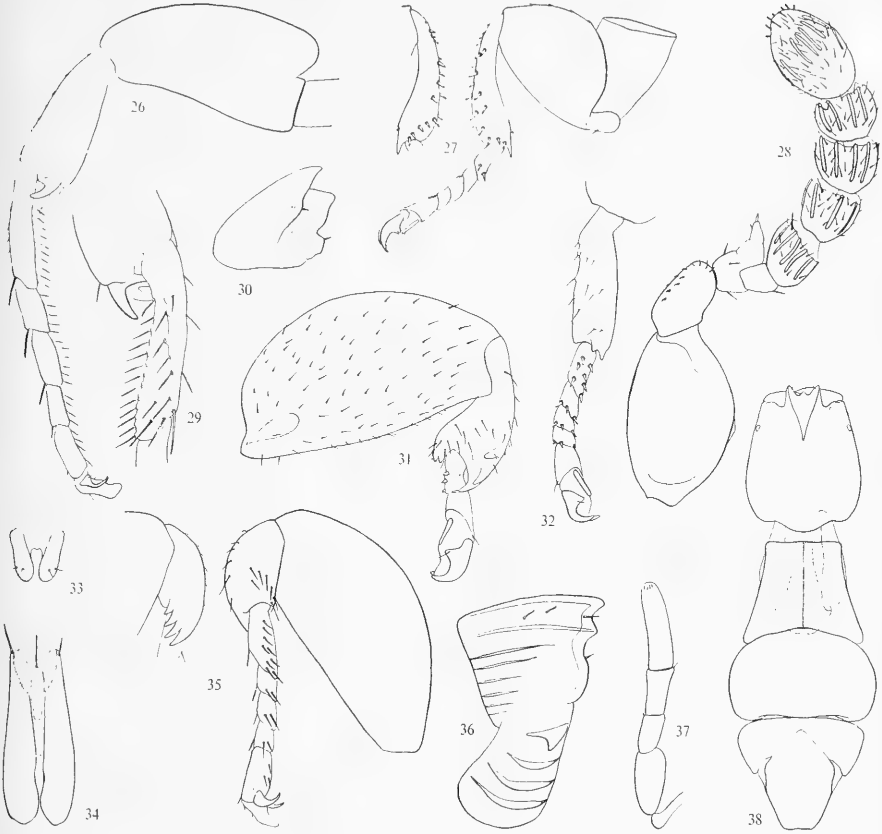
[1]) The wasps introduced to Hawaii, with Malayan *Ficus fistulosa* (cf. CORNER, 1958, p. 18), probably belong to *C. hewitti* Waterston.

[2]) = *Ficus fistulosa* Reinw.

[3]) see p. 96.



Figs. 26—38, *Ceratosolen grandii,* New Guinea, 26, female hind leg, 27, male mid leg, and detail in axial aspect, 28, female antenna, axial aspect, 29, detail of female hind leg, axial aspect, 30—33, male, 30, mandible, 31, fore leg, 32, detail of hind leg, 33, labium and maxillae, 34—36, female, 34, labium and maxillae, 35, fore leg, axial aspect, and detail in antaxial aspect, 36, mandible, 37, male antenna, 38, male. Figs. 38, × 40; 27, 31, 32, 37, × 90; 26, 28, 30, 33, 35, × 115; 29, 34, 36, × 160

(Sumatra), leg. W. Meijer, III—V.1956, no. 3473; coll. nos. 465, 467, 469; ♂, slide 465a, ♀, ♂, 465b.

? Series ♀, ♂, ex *Ficus fistulosa* Reinw. var. *tengerensis* O.K. (det. E. J. H. Corner), Mt. Kinabalu East (N. Borneo), 3000 ft. alt., leg. E. J. H. Corner, 25.VII.1961, RSNB no. 967; coll. no. 626; ♀, slide 626a, ♂, 626b.

Description — Additional note.

The males have small eyes, near the insertion of the mandibles. Maxilla with two lateral hairs. Head, thorax, and propodeum, fig. 2. Fore tibia with seven apical teeth: two stout teeth at the dorsal edge, with a smaller one in between, one dorsally on the disk, and three more slender teeth at the ventral edge. Mid tibia with five apical teeth. Hind tibia with three dorso-apical teeth. The aedeagus (fig. 5) is slightly dilated, and the cerci of the tenth urite bear two large claws.

Female. Mandibular appendage with five or six ventral ridges. Maxilla with one lateral hair, and a subapical one. Fore wing (2 : 1), 1.2 mm long. Submarginal, marginal, stigmal, and postmarginal veins approximately in ratio 20 : 7 : 6 : 8. Submarginal vein with three pustulus, stigmal vein with four. Hind wing (10 : 3), 0.7 mm long. Fore tibia, fig. 3; there are four apical teeth at the dorsal edge. Ventral edge without a long spur. Mid leg long and slender. Femur two-thirds the length of the tibia, which is as long as the tarsal segments combined. First tarsal segment one fourth longer than the fifth, the intermediates subequal and approximately half as long as the first. Tibia without prominent apical teeth, but with some very stout hairs at the ventro-apical edge. Hind leg, fig. 4. Ovipositor scarcely projecting beyond the apex of the gaster.

Remark.

The specimens from Sumatra, ex *F. dimorpha* King, resemble the Javanese specimens in all details. The sample from Mt. Kinabalu is provisionally referred to *C. constrictus*, although the females differ slightly from the Javanese specimens: antenna with short segments as in *C. constrictus*, but the sensilla rather long, as in *C. hewitti,* fore tibia with two dorso-apical teeth.

Ceratosolen hewitti Waterston (fig. 1)

Ceratosolen hewitti Waterston, 1921, pp. 35—38, fig. 1 [descr. ♀, ♂, ex *Ficus* spec., Sarawak (Borneo), leg. J. Hewitt, VII.1907; type: ♀].

Ceratosolen imbecillus Grandi, 1927a, pp. 315—317, Pl. 3 figs. 33—42, Pl. 4 figs. 43—49 [descr. ♀, ♂, ex *Ficus chartacea* Wall.[1]), Singapore, leg. C. F. Baker]; 1928c, p. 223 [= *C. hewitti* Waterston].

Material.

One ♀, 1 ♂, "from a fruiting trunk. *Ficus*. July 1907. J. HEWITT", Sarawak (Borneo), from type lot of *C. hewitti* Waterston; coll. BM, 1 slide.

Series ♀, ♂, ex *Ficus* aff. *fistulosa* Reinw. (det. E. J. H. CORNER), Bau (Kuching, Borneo), leg. E. J. H. CORNER, 25.IX.1961; coll. no. 640; ♀, slide 640a, ♂, 640b.

Series ♀, ♂, ex *Ficus chartacea* Wall.[1]), Singapore, from type lot of *C. imbecillus* Grandi; coll. USNM.

Series ♂, ex *Ficus fistulosa* Reinw. (det. E. J. H. CORNER), Singapore, Bot. Gdn., 1932; coll. no. 422; ♂, slides 422a, b.

Series ♀, ♂, ex *Ficus fistulosa* Reinw. (det. E. J. H. CORNER), Sungei Gombah (Selangor, Malaya), leg. E. J. H. CORNER, 4.X.1961; coll. no. 638; ♀, slide 638a, ♂, 638b.

Ceratosolen gravelyi Grandi

Ceratosolen gravelyi Grandi, 1916a, pp. 150, 152 [descr. ♀, ♂, in key]; 1916b, pp 201—207, figs. IX—XI [descr. ♀, ♂, ex *Ficus cunia* Hann.[2]), Paresnath Hill (Chota Nagpur, India), 4300 ft. alt., leg. N. Annandale, 9 & 14.IV.1909]; Joseph, 1954, p. 409, figs. IV, 36—41 [descr. note ♂, ex *Ficus cunia* Hann.[2]), Dehra Dun (India), Forest Research Inst. Estate, New Forest, leg. K. J. Joseph, 25.VI.1953].

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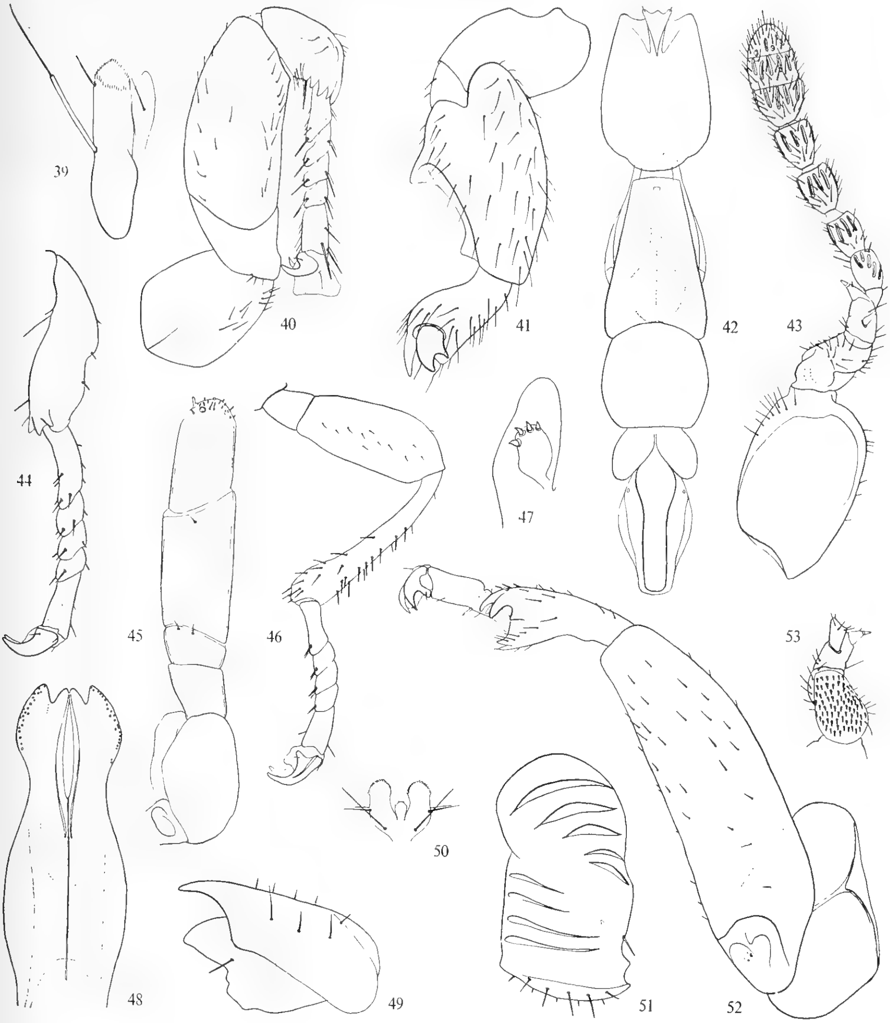
[1]) Probably incorrect, see p. 97.

[2]) = *Ficus semicordata* Ham. ex Smith.



Figs. 39—53, *Ceratosolen boschmai,* Bougainville I., 39—41, female, 39, labium and maxilla, 40, fore leg, 41, hind leg (tarsus omitted), 42, male, 43, female antenna, 44—50, male, 44, detail of hind leg, 45, antenna, 46, mid leg, 47, cercus of tenth urite, and paramere, 48, aedeagus, 49, mandible, 50, labium and maxillae, 51, female mandible, 52, male fore leg, 53, detail of female antenna in axial aspect. Figs. 42, × 40; 40, 41, 43, 44, 46, 52, 53, × 90; 39, 51, × 115; 45, 47—50, × 160

Material.

One ♀, 2 ♂, ex *Ficus cunia* Hann.[1]), Paresnath Hill (Chota Nagpur, India), ex coll. Grandi; coll. ML, no. 509.

Nine ♂, India, ex coll. Joseph; coll. ML, no. 566.

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[1]) = *Ficus semicordata* Ham. ex Smith.

Remark.

This species shows some resemblance to both *C. pygmaeus* and *C. emarginatus*, but it appears to be more closely related to the latter.

Ceratosolen emarginatus Mayr

Ceratosolen emarginatus Mayr, 1906, pp. 153—154 [descr. ♀, ♂, ex *Ficus* spec., Tonkin (N. Vietnam), leg. P. Marchal, no. 20b]; Grandi, 1928c, pp. 189—190, figs. XXXIII—XXXIV [redescr. ♀, ♂, type specimens of *C. emarginatus* Mayr = *C. effractarius* Grandi]; Joseph, 1954, p. 409 [♀, ♂, ex *Ficus roxburghii* Wall.[1]), Dehra Dun (India), leg. K. M. Vaid & K. J. Joseph, 30.VI.1953].

Ceratosolen effractarius Grandi, 1927b, pp. 169—174, figs. I—II [descr. ♀, ♂, ex *Ficus Roxburgi*[1]), Hanoi (Indo-China), leg. F. Silvestri, 4.III.1925].

Material.

Five ♀, 1 ♂, Calcutta (India); coll. USNM, incorrectly identified with *Blastophaga appendiculata* Mayr.

Series ♀, ♂, India, ex coll. JOSEPH; coll. ML, no. 565; ♂, slide 565a, ♀, 565b.

Series ♀, ♂, ex *Ficus* spec., Chiangmai (N.W. Thailand), Fang, 500 m alt., leg. T. C. MAA, 12/19.IV.1958, no. 380; coll. BMH.

Series ♀, ♂, ex *Ficus oligodon* Miq.[2]) (det. E. J. H. CORNER), Fraser's Hill (Selangor, Malaya), 4000 ft. alt., leg. E. J. H. CORNER, 3.X.1961; coll. no. 609; ♂, slides 609a, b, ♀, 609c.

Remark.

This species is very close to *C. fusciceps* (Mayr). It differs, however, in having an extra ring segment in the male antenna, and in the absence of spines from the disk of the male hind tibia.

Ceratosolen fusciceps (Mayr)

Blastophaga spec., Mayer, 1882, p. 570 [♀, ex *Covellia glomerata* Willd.[3]), Bogor (Java), Bot. Gdn., no. 4a].

Blastophaga (Ceratosolen) fusciceps Mayr, 1885, pp. 154, 161, 164, 167—168, Pl. XI fig. 3 [key ♀, ♂, descr. ♀, ♂, ex *Ficus (Sycomorus) glomerata* horti Bogor., nec Roxb. (det. Solms), P. Mayer, no. 4a; type: ♂].

Blastophaga (Ceratosolen) fuscipes Mayr, 1885, p. 249 [incorrect spelling].

Ceratosolen fusciceps: Mayr, 1906, p. 153 [descr. note ♂, ex *Ficus Covellii*[4]), Bogor (Java), Bot. Gdn., leg. C. Aurivillius, no. 1; also ? ♀, ex *Covellia glomerata* Miq., and *Urostigma lucescens* Miq.[4]), same locality, leg. C. Aurivillius, nos. 5 and 6, respectively]; Grandi, 1928a, pp. 79—80 [♀, ♂, ex *Ficus glomerata* Roxb., Chambaganour (Pulneys, India)[5]), 4000 ft. alt., leg. E. Gombert, 7.VI.1914]; 1928c, p. 171 [type specimens studied]; Joseph, 1953a, p. 61 [♀, ♂, ex *Ficus glomerata* Roxb., Agra (India), leg. K. J. Joseph, 12.IV.1952]; 1953b, p. 137 [♀, ♂, ex *Ficus glomerata* Roxb., Agra, 28.VIII.1950, and Trivandrum, 5.VII.1950 (India), leg. K. J. Joseph].

Ceratosolen fuscipes: Grandi, 1916a, pp. 151—152 [♀, ♂, in key]; 1916b, pp. 194—201,

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[1]) = *Ficus auriculata* Lour.

[2]) The question of the host *Ficus* is discussed on p. 97.

[3]) = *Ficus racemosa* Linn.

[4]) see p. 98.

[5]) ? = Shembaganur, Palni Hills, South India?

figs. V—VIII [descr. ♀, ♂, ex *Ficus glomerata* Roxb., Bogor (Java), Bot. Gdn., leg. E. Jacobson, I.1915; and Colombo (Ceylon), leg. O. Beccari, 1870]; 1923a, p. 299 [♀, India, leg. H. M. Lefroy].

Ceratosolen mysorensis Joseph, 1953c, pp. 277—282, figs. IV—V [descr. ♀, ♂, ex *Ficus mysorensis* Hayne[1]), Trivandrum (India), Bot. Gdn., leg. K. J. Joseph, 12.VII.1950].

?*Blastophaga niveipes* Girault[2]), 1927, p. 338 [descr. (♀), ex *Ficus glomeratus*, Roper River (N. Terr., Australia), leg. N. B. Tindale].

Material.

Series ♀, ♂, ex *Ficus racemosa* Linn., Bogor (Java), Bot. Gdn., VI—VIII.1954; coll. no. 83; ♂, slide 83a, ♀, ♂, 83b.

Series ♀, ♂, ex *Ficus racemosa* Linn., Bogor (Java), Bot. Gdn., near warung, 24.IX.1954; coll. no. 479.

Series ♀, ♂, ex *Ficus racemosa* Linn. var. *elongata* (King) Barrett (det. E. J. H. CORNER), Bogor (Java), Bot. Gdn., 18.X.1954; coll. no. 236; ♂, slide 236a, ♀, 236b.

Series ♀, ♂, ex *Ficus racemosa* Linn. (det. E. J. H. CORNER), Timor, leg. M. E. WALSH, no. 95; coll. no. 386; ♂, slide 386a, ♀, 386b.

Series ♀, ♂, ex *Ficus racemosa* Linn., Sudadji (Bali, distr. Sawahan, 16 km SE of Singaradja), leg. NJOMAN TOJA; coll. no. 59; ♂, slide 59a, ♀, slide 59b.

Series ♀, ♂, ex *Ficus racemosa* Linn.[3]), Udjung Kulon (Java), leg. A. HOOGERWERF, XI.1954, no. 1; coll. no. 276; ♀, ♂, slide 276a.

Series ♀, ♂, ex *Ficus racemosa* Linn.[3]), Udjung Kulon (Java), leg. A. HOOGERWERF, XI.1954, no. 2; coll. no. 292; ♂, slide 292a, ♀, 292b.

Series ♀, ♂, ex *Ficus racemosa* Linn.[3]), Udjung Kulon (Java), leg. A. HOOGERWERF, XI.1954[4]); coll. no. 279; ♀, ♂, slide 279a.

Fifteen ♀, series ♂, ex *Ficus racemosa* Linn. var. *elongata* (King) Barrett[5]) (det. E. J. H. CORNER), Koung, Mt. Kinabalu (N. Borneo), ± 400 m alt., 17.V.1933, Sing. F. no. 27322; coll. no. 420; ♂, slide 420a, ♀, ♂, 420b.

Series ♀, ♂, ex *Ficus racemosa* Linn. var. *elongata* (King) Barrett (det. E. J. H. CORNER), Kota Belud (N. Borneo), leg. E. J. H. CORNER, 23.IX.1961; coll. no. 622.

Three ♀, 10 ♂, ex *Ficus racemosa* Linn. (det. E. J. H. CORNER), Sungei Nenggiri (Kelantan, Malaya), leg. E. McCLURE, 13.XI.1961; coll. no. 667.

Fourteen ♀, 2 ♂, ex *Ficus racemosa* Linn. (det. E. J. H. CORNER), Negri Sembilan (Malaya), 1932, Sing. F. no. 26135; coll. no. 416; ♀, ♂, slide 416a; do., 12 ♀ from a young fig; coll. no. 418.

Series ♀, 7 ♂, ex *Ficus glomerata* Roxb.[6]), Pusa, Bihar (India), leg. D. T. FULLAWAY, 13.II.1921; coll. HSPA.

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[1]) see p. 98.

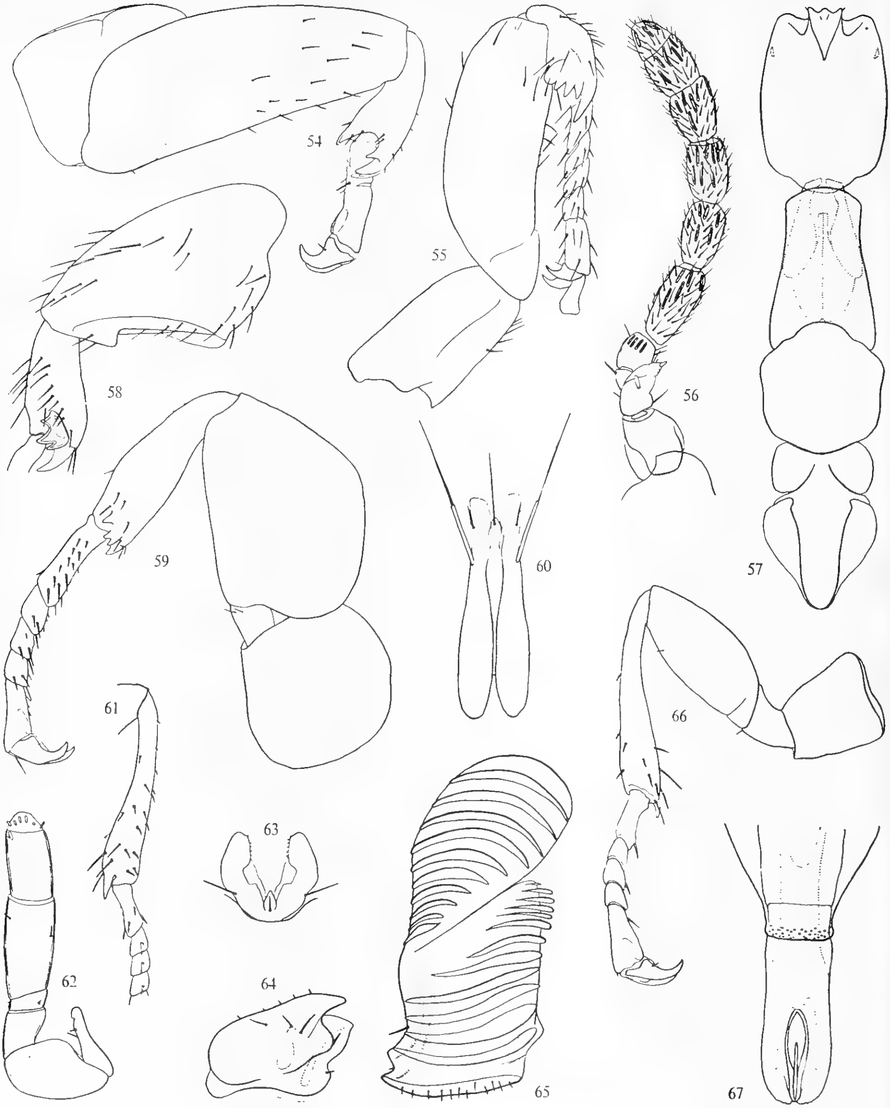
[2]) I saw one ♀ from the type series (S. Australian Museum, Adelaide), but the (as yet unknown) male should be studied for a definitive identification. Another Australian sample of *C. fusciceps* seen by me is: series ♀, ♂, ex *Ficus glomerata* Roxb. (= *F. racemosa* Linn.), Greenhills, Meringa (Queensland, Australia), leg. C. E. PEMBERTON, 28.XI.1921; coll. HSPA; coll. ML, no. 589: series ♀, ♂; ♀, ♂, slide 589a.

[3]) identification uncertain.

[4]) locality uncertain.

[5]) *Ficus acidula* King.

[6]) = *Ficus racemosa* Linn.



Figs. 54—67, *Ceratosolen bianchii,* Fiji, 54, male fore leg, 55, female fore leg, 56, female antenna, 57, male, 58, detail of female hind leg, 59, male hind leg, 60, female labium and maxillae, 61—64, male, 61, detail of mid leg, 62 antenne, 63, labium and maxillae, 64, mandible, 65, female mandible, 66, male mid leg, axial aspect, 67, apex of male abdomen. Figs. 57, × 40; 54—56, 58, 59, 61, 66, × 90; 60, 62—65, 67, × 115

Five ♀, 5 ♂, ex *Ficus glomerata* Roxb. [1]), Pusa, Bihar (India), leg. I. R. DUTT, 2.III.1923; coll. HSPA; ♂, ♀, slide mounted.

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[1]) = *Ficus racemosa* Linn.

One ♀, 4 ♂, India, ex coll. JOSEPH; coll. ML, no. 563; ♀, slide 563a, ♂, 563b.

Two ♀, 4 ♂, ex *Ficus glomerata* Roxb.[1]), Poona (India), leg. P. VARMA; coll. USNM.

Ten ♀, 5 ♂, ex *Ficus* spec., Bangalore (India), leg. G. COMPÈRE, VIII.1907; coll. USNM.

Nine ♀, ex *Ficus glomerata* Roxb.[1]), Bangalore (India), leg. D. T. FULLAWAY, 25.II.1921; coll. HSPA.

Five ♀, 8 ♂, ex *Ficus glomerata* Roxb.[1])[2]), Bangalore (India), II.1921; coll. HSPA.

Ten ♀, Peradeniya (Ceylon), leg. A. RUTHERFORD; coll. USNM.

One ♂, ex *Ficus glomerata* Roxb.[1]), Colombo (Ceylon), leg. STAINFORTH GREEN; coll. OUM, 1 slide.

Ceratosolen appendiculatus (Mayr) and C. striatus Mayr

In 1885, MAYR described *Blastophaga* (*Ceratosolen*) *appendiculata* from the Botanical Gardens at Bogor, Java. It was not recognized by subsequent authors, although GRANDI, in his revision of the Agaonidae (1928c), redescribed typical specimens from MAYR's collection[3]).

C. striatus Mayr was described, in 1906, as being different from *C. appendiculatus* in the shape of the head, and in the striate head and pronotum of the male. Later, GRANDI (1917) described *C. striatus notandus*, the male of which is essentially the same as in the nominate form, but for the non-striate head and pronotum, the shape of the head, and the relative length of the antennal segments. According to GRANDI, this new form could not be identical with *C. appendiculatus*, because the female had the ovipositor three quarters the length of the gaster, whereas in *C. appendiculatus* this relative length was given by Mayr as approximately one third. In 1928, GRANDI referred *C. striatus notandus* again, with some doubts, to the nominate form.

In my opinion, *C. striatus notandus* Grandi belongs indeed in the synonymy of *C. striatus* Mayr, as I find characters of both (viz., the striate head and pronotum, and the relative proportions of the antenna) in the same specimen. Moreover, after having studied the type series of *C. appendiculatus* (Mayr), I am convinced of the identity of *C. striatus* and *C. appendiculatus.* The length of the ovipositor in the only female of *C. appendiculatus* before me is four-sevenths the length of the gaster, which falls entirely within the variability of *C. striatus.*

Ceratosolen appendiculatus (Mayr)

Blastophaga spec., Mayer, 1882, pp. 570—571 [♀, ♂, ex *Ficus umbellata* Vahl (or *umbonata* Reinw.?)[4]), Bogor (Java), Bot. Gdn., no. 8a].

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[1]) *Ficus racemosa* Linn.

[2]) This sample bears another label: "*F. mysorensis?* COLEMAN's comp. Bangalore". See the remark on *Ficus mysorensis,* p. 98.

[3]) A sample from Calcutta, in the USNM collection identified with *Blastophaga appendiculata* Mayr, belongs to *Ceratosolen emarginatus* Mayr.

[4]) For a discussion of this host record, see p. 97.

Blastophaga (Ceratosolen) appendiculata Mayr, 1885, pp. 154, 161, 162, 164—166, Pl. XI figs. 1—2 [key ♀, ♂, descr. ♀, ♂, ex *Ficus (Sycomorus) umbellata* horti Bogor., nec Vahl (det. Solms)¹), P. Mayer, no. 8a; type: ♂].

Ceratosolen spec., Williams, 1928, p. 12 [biological note on the wasps from *Ficus integrifolia* Elmer²), Philippine Is.].

Ceratosolen appendiculatus: Grandi, 1928c, pp. 176—179, figs. XXVII—XXVIII [redescr. ♀, ♂, type specimens of *B. appendiculata* Mayr].

Ceratosolen striatus Mayr, 1906, p. 153 [descr. (♀), ♂, ex *Ficus variegata* Bl. var., Bogor (Java), Bot. Gdn., leg. C. Aurivillius, no. 3]; Grandi, 1916a, p. 153 [♂, in key]; 1917, pp. 32—34, fig. XI [descr. ♂, ex *Ficus variegata* Bl., Bogor (Java), Bot. Gdn., leg. E. Jacobson, I.1915]; 1928c, pp. 179—180 [type specimens of *C. striatus* Mayr studied; ? = *C. striatus notandus* Grandi].

Ceratosolen striatus notandus Grandi, 1916a, pp. 151, 153 [♀, ♂, in key]; 1917, pp. 34—40, figs. XII—XIII [descr. ♀, ♂, ex *Ficus variegata* Bl., Bogor (Java), Bot. Gdn., leg. E. Jacobson, I.1915].

?*Ceratosolensia ficophaga* Girault³), 1915, pp. 311, 312 [descr. ♀, ♂, ex *Ficus* spec., Gordonvale (Cairns, Queensland), I, and 18.IX.1912].

Material.

One ♀, 17 ♂, from type series of *Blastophaga appendiculata* Mayr; coll. NMW.

Series ♀, ♂, ex *Ficus variegata* Bl., Bogor (Java), Bot. Gdn., fern garden, 28.XI.1954; coll. no. 222; ♀, ♂, slide 222a.

Series ♀, ♂, ex *Ficus variegata* Bl., Bogor (Java), Bot. Gdn., 24.IX.1954; coll. no. 237; ♀, ♂, slide 237a.

Series ♀, ♂, ex *Ficus variegata* Bl., Tjiwaringin, Bogor (Java), 22.IX.1954; coll. nos. 40, 125; ♀, ♂, slide 40a.

Series ♀, ♂, ex *Ficus variegata* Bl. (det. E. J. H. CORNER), Tjibodas (Java), 30.XI.1954; coll. no. 230; ♀, ♂, slide 230a.

Fragments ♀, ♂, ex *Ficus variegata* Bl. var. *garciae* (Elmer) Corner (det. E. J. H. CORNER), Mt. Iraya (Batan I., Philippine Is.), Bur. Sci. no. 80191; coll. no. 430; ♀, ♂, slide 430a.

Series ♀, ♂, ex *Ficus integrifolia* Elmer²), Los Baños (Luzon, Philippine Is.), leg. F. X. WILLIAMS, 17.V.1921; coll. HSPA; coll. ML, no. 593: 5 ♂; ♂, slide 593a.

Six ♂, several immature ♀, ex *Ficus variegata* Bl. var. *sycomoroides* (Miq.) Corner (det. E. J. H. CORNER), Mt. Maquiling (Luzon, Philippine Is.), Coll. Agric., Laguna, no. 592; coll. no. 409; ♂, slides 409a, b, immature ♀, 409c.

Four ♀, 4 ♂, ex *Ficus variegata* Bl., Mt. Maquiling (Luzon, Philippine Is.), "on the Calamba-trail", leg. F. X. WILLIAMS, 30.I.1922; coll. HSPA.

Series ♀, ♂, ex *Ficus variegata* Bl., Mt. Maquiling (Luzon, Philippine Is.),

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¹) For a discussion of this host record see p. 97.

²) = *Ficus variegata* Bl. var. *sycomoroides* (Miq.) Corner.

³) I saw 1 ♀ from the type series (Queensland Museum, Brisbane), but the male should be studied for a definitive identification. Other Australian samples of *C. appendiculatus* seen by me are:

Series ♀, ♂, ex *Ficus ehretioides* F. v. Muell. (= *Ficus variegata* Bl.), Hambledon (Queensland), leg. C. E. PEMBERTON, 6.XII.1921; coll. HSPA.

Series ♀, ♂, ex *Ficus ehretioides* F. v. Muell. (= *Ficus variegata* Bl.), Merawa (Queensland), leg. C. E. PEMBERTON, 18.XI.1921; coll. HSPA.

leg. F. X. WILLIAMS, 11 & 14.XII.1921; coll. HSPA; coll. ML, no. 592: 5 ♀, 5 ♂.

Immature ♀, ♂, ex *Ficus viridicarpa* Corner[1]) (det. E. J. H. CORNER), Kemanan (Trengganu, Malaya), 23.XI.1935, Sing. F. no. 30553; coll. no. 478; immature ♀, ♂, slide 478a.

Immature ♀, ♂, fragments, ex *Ficus viridicarpa* Corner[1]) (det. E. J. H. CORNER, type no.), Jelebu (Negri Sembilan, Malaya), 29.X.1932, Sing. F. no. 26032; coll. no. 432; immature ♀, ♂, slide 432a, ♂, fragments, 432b.

Ceratosolen grandii sp. n. (figs. 26—38)

Material.

Series ♂, a few immature ♀, ex *Ficus semivestita* Corner (det. E. J. H. CORNER, type no.), Morobe district (Terr. New Guinea), 3000 ft. alt., leg. E. J. H. CORNER, 10.X.1955, NGF no. 7358; coll. no. 452; ♂ (holotype), slide 452a, ♀ (allotype), 452b.

Description.

Male. Head (fig. 38) nearly twice as long as wide anteriorly, and longer than its maximum width [6 : 5], with many small triangular bristles. The lateral lobes of the epistomal margin are much longer than the median one, and bear small hairs. Eyes present. Antennal grooves half closed. Antenna (fig. 37) four-segmented. Pedicel (2 : 1) two-thirds the length of the scape (2 : 1), third segment (2 : 1) somewhat longer than the pedicel, and approximately half as long as the apical segment (4 : 1). Mandible, fig. 30. Labium and maxillae, fig. 33; the maxilla bears two subbasal hairs.

Thorax, fig. 38. Pronotum only little longer than wide anteriorly, its maximum width one and a half times the length. Mesonotum wide, the length three-fifths of the width. Metanotum anteriorly nearly as wide as the mesonotum, narrower behind. Propodeum narrow and rather long, indistinctly separated from the metanotum. Tibia of the fore leg (fig. 31) half as long as the femur, tarsus nearly as long as the tibia. Tibia with two dorsal and three ventro-apical teeth; a third dorsal tooth is situated on the disk. Tarsal segments incompletely separated, the first with three conical ventral spines; the second, subequal in length to the first (measured dorsally), without spines. Mid leg, fig. 27. Tibia with one ventro-apical tooth, about as long as the femur, and but little shorter than the tarsus. Dorsal surface of the tibia provided with diverging rows of conical spines; one spine at the ventral margin. First tarsal segment nearly as long as the three following combined, with a pair of ventral spines. Fifth segment shorter than the first [2 : 3], but about twice as long as the intermediate segments. Tibia of the hind leg (fig. 32) with a bidentate ventro-apical tooth; the disk with hairs that are situated on small protuberances. First tarsal segment as long as the three following combined, with seven ventral conical spines. Second to fourth segments with three apical spines each. Fifth segment shorter than the first [3 : 5], without spines.

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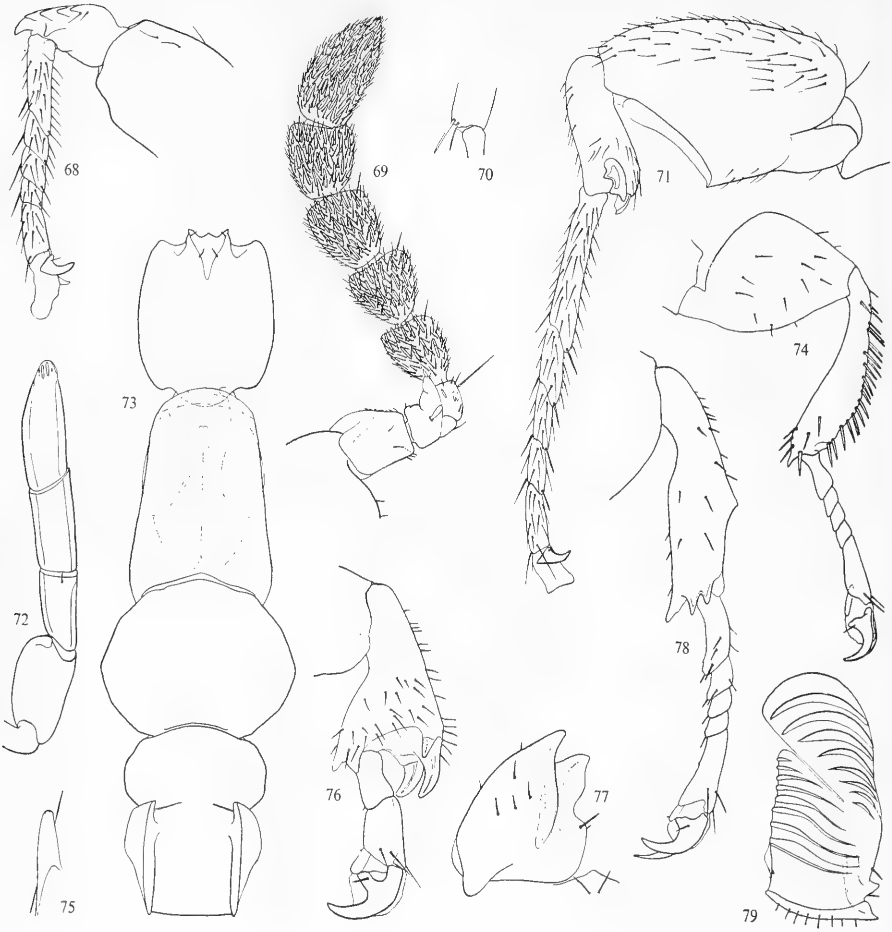
[1]) see p. 97.



Figs. 68—79, *Ceratosolen armipes,* New Guinea, 68—71, female, 68, detail of fore leg, 69, antenna, 70, detail of mid tibia, 71, hind leg, 72—78, male, 72, antenna, 73, male, 74, mid leg, 75, cercus of tenth urite, 76, detail of fore leg, 77, mandible and hypostomal margin, 78, detail of hind leg, 79, female mandible. Figs. 73, × 40; 68—71, 74, 76, 78, 79, × 90; 72, 77, × 115; 75, × 275

Gaster. Genitalia without cerci.

Length, 1.6 mm. Colour yellowish brown.

Female. The description is made from immature specimens taken from the gall-flowers. Head slightly longer than wide across the compound eyes. Longitudinal diameter of the eye one and a half times as long as the cheek. Antenna (fig. 28) with nine free segments. Scape large, twice as long as the pedicel. Flagellum short, with rather wide segments. Funicular segments with one row of sensilla each; the club, consisting of the apical three segments, with one complete and one incomplete row. Mandible, fig. 36: its appendage with four transverse ridges. Labium and maxillae (fig. 34) with one apical hair each.

Thorax very much like that of *C. appendiculatus*, but scutum and scutellum with more hairs: eight and twenty, respectively. Close to the propodeal spiracle there are only a few hairs. Wings still folded; not studied. Femur of the fore leg (fig. 35) nearly as long as tibia and tarsus together. Tibia with four apical teeth visible in antaxial aspect. First tarsal segment not quite as long as the three following combined, second to fourth segments subequal, the fifth as long as third and fourth segments combined. Tarsal segments with stout ventral hairs: ten on the first, others with two apicals only, except for the fifth, which has three ventrals. Tibia of the mid leg nearly as long as femur and trochanter combined, without apical spines, but with many spines on the disk. Tarsal segments in ratio 8 : 5 : 4 : 3 : 8 (with the claws). Hind leg, figs. 26, 29. Coxa and femur subequal, length of the tibia two-thirds of that of the femur. Tibia with two apical bidentate teeth. Tarsal segments in ratio 14 : 5 : 6 : 4 : 6; all segments with rows of ventral spines (fig. 29).

Gaster. Protruding part of the ovipositor approximately half as long as the gaster.

Length, 1.6 mm.

Remark.

This species appears to be close to *C. appendiculatus*, judging from the structure of the female antenna, and of the male genitalia. On the other hand there are several structures in the male suggesting a close affinity to *C. fusciceps*: antenna consisting of four segments, mouthparts not atrophied.

I dedicate this species to Professor GUIDO GRANDI (Bologna), the well-known authority on fig wasps.

Ceratosolen boschmai sp. n. (figs. 39—53)

Material.

Series ♀, ♂, ex *Ficus salomonensis* Rech. (det. E. J. H. CORNER), Arawa, Kieta (Bougainville I.), leg. E. J. H. CORNER, X.1960; coll. no. 532; ♂ (holotype), slide 532a, ♀ (allotype), 532b, ♂, ♀ (paratypes), 532c, d.

Description.

Male. Head (fig. 42) approximately twice as long as wide anteriorly, maximum width two-thirds of the length. Dorsal surface with many small hairs. Lateral lobes of the epistomal margin with one apical hair. Eyes wanting. Antennal grooves half closed. Antenna (fig. 45) five-segmented; the scape (3 : 2) about twice as long as the pedicel (5 : 4), which is not quite twice as long as the next segment (5 : 3). This segment is, in some specimens, half split into two parts, in others it is entire, or shows only a small notch at the antaxial margin. Fourth segment (7 : 4) three to four times as long as the third, the apical segment (2 : 1) thrice as long as the third. Mandible, fig. 49. Labium and maxillae (fig. 50): there are three (one basal and two lateral) hairs on each maxilla.

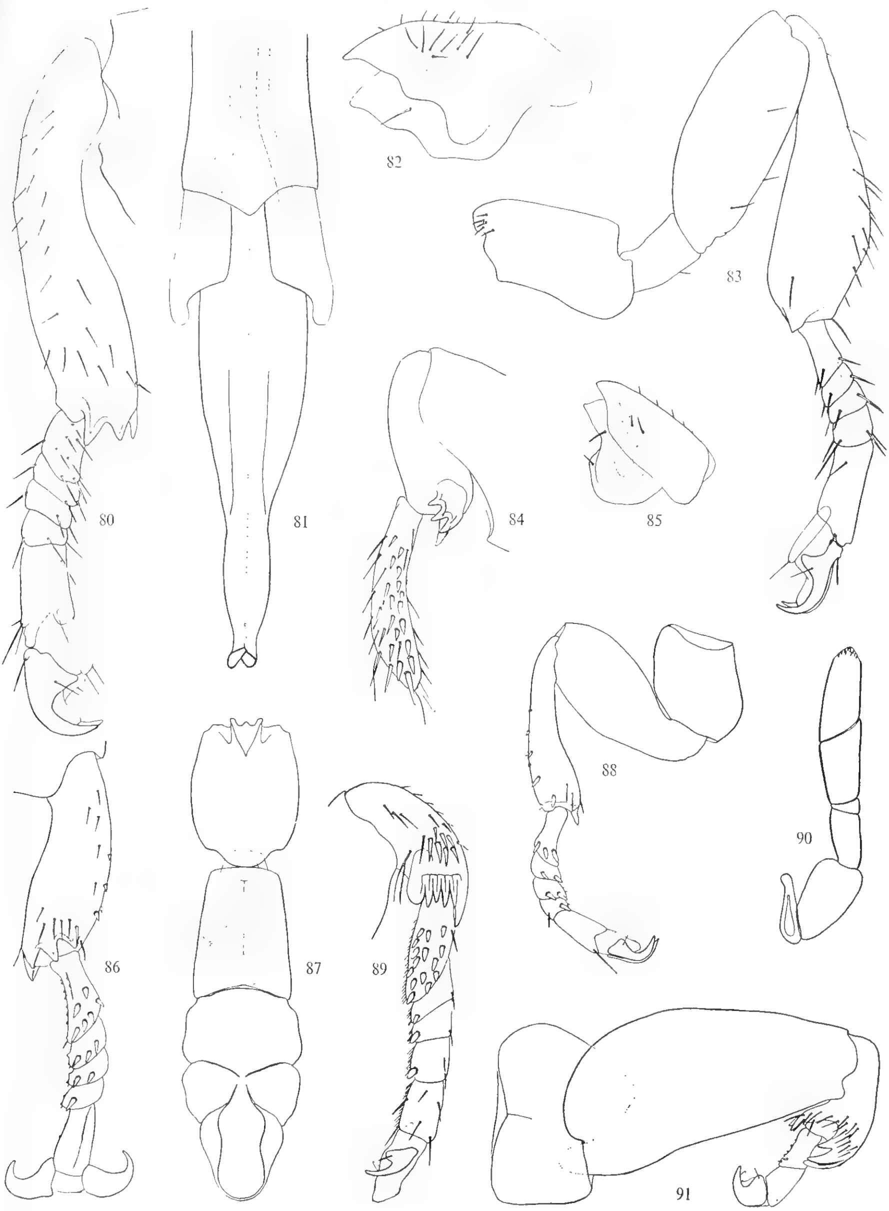
Thorax, fig. 42. The pronotum is rather narrow, and does not quite conceal the propleurae. Posteriorly it is about twice as wide as it is anteriorly; its length is equal to the sum of the anterior and posterior widths. Mesosternum about as long as wide, with rounded lateral edges. Metanotum consisting of two ear-like plates, not quite separated in the mid line, and almost free from the long propodeum. The lateral edges of the propodeum are folded ventrally, leaving a very narrow dorsal surface; the lateral surfaces are almost wholly occupied by the large peritremata. The fore leg (fig. 52) shows a very long femur, much longer than tibia and tarsus combined [3 : 2]. Tibia (without the apical teeth) more than twice as long as the second tarsal segment, which is slightly longer than the first [6 : 5]. Tibial armature consisting of four dorsal and two ventro-apical teeth. Tarsus bimerous, the segments incompletely separated. Mid leg, fig. 46. Tibia as long as femur and trochanter combined, and but little longer than the pentamerous tarsus. Tarsal segments in ratio 7 : 3 : 3 : 3 : 5. Femur of the hind leg (fig. 44) large, tibia not much more than half as long, with three dorso-apical teeth. Tarsus pentamerous, segments in ratio 9 : 3 : 3 : 2 : 6.

Tergites of the gaster distinctly sclerotized. Genitalia (fig. 48) with cerci (four claws) and parameres (fig. 47).

Length, 1.5—1.9 mm. Colour yellowish brown, head and fore legs darker, the propodeal peritremata strikingly black-brown.

Female. Head approximately as long as wide across the eyes. Longitudinal diameter of the eye short, about four-fifths the length of the cheek. Lateral lobes of the epistomal margin rather angular. Antenna (fig. 43): the scape two and a half times as long as the pedicel, which has many minute spines on the axial surface (fig. 53). Fifth to eleventh segments with one row of oblong sensilla; the fifth with five sensilla, the sixth with six, the seventh and eighth with eight, the ninth with nine, the tenth with ten, and the eleventh with four oblong and two circular sensilla. Ninth to eleventh segments combined into a loose club. Mandible (fig. 51) with four ventral ridges, its appendage with five. Labium and maxilla, fig. 39. The bacilliform process is about half as long as the maxilla.

Thorax very finely striate, with long hairs. Scutum not quite as long as its maximum width [3 : 4], with fifteen hairs. Scutellum about as long as wide, with seven hairs on each side. Metanotum not much wider than scutellum and axillae combined, propodeum distinctly wider. Propodeal peritremata large; tufts of about ten hairs occur beneath the spiracles. Fore wing (9 : 4), 1.6 mm long; nearly the whole surface setose. Submarginal, marginal, stigmal, and postmarginal veins in ratio 22 : 6 : 7 : 11; stigmal vein with three or four pustules, submarginal vein with three. Hind wing (5 : 2), 1.0 mm long. Femur of the fore leg (fig. 40) about as long as coxa and trochanter combined, the tibia half as long, with five apical teeth — the first of which is blunt — arranged in a dorsal comb. Tarsal segments with expanded plantar edges, the first segment is distinctly longer than the fifth [7 : 5], and more than twice as long as the subequal intermediates. Tibia of the mid leg about as long as trochanter and femur combined. Tarsus pentamerous, the segments in ratio 17 : 7 : 8 : 7 : 14. Femur of the hind leg (fig. 41) with a very distinct ventral groove. Tibia with one apical axial tooth,



Figs. 80—83, *Ceratosolen abnormis,* West New Guinea, male, 80, detail of hind leg, 81, apex of abdomen, 82, mandible, 83, mid leg, axial aspect, 84—91, *C. sordidus,* Solomon I., 84, detail of female hind leg, 85—88, male, 85, mandible, 86, detail of hind leg, 87, male, 88, mid leg, 89, detail of female fore leg, 90, male antenna, 91, male fore leg. Figs. 87, × 40; 81, 91, × 90; 80, 82—86, 88—90, × 115

and a bidentate antaxial tooth. Tarsal segments in ratio 20 : 8 : 5 : 6 : 11.

Gaster. Ovipositor distinctly projecting.

Length, 1.7—2.1 mm. Colour black-brown, distal parts of the extremities lighter.

Remark.

C. boschmai is easily distinguished from its congeners by the peculiar propodeum of the male. It is a pleasure to dedicate this species to Dr. H. Boschma, Professor of Systematic Zoology at Leiden University.

Ceratosolen bianchii sp. n. (figs. 54—67)

Material.

Series ♀, ♂, ex *Ficus* spec. ("no. 2"), Fiji I., leg. C. E. Pemberton, 1920; coll. HSPA, slide mounted: ♂ (holotype), ♀ (allotype), ♀, ♂ (paratypes); coll. ML, no. 598: 5 ♀, 2 ♂.

Description.

Male. Head (fig. 57): the width two-thirds of the length. Median lobe of epistomal margin broad. Eyes present. Antennal grooves half closed. Antenna (fig. 62) five-segmented; the scape not quite twice as long as its maximum width, the pedicel as long as the width of the scape, and half as wide. Third segment (1 : 2) annuliform, fourth and fifth segments subequal in length, the latter (2 : 1) is narrower than the former. Labium and maxillae, fig. 63; labium with one ventral hair, maxilla with one lateral hair. The maxillae are rather long; and they fold easily in the slides. Mandible, fig. 64.

Thorax, fig. 57. Pronotum approximately twice as long as wide anteriorly, wider behind. Mesonotum large; metanotum narrower, incompletely separated from the long propodeum. Propodeal peritremata large. Femur of the fore leg (fig. 54) more than twice as long as the tibia. Apical dentation of the tibia consisting of four dorsal and two ventro-apical teeth. Tarsus bimerous, though the two segments are not completely separated. Segments in ratio 5 : 7. Mid leg, figs. 61, 66. Femur longer than coxa and trochanter combined, but shorter than the tibia [8 : 11]. Tibia with a few stout hairs and spines, especially on the antaxial surface, and one ventro-apical tooth. Tarsus pentamerous, segments in ratio 9 : 3 : 4 : 3 : 12. Coxa of the hind leg (fig. 59) semiglobular, trochanter small; the femur expanded dorsally. Tibia not quite as long as the femur, with four antaxial ventro-apical teeth. Tarsus pentamerous, the segments in ratio 24 : 9 : 8 : 8 : 15.

Gaster. Genitalia (fig. 67) without cerci or parameres; apex of the aedeagus scarcely dilated.

Length, 2.0—2.1 mm. Colour uniformly dark yellow-brown.

Female. Head approximately as long as wide across the eyes. Eyes small, the longitudinal diameter distinctly shorter than the cheek [7 : 9]. Face with rather

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[1] As the material has been desiccated, some characters are not easily to be observed, and some must remain undescribed.

long pubescence. Antenna, fig. 56[1]). Scape two and a half times as long as the pedicel. Fifth segment with five oblong subapical and two circular sensilla. Sixth segment twice as long as the fifth, seventh and eighth segments subequal, shorter than the sixth. Apical three (or two?) segments shaped so as to form a club, ninth and tenth segments subequal, the eleventh shorter. Sixth to eleventh segments with irregular rows of oblong sensilla. Mandible (fig. 65) with twelve ventral ridges, its appendage with ten. Labium and maxillae, fig. 60. Labium with one apical hair, maxilla with a subapical hair and a bacilliform process. The latter has not quite one third the length of the maxilla, and bears a long apical hair.

Thorax pubescent, relative proportions much as in *C. boschmai*. Propodeum with five hairs below the large peritremata. Fore wing, 2.0 mm long, more than twice as long as wide. Submarginal, marginal, stigmal, and postmarginal veins in ratio 15 : 6 : 4 : 6. Stigmal vein with four pustules, submarginal vein with three. Postmarginal vein rather robust and dark. Hind wing (6 : 1), 1.3 mm long. Fore leg (fig. 55): femur and trochanter together as long as tibia and tarsus combined, and not quite twice as long as the coxa. Apical dentation of the tibia consisting of five teeth, the ventral one of which is blunt; the dorsal one is the longest. Tarsus five-segmented; first and fifth segments subequal in length, fourth segment approximately half as long, second and third segments shorter, subequal. Coxa of the mid leg semiglobular; the trochanter small, the femur thrice as long; the tibia a little longer than the femur, with one ventro-apical spur. Tarsal segments in ratio 42 : 20 : 21 : 16 : 25. Hind leg, fig. 58. Femur with a distinct ventral groove. Antaxial apical tooth of the tibia tridentate (the median tooth the longest); the axial apical tooth long and curved. Tarsal segments in ratio 15 : 7 : 5 : 4 : 7, rather pubescent.

Gaster. Ovipositor slightly projecting beyond the apex of the gaster.

Length, 2.3 mm. Colour olive-brown, thorax and apical part of the gaster darker.

Remark.

This species appears to be close to *C. boschmai,* but it differs in the relative proportions of the male thorax, the absence of cerci and parameres from the male genitalia, the female antenna, the dentation of the fore and hind tibiae, etc.

I have great pleasure in naming the new species after F. A. BIANCHI, Principal Entomologist, Experiment Station, HSPA, Honolulu, who gave much help by making F. X. WILLIAMS' collection of fig wasps available for examination.

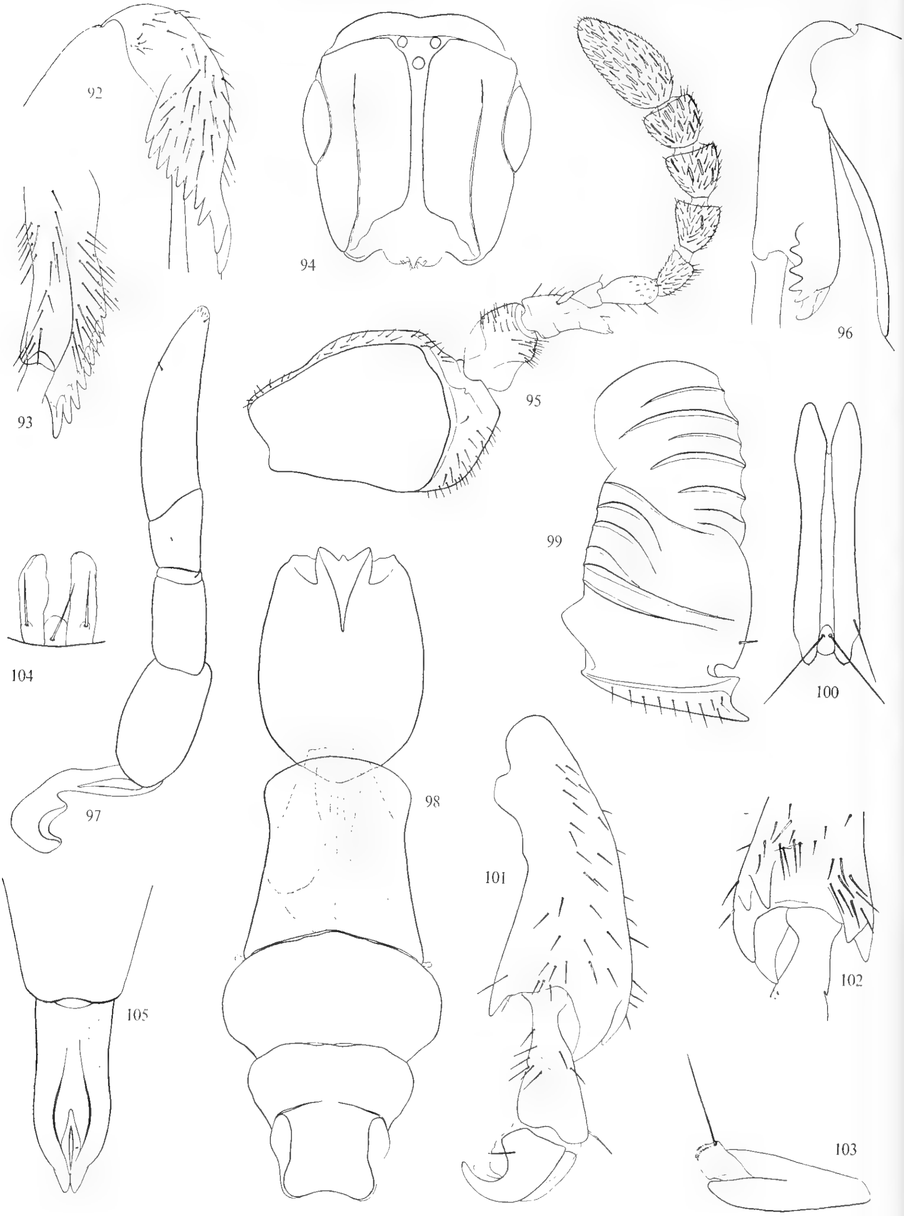
Ceratosolen armipes sp. n. (figs. 68—79)

Material.

Series ♀, ♂, ex *Ficus itoana* Diels (det. E. J. H. CORNER), Wau (Terr. New Guinea), 3000 ft. alt., leg. E. J. H. CORNER, 13.IX.1960; coll. no. 546; ♂ (holotype), slide 546a, ♀ (allotype), 546d, ♀, ♂ (paratypes), 546b, c, e.

Description.

Male. Head (fig. 73) nearly rectangular, longer than wide [5 : 4]. Dorsal



Figs. 92—103, *Ceratosolen abnormis,* West New Guinea (94, 103: specimens from East New Guinea), 92—96, female, 92, detail of fore leg, 93, fore tibia, axial aspect, 94, head, 95, antenna, 96, detail of hind leg, 97, male antenna, 98, male, 99, female mandible, 100, female labium and maxillae, 101—103, male, 101, detail of fore leg, axial aspect, 102, apex of fore tibia, 103, labium and maxillae, lateral aspect, 104—105, *C. bakeri,* Luzon, male, 104, labium and maxillae, 105, apex of abdomen. Figs. 94, 98, × 40; 95, × 90; 92, 93, 96, 97, 99—103, 105, × 115; 104, × 160

surface anteriorly with small hairs. Epistomal margin broadly tridentate, the lateral lobes with one subapical hair, and one hair at mid length. Antennal grooves half closed. Antenna (fig. 72) four-segmented. Pedicel (2 : 1) two-thirds the length of the scape (2 : 1), and little shorter than the third segment (2 : 1). Apical segment (14 : 5) nearly one and a half times as long as the third segment. Mandible, fig. 77. Labium and maxillae atrophied, the hypostomal margin with two long hairs.

Thorax, fig. 73. Pronotum approximately twice as long as wide anteriorly, the posterior width two-thirds of the length. Mesonotum sub-oval, wider than long [5 : 4]. Metanotum narrower than the mesonotum, about twice as wide as long. Propodeum incompletely separated from the metanotum, longer than wide [13 : 9], with the large spiracular peritremata protruding laterally. Fore leg, fig. 76. Femur twice as long as the tibia. Tibia with three dorsal and three ventro-apical teeth. Tarsus bimerous, segments in ratio 7 : 8. Tibia of the mid leg (fig. 74) longer than the femur [5 : 4], the ventro-apical edges produced; the dorsal edge with many stout spines, which also occur on the axial and antaxial disks, and at the ventral apex. Tarsus pentamerous, segments in ratio 14 : 5 : 5 : 5 : 16. Tibia of the hind leg (fig. 78) shorter than the large femur [8 : 11], with three ventro-apical teeth. Dorsal edge produced at mid length. Tarsus pentamerous, segments in ratio 21 : 7 : 5 : 5 : 19, with ventral protuberances and few hairs.

Gaster. Tergites weakly sclerotized. Genitalia with very small, hyaline cerci (fig. 75), which seem to bear two claws.

Length, 2.2—2.3 mm. Colour dark brown.

Female. Head approximately as long as wide across the eyes. Longitudinal diameter of the eye not quite as long as the cheek. Pubescence scattered, denser towards the inner rims of the eyes. Antenna (fig. 69) rather short, the scape large, nearly thrice as long as the pedicel. Axial surface of the pedicel with about one hundred and fifty small spines. Fifth segment with six short sensilla. The other segments bear two to three irregular rows of small sensilla, and they are heavily pubescent. Sixth to ninth segments subequal, tenth and eleventh segments united into a club. Mandible (fig. 79), and its appendage, with eight ventral ridges. The labium bears two long apical hairs.

Thorax. Pronotum wide. Scutum as long as wide at mid length, wider anteriorly, and tapering behind. Width of the scutellum four-fifths of the length; scutellum with about twenty hairs. Metanotum with a few lateral hairs. Propodeum with ten hairs next to the spiracular peritremata, and four larger hairs beneath. Fore wing (2 : 1), 2.1 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 9 : 3 : 2 : 6. Submarginal vein with two pustules, stigmal vein with three. Hind wing (7 : 2), 1.2 mm long. Wings pubescent. Fore leg, fig. 68. Femur more than one and a half times as long as the coxa, and nearly twice as long as the tibia. Tibia apically with a dorsal comb of five teeth, the first of which is blunt. Tarsus pentamerous, rather pubescent, segments in ratio 5 : 2 : 2 : 1 : 3. Tibia of the mid leg nearly as long as trochanter and femur combined, with two apical spurs (fig. 70). Tarsal segments in ratio 16 : 7 : 6 : 4 : 8. Hind leg, fig. 71: the femur about one and a half times as long as the coxa, and nearly twice as long as the tibia. Ventral edge of the femur with a distinct groove. Apex of tibia with a shovel-shaped axial tooth and a three-dentate antaxial tooth. Tarsus pubescent, segments in ratio 16 : 7 : 6 : 5 : 7.

Gaster. Projecting part of the ovipositor approximately one third the length of the gaster.

Length, 2.0—2.3 mm. Colour dark brown, with lighter extremities.

Remark.

C. armipes is remarkable in having, among other differential characters, the armature of the male mid leg rather heavy, the propodeum of a peculiar shape, and the apical two segments of the female antenna united into a club. Apparently, it is related to *C. boschmai, C. bianchii*, and *C. sordidus*, and to some extent also to *C. abnormis.*

Ceratosolen sordidus sp. n. (figs. 84—91)

Material.

Series ♂, 1 immature ♀, ex *Ficus cynaroides* Corner (det. E. J. H. CORNER), Bougainville I. (Solomon Is.), leg. J. K. L. WATERHOUSE, 1933, no. 845; coll. no. 552; ♂ (holotype), slide 552b, ♂ (paratype), 552a, ♀, ♂ (allotype and paratype, in copula), 552c.

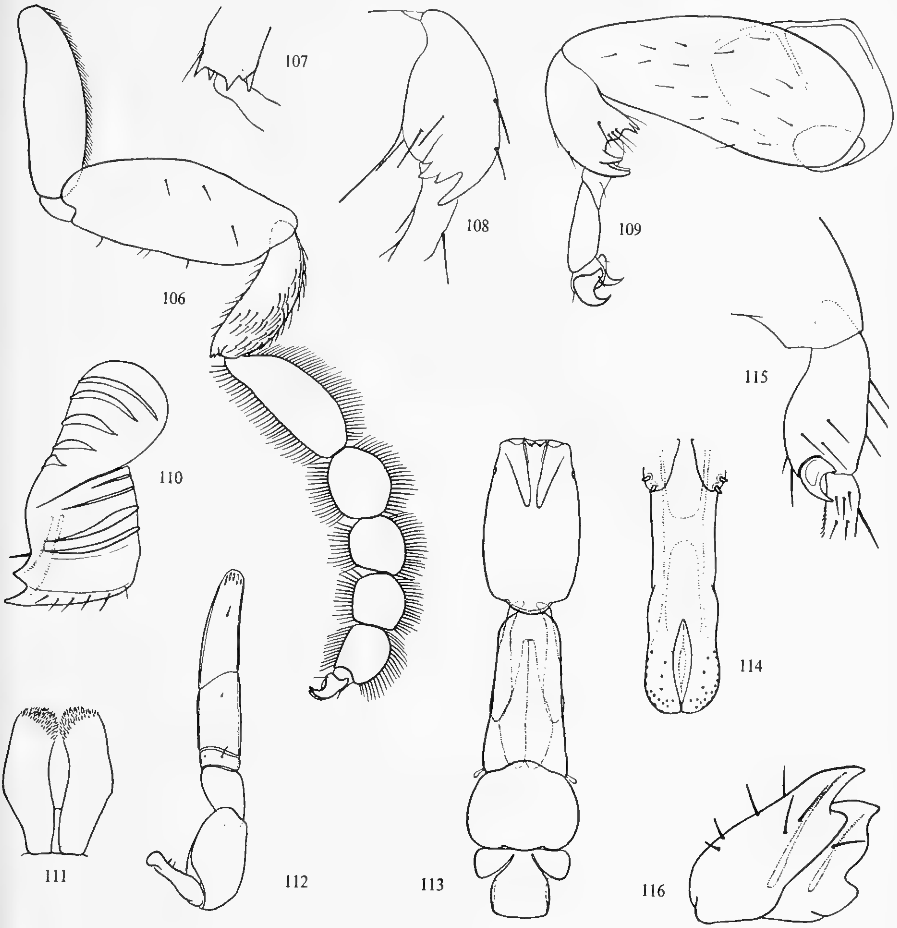
Description.

Male. Head (fig. 87): width at mid length three quarters of the length, slightly narrower in front and behind. Lateral lobes of the epistomal margin wide. Eyes absent. Antennal grooves half closed. Antenna (fig. 90) five-segmented; the scape (9 : 5) one and a half times as long as the pedicel (2 : 1), third segment annuliform. Fourth segment (15 : 8) shorter than the apical segment (19 : 8), which is approximately as long as the scape. Mandible, fig. 85. Labium and maxillae present, but not clearly visible in the badly preserved material.

Thorax, fig. 87. Pronotum nearly twice as long as wide anteriorly, and not much longer than wide posteriorly. Mesonotum transverse, incompletely separated from the metanotum, and about as wide. Metanotum and propodeum narrowly fused; propodeum more than twice as long as wide, with large spiracular peritremata. Fore leg, fig. 91. Femur more than twice as long as the tibia, which bears two apical teeth at the ventral edge, and four at the dorsal edge. Tarsus bimerous, segments subequal. First segment with small ventral spines. Femur and tibia of the mid leg (fig. 88) subequal in length; the tibia with a few dorsal spines, the ventral edge produced. Tarsus pentamerous, with stout ventral spines on the first four segments; the segments in ratio 10 : 3 : 4 : 3 : 8. Tibia of the hind leg (fig.86) with four apical teeth, and with small spines along the dorsal edge. First four tarsal segments with ventral spines and small protuberances; the segments in ratio 15 : 5 : 4 : 4 : 12.

Gaster. The genitalia seem to bear no cerci, but the state of preservation does not permit of a close examination.

Length, 1.0—1.1 mm.



Figs. 106—116, *Ceratosolen gracilis,* Luzon, 106, male hind leg, 107, apex of male mid tibia, 108, detail of female fore leg, 109, male fore leg, 110, female mandible, 111—114, male, 111, labium and maxillae, 112, antenna, 113, male, 114, apex of abdomen, 115, detail of female hind leg, 116, male mandible. Figs. 113, × 50; 106, × 80; 109, × 115; 107, 110, 112, 115, × 155; 108, 114, 116, × 215; 111, × 365

Female. The immature female specimen is badly preserved. Some characteristics are: the antennal club consists of the apical three segments, which, however, are not completely fused; the fore tibia (fig. 89) and the fore and hind tarsi are heavily armed with spines; the hind tibia (fig. 84) bears an apical armature, which is shaped as in the other species related to *C. armipes.*

Remark.

Although the specimens are badly preserved, and the new species could not be described in full, *C. sordidus* is easily recognized by the shape of the male head and thorax, and by the armature of male and female legs.

Ceratosolen bakeri Grandi (figs. 104 and 105)

Ceratosolen bakeri Grandi, 1927a, pp. 312—314, Pl. 2 figs. 18—25, Pl. 3 figs. 26—32 [descr. ♀, ♂, ex *Ficus pseudopalma* Blanco, Los Baños (Luzon, Philippine Is.), leg. C. F. Baker]; Williams, 1928, pp. 12—13 [biological note].

Material.

Series ♀, ♂, ex *Ficus pseudopalma* Blanco, Los Baños (Luzon, Philippine Is.), leg. C. F. BAKER; coll. USNM.

Series ♀, ♂, ex *Ficus pseudopalma* Blanco, Manila (Luzon, Philippine Is.), leg. WESTER, 30.IV.1919; coll. HSPA; coll. ML, no. 591: 2 ♀, 2 ♂.

Fragments of 2 ♀, ex *Ficus pseudopalma* Blanco (det. E. J. H. CORNER), Phil. Nat. Herb. no. 16894; coll. ML, slide no. 385a.

Description — Additional note.

Male. Labium and maxillae (fig. 104) with one long hair each. Genitalia (fig. 105) without cerci.

Ceratosolen abnormis sp. n. (figs. 80—83; 92—103)

Material.

Two immature ♀, 6 ♂, ex *Ficus dammaropsis* Diels (det. E. J. H. CORNER), Begowri River (N.W. New Guinea), leg. GJELLERUP, no. 207; coll. no. 408; ♂ (holotype), slide 408a, ♀ (allotype), 408d, ♂ (paratypes), 408b, c.

One immature ♀, ex *Ficus dammaropsis* Diels (det. E. J. H. CORNER), Albatros Bivak (West New Guinea), leg. W. M. DOCTERS VAN LEEUWEN, no. 9162; coll. no. 394.

Three ♀, series ♂, ex *Ficus dammaropsis* Diels var. *obtusa* Corner, Aiyura (Terr. New Guinea), Highland Experiment Station, leg. J. H. ARDLEY, 5.IX. 1961; coll. no. 575; ♀, ♂ (paratypes), slides 575a, b, c.

Description.

Male. Head (fig. 98) one third longer than its maximum width and a little over twice as long as wide anteriorly. Eyes absent. Epistomal margin with two large, wide lateral lobes; the median lobe is smaller. Lateral lobes with many small hairs. Antennal grooves half closed. Antenna (fig. 97) five-segmented; scape (15 : 8) one and a half times as long as the pedicel (5 : 3); third segment annuliform. Fourth segment (4 : 3) shorter than the pedicel, and about one third the length of the apical segment (11 : 3). Mandible, fig. 82. Labium and maxillae (fig. 103); labium with one (coll. no. 575) or three (coll. no. 408) hairs.

Thorax, fig. 98. Pronotum little longer than wide posteriorly. Anterior width nearly three quarters of the length. Mesonotum very wide, distinctly more than twice as wide as long. Metanotum narrower, about as wide as the pronotum posteriorly, incompletely separated from the propodeum. Propodeum approximately as long as wide, with large peritremata. Fore leg, figs. 101, 102. Femur nearly twice as long as the tibia. Tibia with four dorso-apical teeth, and two ventral teeth. Tarsal segments fused, with a small ventral notch reminding one of the usual bimerous condition. Trochanter of the mid leg (fig. 83) half as long as the coxa, the femur not quite as long as the tibia. Tarsus pentamerous, segments in ratio 32 : 12 : 11 : 18 : 50. Coxa and tibia of the hind leg (fig. 80) subequal in length, the femur is considerably longer. Tibia with three apical teeth at the ventral edge, the relative proportions of which vary in the various samples. Tarsus with stout ventral hairs; first segment approximately thrice as long as the second, second to fourth segments subequal, the fifth segment, including the claws, two and a half times as long as the first.

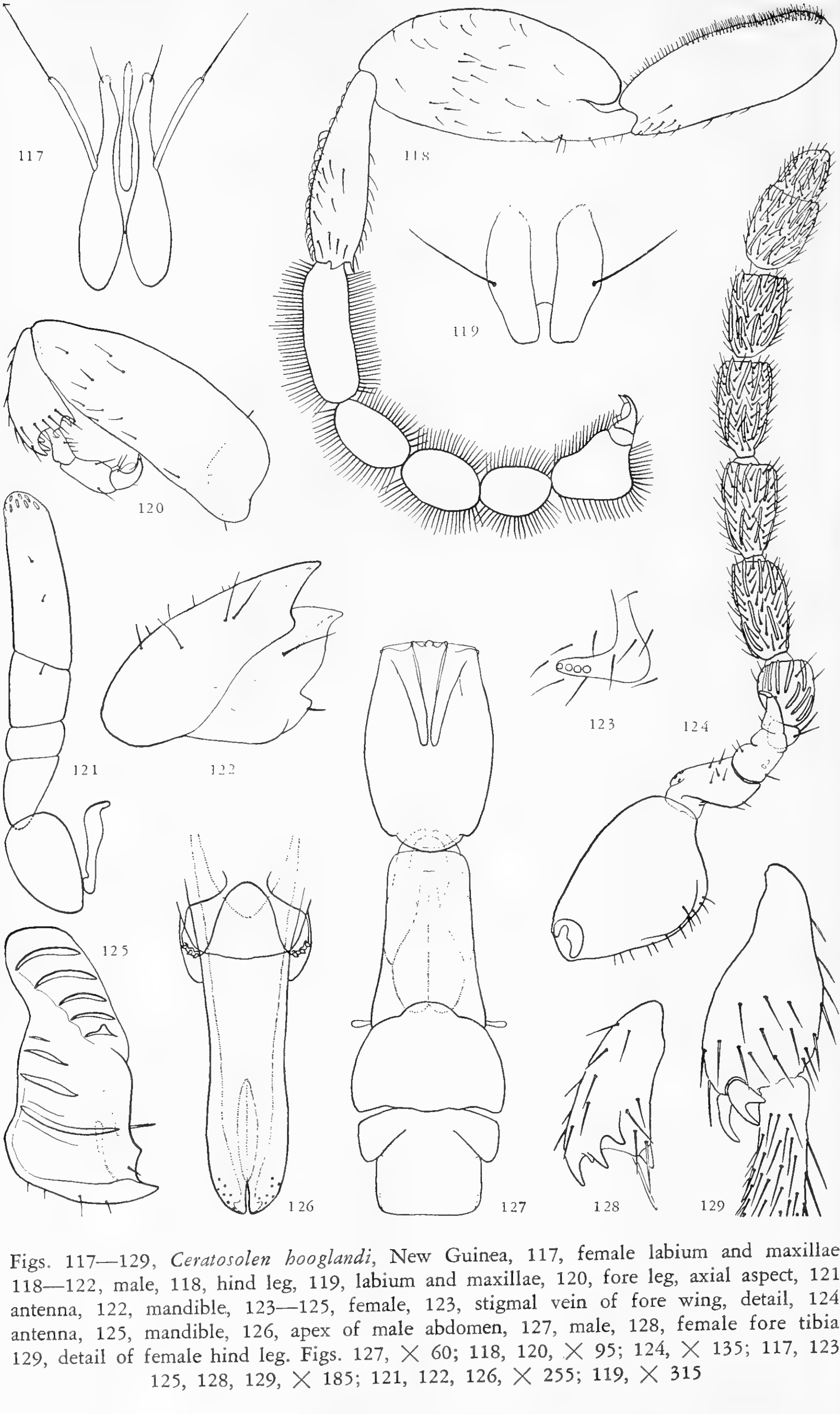
Gaster. Tenth urite, and aedeagus: fig. 81. The genitalia are different from the normal type in having very large parameres. The apodemae aedeagales are rather short and robust.

Length, 2.2 mm. Colour dark brown.

Female. The description was originally made from immature specimens (coll. no. 408), but it was later completed from the mature specimens of sample no. 575.

Head (fig. 94) approximately as long as wide across the eyes. Longitudinal diameter of the eye slightly shorter than the cheek. Antenna (fig. 95) rather short. Scape large, thrice as long as the pedicel. Third segment rather robust, fourth and fifth segments long and slender, the fifth with circular sensillar pits in the apical half. Sixth segment without sensilla, seventh segment with one oblong sensillum. Eighth and ninth segments wide, with two incomplete, irregular rows of sensilla; apical two segments united into a club, with irregular rows of sensilla. Mandible (fig. 99), and its appendage, with six ventral ridges. Labium with two hairs: maxillae in most specimens without hairs, in one specimen (575a) there is one lateral hair on one side only (fig. 100).

Thorax. Pronotum large, approximately twice as wide as long. Scutum not much shorter than wide anteriorly, glabrous. Scutellum as long as wide posteriorly, narrower in front; with about fifteen to twenty hairs. Metanotum short, lateral parts longer, with fifteen hairs. Propodeum large, nearly half as long as wide; spiracles concealed from dorsal view by antero-lateral expansions. Many long hairs occur next to and beneath the peritremata. Fore wing (5 : 2), 2.9 mm long. Surface pubescent, except for some glabrous parts near the base of the wing; with indistinct darker striae radiating from base and stigma. Submarginal, marginal, stigmal, and postmarginal veins in ratio 24 : 6 : 6 : 13. Postmarginal vein distinctly enlarged apically. Submarginal and stigmal veins with three pustules each. Hind wing (4 : 1), 1.65 mm long. Fore leg (fig. 92): femur not quite as long as tibia and tarsus combined. The tibia bears an apical row of eight to ten teeth, the dorsal one of which is particularly long. As seen on the axial side (fig. 93), the tibia appears to be a very slender segment, dorso-antaxially broadened into the wing-shaped shield bearing the apical teeth. Tarsal segments in ratio 14 : 5 : 6 : 9 : 11. Tibia of the mid leg not much longer than the femur, and as long as the tarsus. Tarsal segments in ratio 10 : 6 : 5 : 5 : 8 (including the claws). Hind leg, fig. 96. The femur has a distinct ventral groove. Apically, the tibia bears a quadridentate appendage at the antaxial edge, and a spade-shaped tooth at the axial edge. Tarsal segments in ratio 14 : 5 : 4 : 3 : 6 (including the claws).



Figs. 117—129, *Ceratosolen hooglandi*, New Guinea, 117, female labium and maxillae, 118—122, male, 118, hind leg, 119, labium and maxillae, 120, fore leg, axial aspect, 121, antenna, 122, mandible, 123—125, female, 123, stigmal vein of fore wing, detail, 124, antenna, 125, mandible, 126, apex of male abdomen, 127, male, 128, female fore tibia, 129, detail of female hind leg. Figs. 127, × 60; 118, 120, × 95; 124, × 135; 117, 123, 125, 128, 129, × 185; 121, 122, 126, × 255; 119, × 315

Gaster. The projecting part of the ovipositor three quarters the length of the gaster; the sheaths robust.

Length, 2.35 mm. Colour black-brown; wings infuscated.

Remark.

The female of *C. abnormis* is abnormal in various aspects (e.g., the antenna, dentation of fore and hind tibiae), but the species shows some resemblance to *C. armipes* and relatives.

There is some variation between the specimens from West and East New Guinea, to which more attention should be given when more and better material becomes available.

Ceratosolen crassitarsus (Mayr)

Blastophaga (Ceratosolen) crassitarsus Mayr, 1885, pp. 154, 161, 163, 171—172, Pl. XI fig. 7 [key ♀, ♂, descr. ♀, ♂, ex *Ficus (Cystogyne) Ribes* Reinw. (det. Colms), Sukawana (Tangkuban Prahu, near Bandung, Java), leg. H. Solms-Laubach; type: ♂].

Ceratosolen crassitarsus: Grandi, 1916a, pp. 150, 152 [♀, ♂, in key, Java]; 1917, pp. 40—46, figs. XIV—XV [descr. ♀, ♂, ex *Ficus ribes* Reinw., Tjibodas (Java), Bot. Gdn., leg. J. Boldingh, II.1915]; 1928c, p. 172 [type specimens studied].

Material.

Six ♀, ex *Ficus ribes* Reinw., Tjibodas (Java), leg. J. H. de Gunst, 5.XI.1954; coll. no. 94.

Series ♀, ♂, ex *Ficus ribes* Reinw., Tjibodas (Java), 20 & 23.XII.1954; coll. no. 145; ♂, slide 145a.

Remark.

For the records of *C. ? crassitarsus*: Grandi (1923a, p. 299; 1927b, p. 174), see p. 83.

Ceratosolen gracilis sp. n. (figs. 106—116)

Material.

Series ♂, ex *Ficus ribes* Reinw. var. *cuneata* (Miq.) Corner (det. E. J. H. Corner), Mt. Pinatubo (Prov. Pampanga, Luzon, Philippine Is.), Elmer no. 21980; coll. no. 401; ♂ (holotype), slide 401a, ♂ (paratypes), 401b.

Series ♀, ♂, ex *Ficus ? merrilli*1), Mt. Maquiling (Luzon, Philippine Is.), leg. F. X. Williams, 11.V.1921, no. 202; coll. HSPA, ♀ (allotype and paratypes), and ♂ (paratypes) slide mounted; coll. ML, no. 681: 10 ♀, 10 ♂.

Series ♀, ♂, ex *Ficus merrilli*1), Mt. Maquiling (Luzon, Philippine Is.), leg. F. X. Williams, 11.V.1921, no. 303; coll. HSPA, ♀ (paratype) slide mounted.

Series ♀, ♂, ex *Ficus ribes*2), Mt. Maquiling (Luzon, Philippine Is.), leg. F. X. Williams, 10.V.1921, no. 404; coll. HSPA.

Seven ♀, 6 ♂, ex *Ficus ribes*2), Mt. Maquiling (Luzon, Philippine Is.), leg. F. X. Williams, 26.XI.1921; coll. HSPA.

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1) *Ficus merrilli* Elmer = *F. ribes* Reinw. var. *cuneata* (Miq.) Corner.

2) True *Ficus ribes* Reinw. does not occur in the Philippines.

Description.

Male. Head (fig. 113) more than twice as long as wide anteriorly, its maximum width nearly two-thirds of the length. Lateral lobes of the epistomal margin rather sharp. Pubescence sparse and short. Eyes distinct. Antennal grooves open, wide behind. Antenna (fig. 112) five-segmented; scape (2 : 1) slightly more than one and a half times as long as the pedicel (2 : 1), the first flagellar segment short, about one fifth the length of the second (10 : 7), which is three quarters the length of the apical segment (8 : 3). Mouthparts, figs. 111, 116.

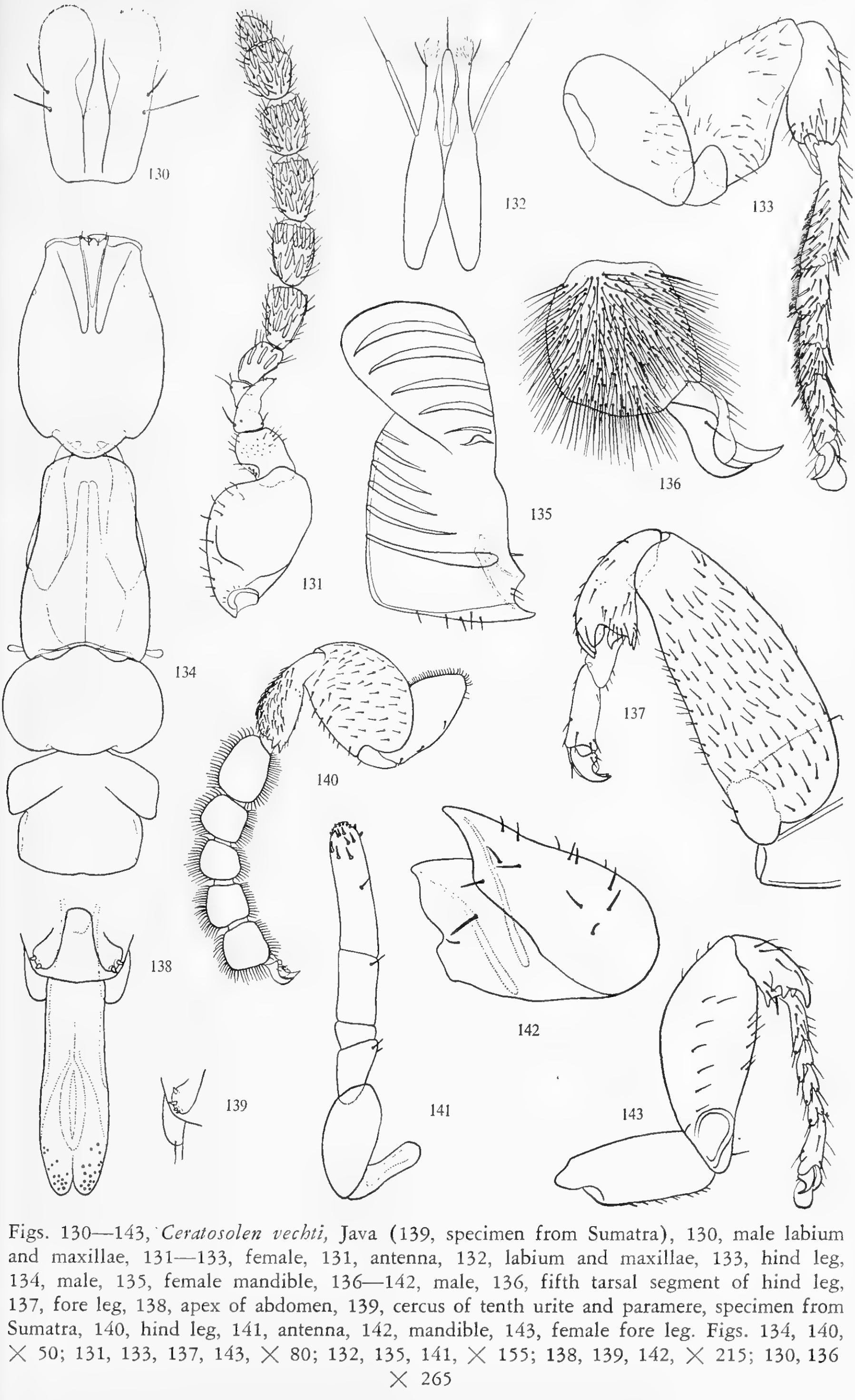
Thorax, fig. 113. Pronotum more than two and a half times as long as wide anteriorly, and twice as long as its maximum width. Mesonotum wider than long [5 : 4]. Metanotum not quite as wide as the mesonotum, and incompletely separated from the propodeum, which is nearly as long as wide. Fore leg (fig. 109): femur more than twice as long as the tibia. Tibial armature consisting of four dorso-apical teeth, one of which is very small, and two ventral teeth. Tarsal segments in ratio 5 : 6. Mid leg slender, the coxa nearly as long as trochanter and femur combined, and as long as the clavate tibia. The tibia apically armed with a series of sharp teeth (fig. 107). Tarsus pentamerous, the first segment slightly longer than the fifth [14 : 13], the intermediates subequal, not quite half as long as the fifth [5 : 12]. Hind leg (fig. 106) rather long, the femur as long as coxa and trochanter combined; all these segments slender. Tibia nearly two-thirds the length of the femur, with a dorsal hyaline ridge. Ventro-apical armature and pubescence as in the figure. Tarsus dilated, the first segment as long as the tibia, the second half as long; third to fifth segments subequal, two-thirds the length of the second. Pubescence half as long as the width of the segments.

Gaster. Cerci of the tenth urite with two claws, aedeagus slightly dilated subapically and apically (fig. 114).

Length, 1.1 mm. Colour uniformly yellow-brown.

Female. Antenna consisting of eleven segments, of which the apical two form a loose club. Scape approximately twice as long as the pedicel, appendage of the third segment rather short and robust. Fifth segment three quarters the length of the seventh, the eighth segment slightly longer than the seventh, ninth to eleventh segments gradually diminishing in size. The funicular segments bear two irregular rows of long sensilla. Maxilla without a bacilliform process, but with a long, subapical hair. Mandible (fig. 110) with four ventral ridges, its appendage with five ridges.

Thorax. A few hairs occur above and beneath the propodeal spiracle. Fore wing (2 : 1), 1.4 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 20 : 7 : 7 : 11, the submarginal vein with three pustules, the stigmal vein with four pustules. Hind wing (4 : 1), 0.8 mm long. Coxa of the fore leg (fig. 108) two-thirds the length of the femur, the tibia not quite half as long as the femur. Tibial armature consisting of four dorsal teeth. Tarsal segments approximately in ratio 11 : 7 : 5 : 4 : 5. Mid leg slender, the subclavate tibia not quite as long as femur and trochanter combined. First tarsal segment twice as long as the second, second to fifth segments subequal. Hind leg (fig. 115): length of the coxa two-thirds of that of the femur, which is not nearly twice as long as the



Figs. 130—143, *Ceratosolen vechti,* Java (139, specimen from Sumatra), 130, male labium and maxillae, 131—133, female, 131, antenna, 132, labium and maxillae, 133, hind leg, 134, male, 135, female mandible, 136—142, male, 136, fifth tarsal segment of hind leg, 137, fore leg, 138, apex of abdomen, 139, cercus of tenth urite and paramere, specimen from Sumatra, 140, hind leg, 141, antenna, 142, mandible, 143, female fore leg. Figs. 134, 140, × 50; 131, 133, 137, 143, × 80; 132, 135, 141, × 155; 138, 139, 142, × 215; 130, 136 × 265

tibia [12 : 7]. The antaxial tibial tooth is bidentate; the axial tooth, usually found in the species of *Ceratosolen*, is lacking in all specimens studied. Tarsus pubescent, especially along the plantar edge, the segments with heavy ventro-apical spines. Tarsal segments approximately in ratio 25 : 5 : 5 : 4 : 5.

Gaster. The ovipositor distinctly projecting beyond the apex of the gaster.

Length, 1.3—1.4 mm.

Remark.

Due to the fact that the samples have been desiccated, this species could not be described and figured in the usual detail. Notably the chaetotaxy must for the greater part remain undescribed. Yet, *C. gracilis* is easily recognizable by its size, by the relatively long hind legs of the male, and by the absence of a bacilliform process from the female maxilla.

Ceratosolen hooglandi sp. n. (figs. 117—129)

Material.

Series ♀, ♂, ex *Ficus bernaysii* King (det. E. J. H. CORNER), Mawan Village (Gogol Valley, Madang distr., Terr. New Guinea), leg. R. D. HOOGLAND, 16.VI.1955, no. 4890; coll. no. 362; ♂ (holotype), slide 362a, ♀ (allotype), 362c, ♂, ♀ (paratypes), 362b, d.

Series ♀, ♂, ex *Ficus bernaysii* King (det. E. J. H. CORNER), Lae (Terr. New Guinea), Busu River, leg. E. J. H. CORNER, 8.IX.1960, NGF 12471; coll. no. 517.

Description.

Male. Head (fig. 127) more than twice as long as wide anteriorly, and one and a half times as long as its maximum width. Pubescence short and sparse. Epistomal margin with four short hairs. Eyes absent. Antennal grooves open, not very wide behind. Antenna (fig. 121) consisting of five segments. Pedicel (5 : 3) more than half as long as the scape (8 : 5); the first funicular segment (5 : 8) half as long as the pedicel, the second flagellar segment (5 : 4) half as long as the first; the apical segment (3 : 1) more than twice as long as the second. Mandible, fig. 122. Maxilla and labium, fig. 119; maxilla with one lateral hair.

Thorax, fig. 127. Pronotum nearly twice as long as wide anteriorly; the maximum width four-fifths of the length. Length of the mesonotum three quarters of the width. Metanotum incompletely separated from the propodeum, slightly narrower than the mesonotum. Tibia of the fore leg (fig. 120) not nearly half as long as the femur, with three large dorsal and three ventro-apical teeth. Second tarsal segment slightly longer than the first. Coxa of the mid leg as long as the femur, tibia nearly as long as femur and trochanter combined. Tibia with only one inconspicuous apical tooth. Tarsal segments in ratio 3 : 1 : 1 : 1 : 3. Hind leg, fig. 118. Coxa and tibia shorter than the femur [7 : 8]. Tibia one third longer than the first tarsal segment, which is as long as third and fourth segments combined. Second, third, and fifth segments subequal, fourth smaller. Tarsal pubescence distinctly shorter than half the width of the segments; dilatation not very wide.

Gaster. Cerci of the tenth urite with three short claws, aedeagus not dilated at apex (fig. 126).

Length, 1.4 mm. Colour uniformly yellowish brown.

Female. Head longer than wide between the external margins of the eyes [10 : 9]. Longitudinal diameter of the eye little shorter than the cheek. Pubescence rather long. Antenna (fig. 124): the scape relatively small, about as long as third to fifth segments combined. Pedicel slender, and little more than one third the length of the scape. Fourth segment very small, the fifth more than twice as long. Sixth segment more than one and a half times as long as the fifth, seventh to tenth segments gradually diminishing in size; the eleventh as long as the fifth. Funicular segments with two rows of long narrow sensilla. Mandible (fig. 125) with four ventral ridges; the appendage shorter than the mandible, with five ridges. Maxilla (fig. 117) with a long bacilliform process, which is nearly half as long as the maxilla. Maxilla as well as its process with a long hair; labium without hairs.

Thorax slender, its parts with many long hairs. Scutum as long as wide anteriorly, with approximately ten hairs on each side. Scutellum little longer than wide anteriorly, with lateral rows of fifteen to twenty hairs. Metanotum with five hairs on each side of the mid-line. Propodeum wide; little groups of hairs are situated above and beneath the spiracle. Forewing (7 : 3), 1.4 mm long. Submarginal, marginal, stigmal, and postmarginal veins approximately in ratio 30 : 9 : 11 : 17. Submarginal vein with three pustules, stigmal vein (fig. 123) with four. Hind wing (5 : 1), 0.8 mm long. Fore leg, fig. 128. Coxa nearly as long as the femur, tibia half as long. Tibia with four teeth along the dorsal edge, ventral edge with one tooth. Tarsal segments in ratio 3 : 2 : 2 : 2 : 3. Mid leg slender, tibia shorter than trochanter and femur combined [7 : 8]; tarsal segments in ratio 12 : 5 : 4 : 4 : 7. Coxa and femur of the hind leg (fig. 129) subequal in length, the tibia shorter [8 : 11]. Tibia with the usual two apical teeth, the one bidentate, and the other unidentate. First tarsal segment as long as the tibia, and nearly thrice as long as the fifth tarsal segment. Intermediate segments shorter than the fifth [2 : 3]. Ventral edge of the tarsus fimbriated.

Gaster. Ovipositor scarcely projecting beyond the apex of the gaster.

Length, 1.4 mm. Colour dark brown, with lighter ventral surface and legs. Nervures of wings yellowish brown.

Remark.

C. hooglandi is recognizable by the long and slender tibia and metatarsus of the male hind leg, and by the relatively long bacilliform process of the female maxilla.

It is a pleasure to name the species after its collector, Dr. R. D. HOOGLAND.

Ceratosolen vechti sp. n. (figs. 130—143; Pl. 1)

Material.

Series ♀, ♂, ex *Ficus lepicarpa* Bl.[1]) (det. E. J. H. CORNER), Tjibodas (Java),

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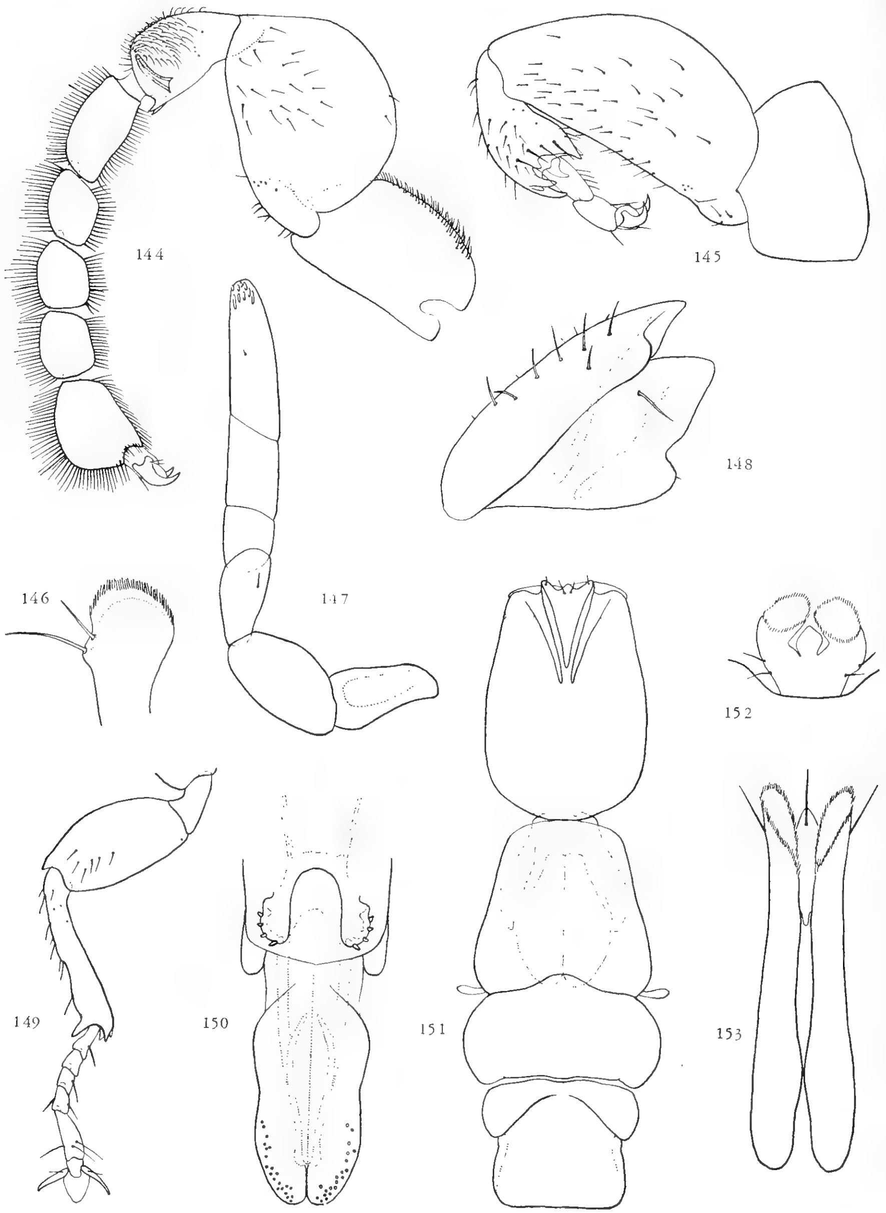
[1]) Discussion of host record, see p. 98.



Figs. 144—151, *Ceratosolen nugatorius*, Kelantan, male, 144, hind leg, 145, fore leg, 146, maxilla, 147, antenna, 148, mandible, 149, mid leg (coxa omitted), 150, apex of abdomen, 151, male, 152—153, *C. bisulcatus*, Java, 152, male labium and maxillae, 153, female labium and maxillae. Figs. 151, × 60; 144, 145, 149, × 95; 147, × 185; 148, 150, 152, 153, × 255; 146, × 315

along stream, 1500 m alt., leg. J. H. DE GUNST, 16.XI.1954; coll. no. 98; ♂ (holotype), slide 98a, ♀ (allotype), 98d, ♂, ♀ (paratypes), 98b, c, e, f.

Six ♀, 5 ♂, ex *Ficus lepicarpa* Bl., Tjibodas (Java), Mt. Gedeh, 1400 m alt., leg. J. H. DE GUNST, 16.XI.1954; coll. no. 6.

Fragments ♀, ex *Ficus lepicarpa* Bl., Tjibodas (Java), leg. J. H. DE GUNST, 5.XI.1954; coll. no. 70.

Eleven ♀, ex *Ficus lepicarpa* Bl., Tjibodas (Java), leg. J. H. DE GUNST, 11.II.1955; coll. no. 300.

Four ♀, series ♂, ex *Ficus lepicarpa* Bl. (det. E. J. H. CORNER), Pajakumbuh (Sumatra), Mt. Sago, leg. W. MEIJER, 14.V.1955, no. 3334; coll. no. 371; ♂, slide 371a.

? Six ♀, ex *Ficus lepicarpa* Bl. (det. E. J. H. CORNER), Kundasan (N. Borneo), 4000 ft. alt., leg. E. J. H. CORNER, 6.IX.1961; coll. no. 624.

Description.

Male. Head (fig. 134) more than twice as long as wide anteriorly, its maximum width three quarters of the length. Epistomal margin with four short hairs. Pubescence short. Eyes small. Antennal grooves open, not very wide behind. Antenna (fig. 141) five-segmented; pedicel (5 : 3) half as long as the scape (2 : 1). First flagellar segment (2 : 3) small, the apical (11 : 3) somewhat longer than the scape, and more than one and a half times as long as the subapical segment (7 : 4). Mandible, fig. 142. Labium and maxillae, fig. 130; maxilla with two hairs at mid length.

Thorax, fig. 134. Pronotum twice as long as wide anteriorly, the maximum width nearly three quarters of the length. Mesonotum with rounded edges, one and a half times as wide as long. Metanotum incompletely separated from the propodeum, approximately as wide as the mesonotum; propodeum narrower, and more than twice as long as the metanotum. Femur of the fore leg (fig. 137) more than twice as long as the tibia, which bears four dorsal and three ventro-apical teeth. Tarsus bimerous, the second segment is the longer. Coxa of the mid leg nearly as long as the femur [5 : 6], the trochanter small. Tibia longer than the femur [7 : 6], apically with three teeth, the dorsal one of which is particularly long. Tarsal segments in ratio 3 : 2 : 2 : 2 : 5. Hind leg, fig. 140; coxa, femur, and tibia about equal in length [10 : 11 : 9], the tibia as long as the first and second tarsal segments combined. First tarsal segment one and a half times as long as the fifth (fig. 136), the fourth as long as the fifth, second and third segments smaller. Tarsus dilated, with pubescence approximately as long as one third the width of the segments.

Gaster. Cerci of tenth urite with two claws, aedeagus not dilated at apex (fig. 138). Some specimens from Sumatra differ in having the cerci with three or four claws, and the parameres with a subapical hair (fig. 139).

Length, 1.7 mm. Colour yellowish, with darker hind tarsi in some specimens, or only the distal segments brown.

Female. Head as long as wide across the compound eyes. Longitudinal diameter of the eye about as long as the cheek. Pubescence short. Antenna (fig. 131) with the scape as long as third to sixth segments together; the pedicel half as long as the scape, the fourth segment small, the fifth approximately twice as long. Segments six to ten subequal, the eleventh smaller. Two apical segments shaped so as to form together a club. Sensilla of the funicle numerous, rather wide, mainly situated in the distal parts of the segments. Mandible (fig. 135) with six ventral ridges, the appendage but little shorter than the mandible, with six ridges. Maxilla (fig. 132) with a bacilliform process, which is one third the length of the maxilla, and a subapical hair; labium and the process with an apical hair.

Thorax. Pronotum wide and bristly. Scutum shorter than wide anteriorly [2 : 3], scutellum nearly one and a half times as long as wide anteriorly. Scutum with three hairs, scutellum with seven to ten hairs along each lateral margin. Metanotum with eight hairs on each side of the mid line. Propodeum with little groups of hairs above and beneath the spiracle. Fore wing (2 : 1), 2.0 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 42 : 15 : 13 :23. Submarginal vein with two or three pustules, stigmal vein with four (or sometimes five). Hind wing (5 : 1), 1.2 mm long. Coxa of the fore leg (fig. 143) two-thirds the length of the femur; the tibia not half as long as the femur, with four dorsal and one ventro-apical teeth. First tarsal segment a little longer than the fifth [5 : 4], intermediates subequal, half as long as the fifth. Coxa and trochanter of the mid leg short, the tibia longer than the femur [4 : 3], tarsal segments in ratio 7 : 3 : 3 : 2 : 4. Tibia and tarsus rather bristly. Coxa of the hind leg (fig. 133) nearly as long as the femur, trochanter small. Tibia with the usual two apical teeth, more than half as long as the femur. Tarsal segments in ratio 11 : 4 : 3 : 3 : 6, with fimbriated ventral edges.

Gaster. Ovipositor barely projecting beyond the apex of the gaster.

Length, 2.2 mm. Colour dark brown, legs and ventral surface lighter. Nervures of the wings light brown.

Remark.

This species is remarkable by the robust hind legs of the males, and by the wide sensilla of the female antenna.

It is a pleasure to name this species after Dr. J. VAN DER VECHT, Professor of Systematic Zoology at Groningen University, Curator of Hymenoptera, Rijksmuseum van Natuurlijke Historie, Leiden, who recognized it as new when studying the samples from Java.

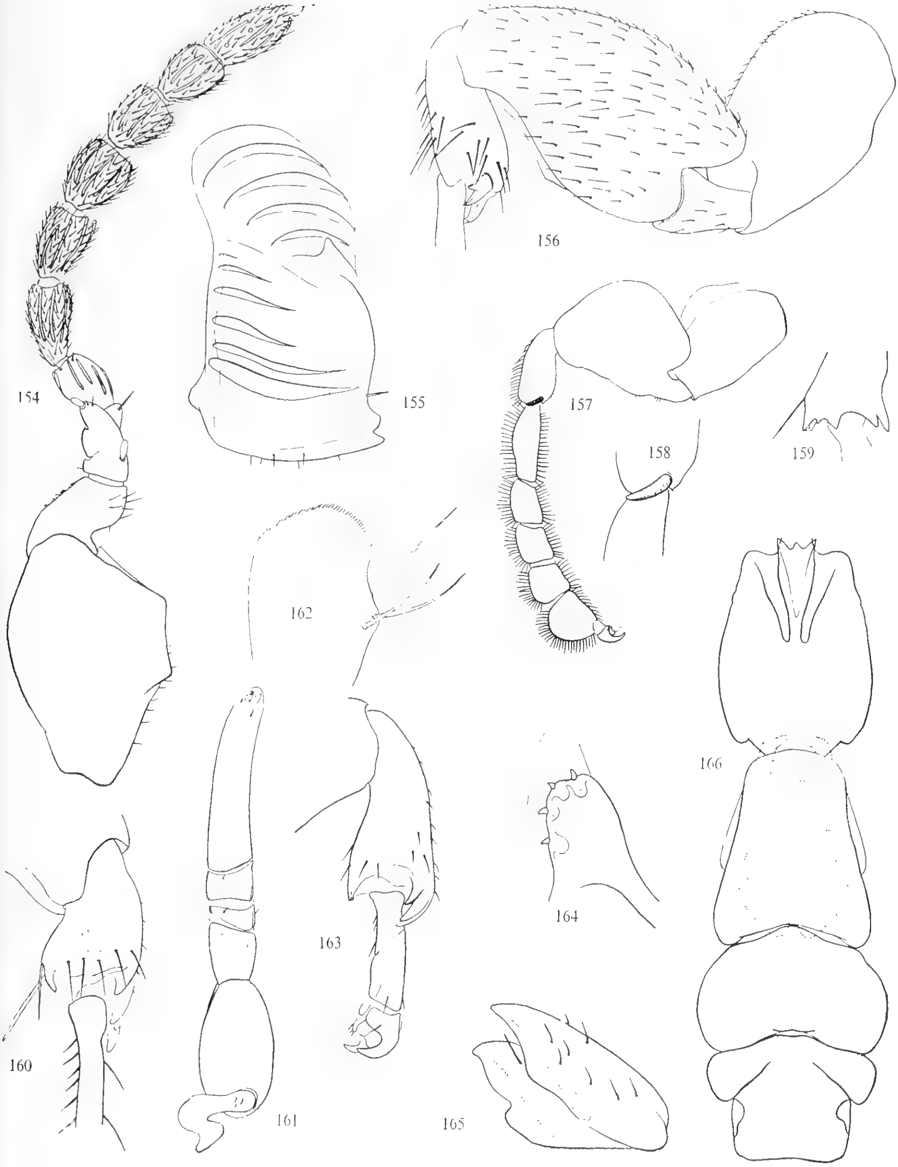
Ceratosolen nugatorius Grandi (figs. 144—151)

Ceratosolen nugatorius Grandi, 1952b, pp. 55—57, figs. V—VI [descr. ♀, ex *Ficus* spec., Kuala Lumpur (Malaya), IX.1948].

Material.

Three ♀, Kuala Lumpur (Malaya), ex coll. GRANDI; coll. ML, no. 510.

Series ♀, ♂, ex *Ficus obpyramidata* King (det. E. J. H. CORNER), Batu Papan (Kelantan, Malaya), leg. E. J. H. CORNER, Sing. F. no. 29526; coll. no. 368; ♂ (allotype), slide 368a, ♀, ♂, 368b-e.



Figs. 154—166, *Ceratosolen dentifer,* New Guinea, 154—156, female, 154, antenna, 155, mandible, 156, detail of hind leg, 157—159, male, 157, hind leg, 158, detail of hind leg, 159, apex of mid tibia, 160, detail of female fore leg, 161—166, male, 161, antenna, 162, maxilla, 163, detail of fore leg, 164, cercus of tenth urite and paramere, 165, mandible, 166, male. Figs. 157, 166, × 50; 154, 156, 158, 163, × 115; 155, 159—161, 165, × 155; 162, 164, × 365

Two ♀, 7 ♂, ex *Ficus obpyramidata* King (det. E. J. H. CORNER), Kemanan (Trengganu, Malaya), leg. E. J. H. CORNER, Sing. F. no. 25843; coll. no. 365; ♂, slide 365a.

Description — Additional note.

I consider the specimens from *Ficus obpyramidata* conspecific with *C. nugatorius* Grandi, and describe the hitherto unknown male.

Male. Head (fig. 151) twice as long as wide anteriorly, its maximum width more than two-thirds the length. Pubescence short. Epistomal margin with four short hairs. Eyes very small. Antennal grooves open, narrow behind. Antenna (fig. 147) five-segmented; the pedicel (2 : 1) two-thirds the length of the scape (9 : 5), the first flagellar segment (7 : 6) three quarters the length of the second (2 : 1), the apical segment (7 : 2) nearly twice as long as the subapical one. Mandible, fig. 148. Maxilla (fig. 146) with two lateral hairs.

Thorax, fig. 151. Pronotum one and a half times as long as wide anteriorly, and but little longer than its maximum width. Maximum width of the mesonotum approximately five-thirds of the length. Metanotum almost completely separated from the propodeum, propodeum subquadrate. Fore leg (fig. 145): the tibia approximately half as long as the femur, with four dorsal and two ventro-apical teeth. Tarsal segments in ratio 4 : 3. Coxa and femur of the mid leg subequal in length, the tibia much longer [4 : 3], with four sharp, apical teeth (fig. 149). Tarsal segments in ratio 11 : 7 : 7 : 8 : 17. Hind leg, fig. 144. Coxa little shorter than the femur, and nearly one and a half times as long as the tibia. Tibia with a large motile spur on the disk. First tarsal segment little shorter than the tibia, but longer than the fifth, intermediate segments shorter, subequal. Tarsus dilated, the pubescence nearly as long as half the width of the segments.

Gaster. Cerci of the tenth urite with four short claws (two of which are small and sometimes difficult to be observed), the aedeagus dilated (fig. 150).

Length, 1.3 mm. Colour reddish brown. Head darker than the other parts of the body, hind tarsi light brown.

Remark.

The peculiar spur of the male hind leg, the short and robust male thorax, and the very few sensilla of the female antenna, distinguish this species from its congeners.

Ceratosolen dentifer sp. n. (figs. 154—166)

Material.

Series ♀, ♂, ex *Ficus hispidioides* S. Moore var. *succosa* Corner (det. E. J. H. CORNER), Lae (Terr. New Guinea), leg. E. J. H. CORNER, X.1960; coll. no. 524; ♂ (holotype), slide 524a, ♀ (allotype), 524c, ♀, ♂ (paratypes), 524b, d.

Series ♀, ♂, ex *Ficus hispidioides* S. Moore var. *succosa* Corner (det. E. J. H. CORNER), Lae (Terr. New Guinea), leg. E. J. H. CORNER, 5.IX.1960; coll. no. 522; ♂, slide 522a, ♀, 522b.

Description.

Male. Head (fig. 166) twice as long as wide anteriorly, the maximum width two-thirds of the length. Pubescence short. Eyes small. Antennal grooves open, not very wide behind. Antenna (fig. 161) five-segmented; the scape (2 : 1) more than twice as long as the pedicel (5 : 4), the first flagellar segment short, the second approximately twice as long as the first, and half as long as the pedicel; the apical segment (5 : 1) thrice as long as the pedicel. Mandible, fig. 165. Maxilla (fig. 162) with three lateral hairs, labium without long hairs.

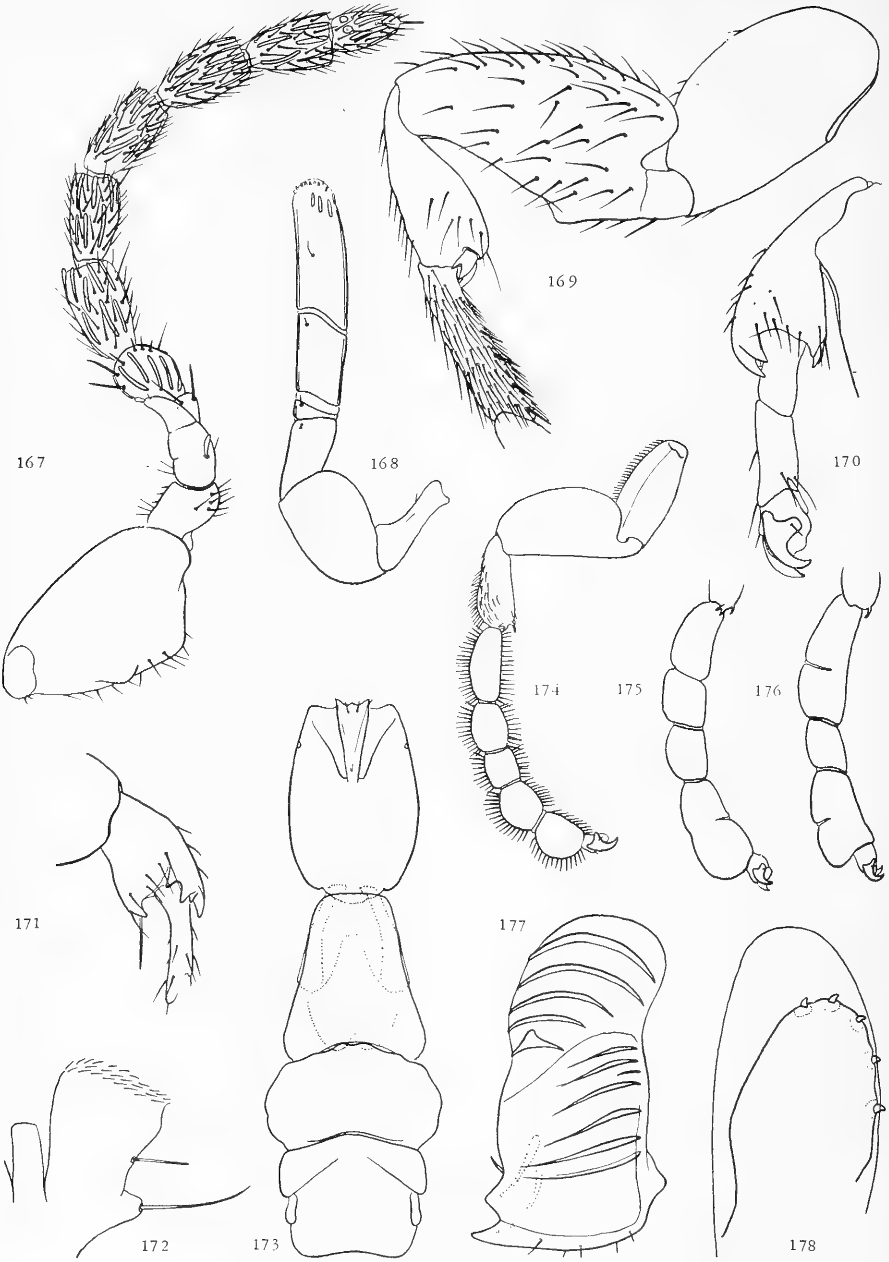
Thorax, fig. 166. Pronotum not quite twice as long as wide anteriorly, the posterior width slightly smaller than the length. Mesonotum nearly twice as wide as long. Metanotum short, incompletely separated from the large propodeum, which is nearly as long as wide [8 : 9]. Fore leg, fig. 163. Femur twice as long as the tibia, which bears four dorso-apical teeth and three ventral teeth. Tarsal segments in ratio 4 : 5. Coxa, femur, and tibia of the mid leg subequal in length, the tibia (fig. 159) with seven apical teeth. Tarsal segments in ratio 5 : 2 : 3 : 3 : 8. Hind leg (figs. 157—158): coxa smaller than the femur, the tibia about half as long. Apex of the tibia with a motile spur (fig. 158). Tarsus dilated, the first segment as long as the tibia, the second segment half as long, third and fourth segments slightly smaller than the second. Fifth segment two-thirds the length of the first. The segments gradually widening distally; pubescence approximately half as long as the width of the segments.

Gaster. Cercus of the tenth urite (fig. 164) with three or four claws.

Length, 1.6 mm; very small specimens measure 1.2—1.3 mm. Colour uniformly yellow-brown, head a trifle darker.

Female. Head as long as wide across the compound eyes, the cheeks as long as the eyes. Pubescence sparce, not very long. Antenna, fig. 154. Scape two and a half times as long as the pedicel; the pedicel with approximately fifty-five small spines on the axial surface. Fifth segment, with six long sensilla, shorter than the sixth, and about as long as the tenth. Seventh to tenth segments gradually diminishing in size, the eleventh, which forms a loose club with the tenth, one and a half times as long as the tenth. Funicular segments with regular rows — one per segment — of seven to nine long sensilla, the apical segment moreover with two circular pits. Mandible (fig. 155) with six ventral ridges, its appendage with five ridges. Maxilla with a subapical hair, and a bacilliform process, which is less than half as long as the maxilla [9 : 22], and bears a long apical hair. Labium without long hairs.

Thorax. Pronotum with sparce, long pubescence. Scutum one and a half times as long as wide maximally, and thrice as long as wide posteriorly, with seven to nine hairs along the lateral margins. Scutellum as long as wide posteriorly, narrower anteriorly, with eight to nine hairs along the lateral edges. Metanotum with ten hairs anteriorly, and two posteriorly, on each side of the mid line. Propodeum wide, with two hairs above, and a group of approximately ten hairs below the spiracle. Fore wing (2 : 1), 1.4 mm long. Submarginal, marginal, stigmal, and postmarginal veins approximately in ratio 14 : 5 : 5 : 12. Submarginal vein with three pustules, stigmal vein with four. Hind wing (9 : 2), 1.1 mm long. Femur



Figs. 167—178, *Ceratosolen moderatus,* Borneo, 167, female antenna, 168, male antenna, 169, detail of female hind leg, 170, detail of male fore leg, 171, detail of female fore leg, 172—176, male, 172, labium and maxilla, 173, male, 174, hind leg, 175, detail of hind leg, 176, detail of hind leg, same specimen as 175, axial aspect of other leg, 177, female mandible, 178, male cercus of tenth urite and paramere. Figs. 173—176, × 60; 169—171, × 140; 167, 168, 177, × 185; 172, 178, × 440

of the fore leg (fig. 160), with long pubescence along the dorsal and ventral margins, nearly twice as long as the coxa, and more than thrice as long as the tibia. Tibia with four dorsal and one ventro-apical teeth. Tarsus pentamerous, with rows of spines; segments in ratio 19 : 6 : 6 : 4 : 9. Mid leg slender; the tibia nearly as long as trochanter and femur combined, tarsal segments in ratio 16 : 9 : 8 : 6 : 9. Tibia and tarsus with long pubescence, tarsal segments with apical spines. Hind leg, fig. 156. Coxa smaller than the femur, the tibia more than half as long [13 : 25]. Femur heavily pubescent. Antaxial tibial spur bidentate, the axial one curved. Tarsus with long pubescence and apical spines; segments in ratio 16 : 8 : 6 : 4 : 7.

Gaster. Ovipositor slightly protruding behind the gaster.

Length, 2.2—2.4 mm (very small specimens measure 1.8 mm). Colour: head and dorsal surface of thorax dark brown, gaster lighter.

Extremities yellow-brown. Nervures of the wings brown.

Remark.

The tibial spur of the male hind leg is a common character of *C. dentifer* and *C. nugatorius*; they are, however, distinguishable by the male and female mouthparts, the relative proportions of the male thorax, etc.

Ceratosolen moderatus sp. n. (figs. 167—178)

Material.

Series ♀, ♂, ex *Ficus moderata* Corner (det. E. J. H. CORNER), Kundasan (N. Borneo), 3500 ft. alt., leg. E. J. H. CORNER, 31.VIII.1961, RSNB no. 2594; coll. nos. 628, 647, 649, 651; ♂ (holotype), slide 628a, ♀ (allotype), 628d, ♂, ♀ (paratypes), 628b, c, e.

Description.

Male. Length of the head (fig. 173) one and a half times the maximum width, and more than twice the anterior width. Eyes small. Antennal grooves open, not very wide behind. Antenna (fig. 168) five-segmented, the scape (3 : 2) one and a half times as long as the pedicel (2 : 1); the first flagellar segment annuliform, the second nearly as long as the pedicel, and more than half as long as the apical segment (5 : 2). Maxilla (fig. 172) with two hairs, the subapical one of which is absent in some specimens; labium without long hairs. Mandible as in the preceding species.

Thorax, fig. 173. Pronotum slightly shorter than wide posteriorly, and twice as long as wide anteriorly. Mesonotum approximately twice as wide as long. Metanotum short, incompletely separated from the propodeum, which is distinctly wider than long (3 : 2). Femur of the fore leg (fig. 170) twice as long as the tibia, with few hairs. Tibia with three dorsal and three ventro-apical teeth. Tarsus bimerous, the segments approximately equal in length; axially with a few stout hairs. Mid leg slender, the femur shorter than the tibia [6 : 7], the coxa shorter than the femur [5 : 6], but wider. Tibia with three apical teeth. Tarsal segments approximately in ratio 10 : 5 : 4 : 5 : 10. Oligomery, in casu, incomplete separation of second, third, and fourth segments, occurs sporadically. Hind leg, figs. 174—176. Coxa and femur subequal in length, the tibia shorter. Tibia with a bidentate apical tooth at the antaxial edge and a ventral spur. Tarsus dilated, segments (in the holotype) in ratio 25 : 16 : 11 : 15 : 16; the pubescence as long as one third the width of the segments. There is a considerable variation in the relative proportions of the tarsal segments, which may be wider than shown in fig. 174, but nearly always the second and fifth segments are subequal, and the first distinctly larger. The third and fourth segments are nearly as long as the second, or longer, or as drawn in fig. 174. Moreover, some of the specimens with large hind feet show oligomery: the first and second, second and third, or fourth and fifth tarsal segments being incompletely separated (figs. 175, 176).

Gaster. Cerci of the tenth urite large, with five small claws (fig. 178).

Length, 1.2—1.3 mm. Colour uniformly light yellow-brown.

Female. Head as long as wide across the compound eyes. Longitudinal diameter of the eye as long as the cheek. Pubescence not very long. Antenna (fig. 167): scape large, four times as long as the pedicel, which bears approximately forty axial spines. Third segment not very long, the fourth small. Fifth segment with ten long sensilla. Sixth to tenth segments subequal, distinctly longer than the fifth, the eleventh shorter, about as long as the fifth. Eleventh segment with six oblong and two circular sensilla, other segments with two rows of six to nine sensilla. Maxilla with one subapical hair, and with a bacilliform process, which is half as long as the maxilla, and bears one apical hair. Mandible (fig. 177) with six large ventral ridges, and five ridges on the appendage.

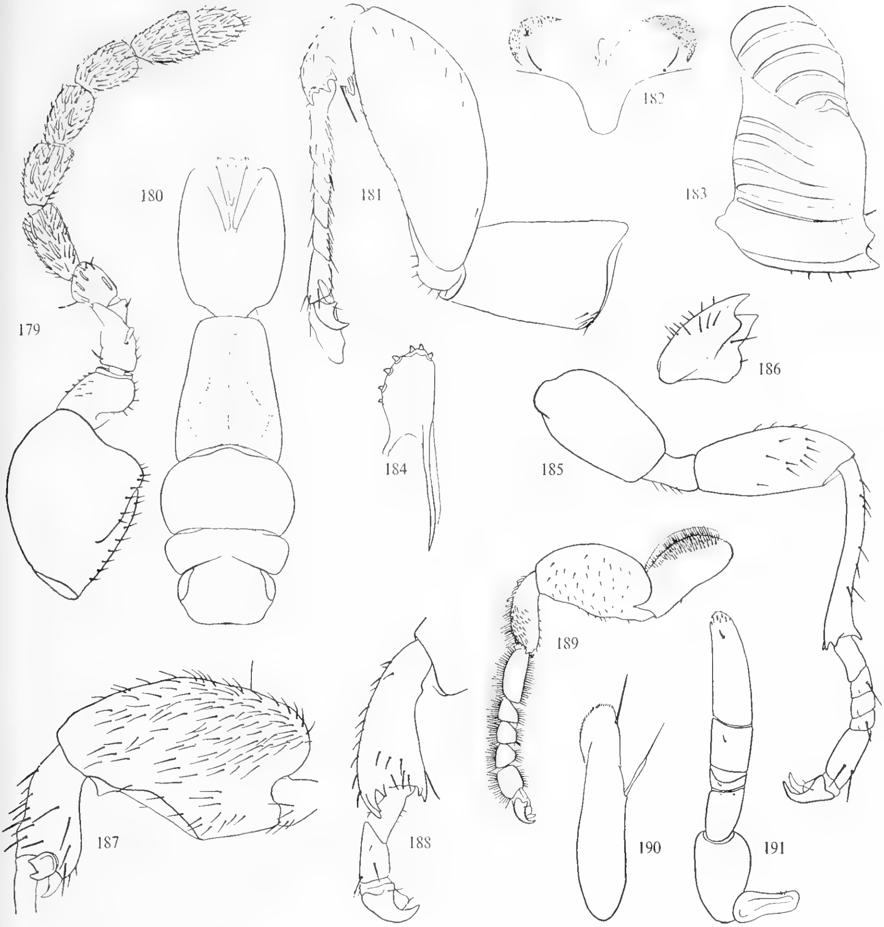
Thorax. Pronotum with sparse, but long pubescence. Scutum as long as wide maximally, the posterior width slightly more than two-thirds the length. Seven to eight hairs occur on each lateral side. Anterior width of the scutellum four-fifths, posterior width six-sevenths of the length, lateral margins with about ten hairs. Metanotum with eight hairs on each side of the mid line; propodeum with three hairs above, and six hairs below the spiracles. Fore wing (7 : 3), 1.65 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 14 : 4 : 5 : 11; submarginal vein with two pustules, stigmal vein with four. Hind wing (5 : 1), 0.95 mm long. Fore leg (fig. 171): length of the coxa three-fifths, length of the tibia two-fifths of that of femur and trochanter combined. Tibia with four dorsal and one ventral teeth. Tarsal segments in ratio 40 : 13 : 13 : 14 : 20. Mid leg slender, the tibia nearly as long as femur and trochanter combined, with long hairs. Tarsus with long pubescence, segments in ratio 15 : 5 : 5 : 5 : 6. Coxa of the hind leg (fig. 169) slightly shorter than the femur; the tibia two-thirds of the femur, with an antaxial bidentate, and an axial unidentate tooth at the ventro-apical edge. Tarsal segments wide, ratio: 30 : 9 : 6 : 5 : 9.

Gaster. Ovipositor slightly projecting beyond the apex of the gaster.

Length, 1.7—1.8 mm. Colour: head and dorsal surface of body grey-brown, ventral surface and extremities lighter. Nervures of the wings brown.

Remark.

C. moderatus is not much larger than *C. crassitarsus*, but it is easily recognized by the relative proportions of the male antenna and hind leg, the heteromery of



Figs. 179—191, *Ceratosolen praestans,* New Britain, 179, female antenna, 180, male, 181, female fore leg, 182, male labium and maxillae, 183, female mandible, 184—186, male, 184, cercus of tenth urite, 185, mid leg, 186, mandible, 187, detail of female hind leg, 188, detail of male fore leg, 189, male hind leg, 190, female maxilla, 191, male antenna. Figs. 180, 189, × 40; 179, 181, 185, 187, 188, × 90; 183, 186, 190, 191, × 115; 182, × 160; 184, × 200

the male hind tarsus, and the presence of five claws on the cerci of the tenth urite. The females have hyaline wings without striae.

Ceratosolen praestans sp. n. (figs. 179—191)

Material.

Series ♀, ♂, ex *Ficus praestans* Corner (det. E. J. H. CORNER), Keravat (New Britain), leg. E. J. H. CORNER, X.1960; coll. no. 533; ♂ (holotype), slide 533a, ♀ (allotype), 533c, ♂, ♀ (paratypes), 533b, d.

Description.

Male. Head (fig. 180) nearly twice as long as wide anteriorly, and one and a half times as long as its maximum width. Epistomal margin prominent, with six hairs. Dorsal and ventral surfaces with sparse, thin hairs. Eyes wanting. Antennal grooves open, not very wide behind. Antenna (fig. 191) five-segmented. Scape (5 : 3) nearly twice as long as the pedicel (3 : 2); the first flagellar segment short, the second (5 : 4) slightly shorter than the pedicel, the apical segment (3 : 1) more than twice as long. Mandible, fig. 186. Labium and maxillae, fig. 182; labium small, maxilla large, with one apical hair.

Thorax, fig. 180. Pronotum not quite twice as long as wide anteriorly, and distinctly longer than wide posteriorly [7 : 6]. Mesonotum with rounded edges, its length two-thirds of the maximum width. Metanotum short, incompletely separated from the propodeum. Propodeum slightly tapering behind, its length three quarters of the maximum width. Femur of the fore leg (fig. 188) twice as long as the tibia. Tibia with four dorsal and three ventro-apical teeth. Tarsus consisting of two segments, the first of which is the longer [6 : 5]. Mid leg (fig. 185): the coxa a little shorter than the femur; the tibia as long as coxa and trochanter combined. Tibia with five apical teeth: three ventrals and two dorsals. Tarsus pentamerous, the segments in ratio 11 : 5 : 5 : 4 : 15. Hind leg (fig. 189): the coxa slightly shorter than the femur, but longer than the tibia. Dorsal edge of the coxa, axial surfaces of femur and tibia, and dorsal edge of the tibia pubescent. Tibia with three ventral apical teeth. Tarsus dilated, with pubescence approximately as long as half the width of the segments. Segments in ratio 29 : 12 : 12 : 13 : 16.

Gaster. Aedeagus dilated apically. Cerci of the tenth urite (fig. 184) with seven claws, parameres tapering distally.

Length, 1.6 mm. Colour uniformly yellow-brown.

Female. Head slightly longer than wide between the external margins of the eyes. Longitudinal diameter of the eye a little longer than the cheek [6 : 5]. Antenna, fig. 179. Scape as long as second to fifth segments combined. Pedicel not quite half as long as the scape, with approximately forty-five slender spines. Fifth segment with two rows of four sensilla, and two apical sensilla which are oriented perpendicularly to the others; the sixth segment with four sensilla in the basal row, and seven apical sensilla, seventh to tenth segments with two rows of six to eight sensilla; the apical segment with five sensilla. Mandible (fig. 183), and its appendage, with five ventral ridges. Labium without hairs. Maxilla (fig. 190) with one subapical hair, and a bacilliform process. The bacilliform process, which is about one fifth the length of the maxilla, seems to be very delicate, and it is, more often than not, broken off close to its base, or even entirely absent.

Thorax. Pronotum wide, with many hairs. Scutum nearly as long as wide anteriorly, scutellum one and a half times as long as wide anteriorly. Metanotum nearly as wide as scutum and scapulae together, with ten hairs on each side of the mid line. Propodeum wider, with six hairs above, and twelve hairs beneath the spiracular peritremata. Fore wing (2 : 1), 2.2 mm long. Submarginal, marginal stigmal, and postmarginal veins in ratio 17 : 7 : 5 : 13. Submarginal vein with three pustules, stigmal vein with four. Hind wing (4 : 1), 1.3 mm long. Coxa of fore leg (fig. 181) not quite two-thirds the length of the femur, tibia much shorter than the femur [2 : 5], with four teeth at the antaxial, dorso-apical edge, and one ventral tooth. Tarsal segments in ratio 16 : 4 : 5 : 6 : 9; first segment with ventral spines, other segments with hairs and apical spines. Coxa and trochanter of the mid leg short; the femur four times as long as the trochanter, the tibia nearly as long as femur and trochanter combined. Tarsal segments in ratio 10 : 4 : 4 : 4 : 5. Hind leg, fig. 187. Coxa slightly smaller than the femur, the tibia half as long as the femur. Tibia with one ventral axial tooth, and a bidentate antaxial tooth. Tarsus pubescent, especially along the plantar edge; segments in ratio 42 : 14 : 10 : 9 : 11.

Gaster. Ovipositor scarcely projecting beyond the apex of the gaster.

Length, 2.4—2.6 mm. Colour dark brown, legs and antennae lighter. Wings with dark striae radiating from the stigma.

Remark.

This species is similar to some other species in which the hind feet of the males are dilated. It is distinguished by the male genitalia (cerci with seven claws) and by the short bacilliform process of the female maxilla.

Ceratosolen iodotrichae sp. n. (figs. 192—203)

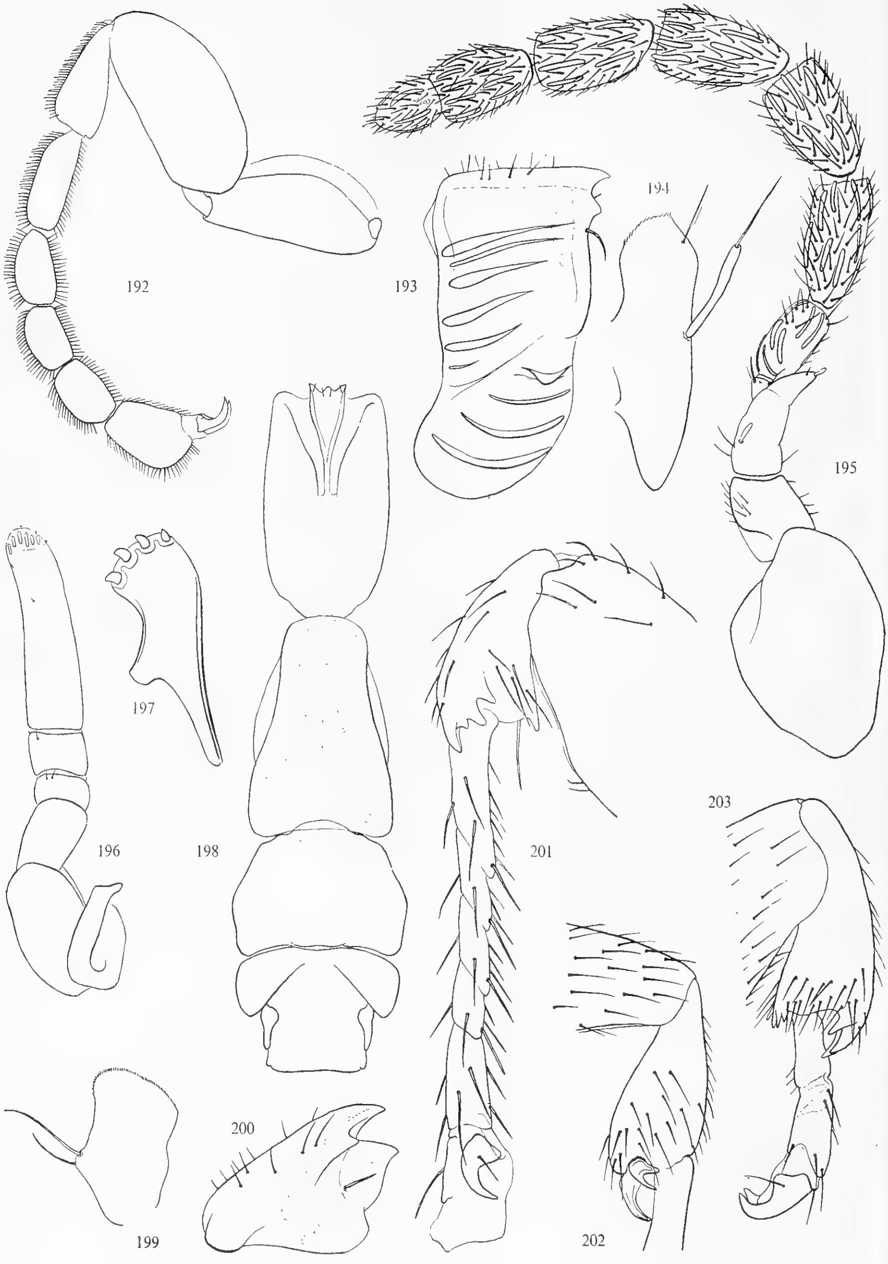
Material.

Series ♀, ♂, ex *Ficus iodotricha* Diels (det. E. J. H. CORNER), Wau (Terr. New Guinea), Edie Creek, leg. E. J. H. CORNER, 19.IX.1960, NGF no. 12498; coll. no. 535; ♂ (holotype), slide 535a, ♀ (allotype), 535c, ♀, ♂ (paratypes), 535b, d, e.

Description.

Male. Head (fig. 198) twice as long as wide anteriorly, with almost parallel sides. Pubescence short and sparse. Eyes wanting. Antennal grooves open, not very wide behind. Antenna (fig. 196) five-segmented; the scape (2 : 1) not quite twice as long as the pedicel (3 : 2); the first flagellar segment (1 : 2) slightly shorter than the second (2 : 3), the apical segment (4 : 1) six times as long as the second. Mandible, fig. 200. Maxilla (fig. 199) with two lateral hairs; labium without long hairs.

Thorax, fig. 198. Pronotum nearly one and a half times as long as wide posteriorly, much narrower anteriorly. Maximum width of the mesonotum distinctly longer than the length [7 : 5]. Metanotum incompletely separated from the propodeum, as wide as the mesonotum. Propodeum approximately as long as wide, its posterior margin nearly straight. Fore leg (fig. 203): the tibia, without the apical teeth, half as long as the femur. Tibia with four dorsal and four ventro-apical teeth. Tarsus bimerous, distal segment slightly longer than the proximal one. Femur and tibia of the mid leg subequal in length, slightly shorter than coxa and trochanter combined. Tibia with seven apical teeth: six at the ventral margin, and one bidentate, dorsal tooth. Tarsus pentamerous, segments in ratio 4 : 2 : 2 : 2 : 5.



Figs. 192—203, *Ceratosolen iodotrichae,* New Guinea, 192, male hind leg, 193—195, female, 193, mandible, 194, maxilla, 195, antenna, 196—200, male, 196, antenna, 197, cercus of tenth urite, 198, male, 199, maxilla, 200, mandible, 201, detail of female fore leg, 202, detail of female hind leg, 203, detail of male fore leg. Figs. 192, 198, × 50; 195, 202, 203, × 115; 193, 194, 196, 200, 201, × 155; 197, 199, × 365

Hind leg (fig. 192) much like that of *C. hooglandi*, but more robust; the tibia with one small apical tooth. Tarsal segments in ratio 14 : 10 : 9 : 9 : 11; dilated, pubescence approximately as long as one third the width of the segments.

Gaster. Cerci of the tenth urite (fig. 197) with four or five claws.

Length, 1.7—1.8 mm. Colour uniformly yellowish brown.

Female. Head as long as wide across the compound eyes. Eyes protruding, about as long as the cheek. Pubescence sparse, but long. Antenna (fig. 195); pedicel not half as long as the scape, with approximately forty short spines axially. Fifth segment twice as long as the short fourth, sixth to ninth subequal, longer than the fifth, tenth and eleventh smaller, together forming a loose club. Funicular segments with rather long sensilla: the fifth with twelve, sixth to tenth with two irregular rows of six to eight sensilla. Apical segment with six oblong and two circular sensilla. Mandible (fig. 193) with six ventral ridges, its appendage with four. Maxilla (fig. 194) with one, or sometimes two, subapical hairs, and a bacilliform process, which is, without the apical hair, between one third and one half the length of the maxilla. Labium bare.

Thorax. Scutum approximately one and a half times as long as wide posteriorly, much wider anteriorly; seven hairs occur along each lateral margin. Scutellum little wider behind than in front, its length four-thirds of the posterior width. Metanotum short, with eight hairs on each side of the mid line. Propodeum with six hairs above, and approximately twice as many behind the spiracle. Fore wing (8 : 3), 2.6 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 24 : 5 : 7 : 13; submarginal vein with three pustules, stigmal vein with four. Hind wing (4 : 1), 1.4 mm long. Femur of the fore leg (fig. 201) nearly twice as long as the coxa, the tibia not half as long as the femur. Tibia with four dorso-apical teeth, and one ventral tooth. Tarsal segments in ratio 12 : 5 : 5 : 5 : 7. Mid leg slender, the subclavate tibia nearly as long as femur and trochanter combined; tarsal segments in ratio 20 : 10 : 9 : 8 : 10, long pubescent. Hind leg robust, the coxa as long as the tibia, but much wider, the femur not quite twice as long. Tibia (fig. 202) with two ventro-apical teeth, the antaxial one of which is bidentate. Tarsus pubescent, especially along the plantar edge; the segments in ratio 19 : 9 : 7 : 6 : 8.

Gaster. Ovipositor distinctly projecting beyond the apex of the gaster.

Length, 2.6 mm. Colour of head and thorax dark brown; abdomen and extremities lighter. Some females have the last three antennal segments, and the distal segments of the legs, of an ivory-white colour, and are evidently not fully mature. Nervures of the wings light brown, three dark striae radiate from the stigma.

Remark.

C. iodotrichae is remarkable in having the apical segment in the male antenna very long. The specimens are rather large, as in *C. vechti*, but they differ distinctly in the relative proportions.

Ceratosolen notus (Baker), C. **orientalis** sp. n. and C. **calopilinae** sp. n.

Ceratosolen notus (Baker), and the new species *C. orientalis* and *C. calopilinae* (described below) are very similar.

There are no distinct structural differences between *C. orientalis* and *C. calopilinae*, yet the two are recognizable by the male trophi, and by the relative proportions of some body-parts, notably the female maxilla and antenna, and the male hind leg.

C. orientalis is much like *C. notus*, but it differs in the relative proportions of the hind leg in the male, of the female antenna, etc.

Examination of more material may prove the three forms to be only subspecifically distinct.

Ceratosolen notus (Baker) (figs. 204—217)

Blastophaga nota Baker, 1913, pp. 65—67, 69, 70—72, 81, 82, figs. 2, 3D, E, 4D [descr. ♀, ♂, ex *Ficus nota* (Blanco) Merrill, Los Baños (Luzon, Philippine Is.), biological notes].

Ceratosolen notus: Williams, 1928, pp. 9—11, 14, Pl. I figs. 2, 5, Pl. II fig. 16 [biological notes].

Material.

Series ♀, ♂, ex *Ficus nota* (Blanco) Merr., Los Baños (Luzon, Philippine Is.), Coll. Agric., leg. F. X. WILLIAMS, 24.VI.1921; coll. HSPA, ♀, ♂ slide mounted; coll. ML, no. 683: 10 ♀, 10 ♂.

Six ♀, 8 ♂, ex *Ficus nota* (Blanco) Merr., Los Baños (Luzon, Philippine Is.), leg. F. X. WILLIAMS, 26.II.1921; coll. HSPA; 2 ♀, 6 ♂, coll. USNM, 1 ♂ slide mounted.

Series[1] ♀, ♂, ex *Ficus nota* (Blanco) Merr., Los Baños (Luzon, Philippine Is.), Coll. Agric., 9.VI.1921; leg. F. X. WILLIAMS, coll. HSPA.

Series ♀, ♂, ex *Ficus nota* (Blanco) Merr. (several trees), Los Baños (Luzon, Philippine Is.), leg. F. X. WILLIAMS, 15/17.VI.1921; coll. HSPA.

Series ♀, ♂, ex *Ficus* spec., Luzon (Philippine Is.), 20 min. SW of Baguio, leg. H. E. MILLIRON, 24.IX.1945; coll. BMH.

Series ♀, 7 ♂, ex *Ficus nota* (Blanco) Merr., Manila (Luzon, Philippine Is.), leg. D. T. FULLAWAY, 1.I.1921; coll. HSPA; 6 ♀, 2 ♂, coll. USNM, 1 ♀ slide mounted.

Series ♀, ♂, ex *Ficus nota* (Blanco) Merr. ("purple fruited"), Mt. Maquiling (Luzon, Philippine Is.), 3000 ft. alt., leg. F. X. WILLIAMS, 25.I.1922; coll. HSPA.

One ♂, ex *Ficus nota* (Blanco) Merr. ("purple ♂"), Mt. Maquiling (Luzon, Philippine Is.), at mud spring, leg. F. X. WILLIAMS, 8.II.1922; coll. HSPA.

Series ♀, ♂, ex *Ficus satterthwaitei*[2]), Mt. Maquiling (Luzon, Philippine Is.), leg. F. X. WILLIAMS, 21.IX.1921; coll. HSPA.

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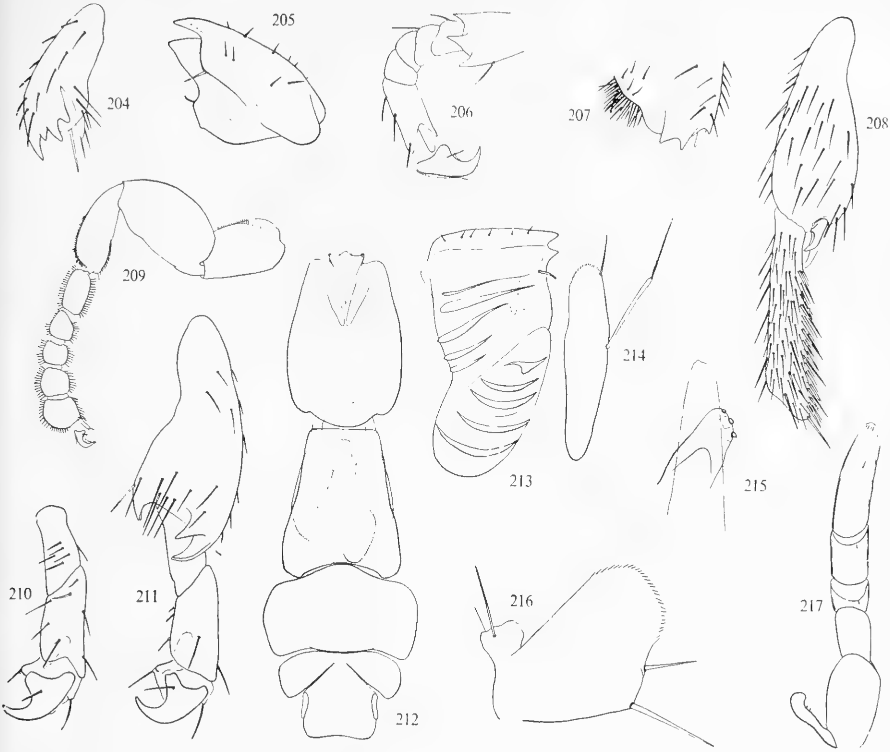
[1]) Except for three or four escapes, this is the total content of one fig: 759 ♀, 255 ♂, no parasites or inquilines.

[2]) *Ficus satterthwaitei* Elmer = *F. congesta* Roxb.



Figs. 204—217, *Ceratosolen notus*, Luzon, 204, female fore tibia, 205—207, male, 205, mandible, 206, detail of mid tibia, and tarsus, 207, apex of hind tibia, 208, female hind tibia and metatarsus, 209—212, male, 209, hind leg, 210, fore tarsus, axial aspect, 211, fore tibia and tarsus, 212, male, 213, female mandible, 214, female maxilla, 215—217, male, 215, cercus of tenth urite, and paramere, 216, maxilla (ventral aspect), and labium (lateral aspect), 217, antenna. Figs. 209, 212, × 40; 204—208, 210, 211, 213, 214, 217, × 115; 215, 216, × 275

Description.

As the original description by Baker is very short, I give a redescription of *C. notus.* The described specimens, taken at the type locality of *C. notus* (College of Agriculture, Los Baños, Williams, 24.VI.1921), were sent to me dry, and I relaxed them in diluted alcohol.

Male. Head (fig. 212) more than twice (9 : 4) as long as wide anteriorly, the maximum width two-thirds of the length. Eyes absent. Epistomal margin wide, with four hairs. Pubescence long. Antennal grooves open, rather wide behind. Antenna (fig. 217) five-segmented: the scape, nearly twice as long as wide, one and a half times as long as the pedicel (2 : 1): the first flagellar segment short, the second (5 : 4) three quarters the length of the pedicel, the apical segment (4 : 1) two and a half times as long as the second. Maxilla (fig. 216) expanded laterally, with two lateral hairs; labium with one subapical hair. Mandible, fig. 205.

Thorax, fig. 212. Pronotum slightly longer than wide posteriorly, and not quite twice as long as wide anteriorly. Mesonotum (8 : 5) much wider than long; metanotum narrower, incompletely separated from the subquadrate propodeum. Fore leg (figs. 210—211): the tibia not quite half as long as the femur [7 : 16], apically with three dorsal and three ventral teeth. Tarsus bimerous, the distal segment slightly longer than the proximal one. Mid leg rather robust; coxa and femur subequal in length; the tibia distinctly longer [4 : 3], with four apical teeth (fig. 206). Tarsus coiled in nearly all specimens, the segments approximately in ratio 5 : 3 : 3 : 4 : 10. Hind leg (fig. 209) pubescent, the coxa three quarters the length of the femur, the tibia slightly longer than the coxa. Tibial armature (fig. 207) consisting of a bidentate antaxial process, a small tooth at the ventral edge, and a motile axial spur. Tarsus dilated, the pubescence slightly longer than one third of the width of the segments. Relative proportions of the segments rather variable, even in specimens from the same sample. First segment always approximately half as long as the tibia, second and third segments subequal, approximately half as long as the first; the fourth distinctly longer than the third; the fifth segment is slightly longer (as in fig. 209) or much longer and wider (as in BAKER's fig. 3D) than the fourth.

Gaster. Cerci of the tenth urite with three claws, parameres narrow (fig. 215).

Length, 1.6 mm. Colour yellowish brown.

Female. Scape of the antenna large, nearly four times as long as the pedicel, which bears some thirty slender spines at the axial surface. Appendage of the third segment robust, the fourth segment small. Fifth to eighth segments gradually increasing in length, the eighth distinctly longer than the fifth [5 : 4]; the ninth segment as long as the fifth, the tenth slightly longer, the eleventh, forming a loose club with the tenth, distinctly shorter [3 : 4]. Funicular segments with two irregular rows of short, wide sensilla. Mandible, and its appendage, with five ventral ridges (fig. 213). Maxilla (fig. 214) with a subapical hair, and a bacilliform process, which is two-fifths the length of the maxilla.

Thorax pubescent; two hairs occur above, and a group of about ten hairs below the propodeal spiracle. Fore wing (5 : 2), 1.8 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 28 : 10 : 9 : 24; submarginal and stigmal veins with four pustules each. Hind wing (5 : 1), 1.1 mm long. Tibia of the fore leg (fig. 204) less than half as long as the femur [5 : 13], and more than half as long as the coxa [5 : 8]. Apical armature consisting of a dorsal comb of four teeth, and one ventral tooth. Tarsal segments in ratio 20 : 10 : 9 : 8 : 15. Mid leg long pubescent, the tibia shorter than femur and trochanter combined [10 : 11]; tarsal segments in ratio 18 : 8 : 9 : 8 : 14. Coxa of hind leg (fig. 208) shorter than the femur [14 : 17], the tibia two-thirds the length of the femur. Antaxial apical tooth bidentate, the axial tooth simple, strongly curved at apex. Tarsus heavily pubescent and spinose, the segments in ratio 20 : 7 : 7 : 6 : 9.

Gaster. Projecting part of the ovipositor one sixth the length of the gaster.

Length, 1.8 mm. Colour brown, head darker, legs yellow-brown. Nervures of the wings light brown.

Remark.

There are some minor differences between the specimens described above and the description by BAKER, notably in the male genitalia (described by BAKER as being "without armed claspers", but the cerci are not distinctly visible) and in the relative proportions of the female hind leg (tibia half as long as the femur, according to BAKER, two-thirds in length of the femur in the specimens measured by me, but probably BAKER measured the part of the tibia visible in situ, and not the whole segment).

I fail to find any differences between the specimens from *Ficus nota* and those from *F. congesta.* For a discussion of the host records, see p. 97.

Ceratosolen orientalis sp. n. (figs. 218—230)

Material.

Series ♀, ♂, ex *Ficus subcongesta* Corner (det. E. J. H. CORNER), Keravat (New Britain), leg. E. J. H. CORNER, 14.X.1960, NGF no. 13783; coll. no. 540; ♂ (holotype), slide 540a, ♀ (allotype), 540c, ♂, ♀ (paratypes), 540b, d.

? Sixteen ♀, 8 ♂, ex *Ficus subcongesta* Corner var. *symmetrica* Corner (det. E. J. H. CORNER), Crown Prince Mts. (Bougainville I.), leg. E. J. H. CORNER, NGF no. 13735; coll. no. 550; ♂, slide 550a, ♀, 550b.

Description.

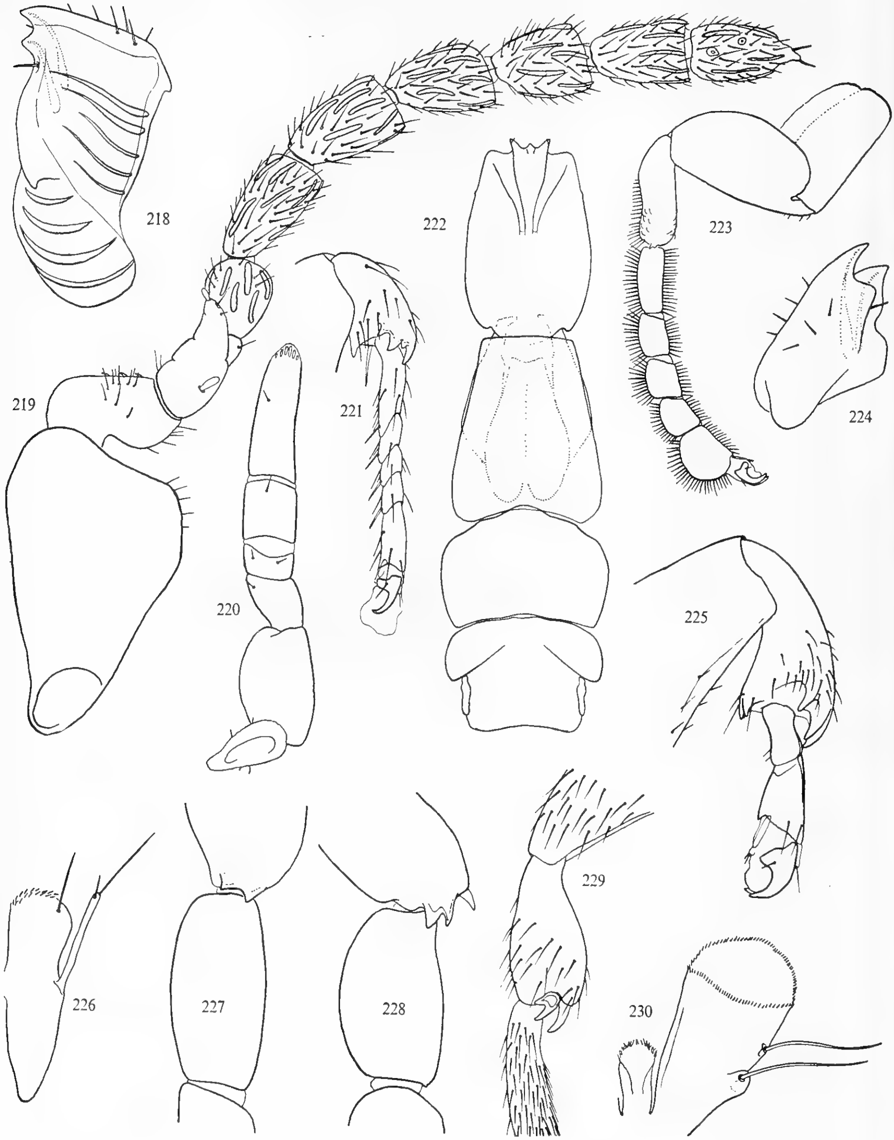
Male. Head (fig. 222) slightly longer than twice the anterior width, maximum width two-thirds of the length. Pubescence short and sparse. Eyes small. Antennal grooves open, not very wide behind. Antenna (fig. 220): the scape (5 : 3) is two and a half times as long as the pedicel (1 : 1), which is twice as long as the first flagellar segment (1 : 2). The following segment (8 : 7) as long as the pedicel, and not quite half as long as the apical one (3 : 1). Maxilla (fig. 230) with two lateral hairs; labium without long hairs. Mandible, fig. 224.

Thorax, fig. 222. Pronotum nearly twice as long as wide anteriorly; the posterior width slightly shorter than the length. Mesonotum transverse (14 : 9); metanotum incompletely separated from the propodeum, which is nearly twice as wide as long. Femur of fore leg (fig. 225) twice as long as the tibia (apical teeth included); the tibia with four dorsal and three ventro-apical teeth. Tarsus bimerous, segments in ratio 5 : 6. Coxa of the mid leg as long as the femur, the tibia as long as femur and trochanter combined, subclavate, with four apical teeth. Hind leg (figs. 223, 227): coxa and femur subequal in length, the tibia little shorter. Tibia with a bidentate process at the antaxial apical edge. Tarsus dilated, segments approximately in ratio 6 : 4 : 4 : 3 : 5. Pubescence longer than half the width of the segments.

Gaster. Cerci of the tenth urite with three or four claws.

Length, 1.5 mm. Colour uniformly yellowish brown.

Female. Head shorter than wide across the compound eyes [15 : 16]. Eye longer than the cheek [11 : 9]. Pubescence short and sparse. Antenna (fig. 219): scape not very wide, and nearly thrice as long as the pedicel, which bears forty-five axial spines. Third segment not very long, the fourth small; the fifth twice, the



Figs. 218—230, *Ceratosolen orientalis,* New Britain (228, specimen from Bougainville I.), 218, female mandible, 219, female antenna, 220, male antenna, 221, female fore leg, 222—225, male, 222, male, 223, hind leg, 224, mandible, 225, detail of fore leg, 226, female maxilla, 227, detail of male hind leg, 228, do., specimen from Bougainville I., 229, detail of female hind leg, 230, male labium and maxilla. Figs. 222, 223, × 50; 221, 225, 229, × 115; 218—220, 224, 226—228, × 155; 230, × 365

sixth and seventh approximately thrice as long as the fourth. Eighth to eleventh segments slightly shorter than the seventh, and gradually diminishing in length. The subapical and apical segments shaped so as to form a loose club. Fifth segment with eight oblong sensilla, sixth to tenth segments with two irregular rows of sensilla (eleven to fourteen per segment), the apical segment with six oblong, and some circular sensilla. Maxilla (fig. 226) with one subapical hair, and a long bacilliform process. Mandible (fig. 218), and its appendage, with five ventral ridges.

Thorax. Pronotum with long hairs. Scutum longer than wide posteriorly [4 : 3], the posterior width slightly longer than half the maximum width. Lateral margins with six hairs. Scutellum one and a half times as long as wide anteriorly, and slightly longer than wide posteriorly; with rows of six or seven hairs along the lateral margins, and approximately ten hairs on the disk. Metanotum rather long, with six hairs on each side of the mid line. Propodeum with two hairs above, and four beneath the large spiracle. Fore wing (7 : 3), 1.7 mm long. Submarginal, marginal, stigmal, and postmarginal veins approximately in ratio 3 : 1 : 1 : 2; submarginal vein with three pustules, stigmal vein with four. Hind wing (5 : 1), 0.9 mm long. Femur of the fore leg (fig. 221) longer than the coxa [3 : 2], and thrice as long as the tibia. Tibia with a dorso-apical row of four teeth, and one ventral tooth. Tarsal segments in ratio 20 : 4 : 4 : 5 : 10. Tibia of the mid leg as long as femur and trochanter combined, with long hairs. First tarsal segment as long as the following two combined, second to fifth segments gradually, but slightly, increasing in length. Femur of the hind leg (fig. 229) slightly longer than the coxa, the tibia two-thirds the length of the femur, with two apical teeth, the antaxial one of which is bidentate. Tarsus rather pubescent, especially along the plantar edge; segments in ratio 12 : 6 : 5 : 5 : 6.

Gaster. Ovipositor slightly projecting beyond the apex of the gaster.

Length, 1.9 mm. Colour brown, ventral surface and extremities lighter. Nervures of the wings brown, stigma with dark radiating striae.

Remark.

The specimens from Bougainville I. (coll. no. 550) differ from those of the typical sample. The females have the third antennal segment more slender, with longer and more slender, hyaline processes, and the pedicel bears less (approximately twenty-five) teeth at the axial surface. In the male, the first flagellar segment of the antenna is only one third the length of the second. The hind leg is shorter than in the New Britain specimens, and the metatarsus is less slender. The tibia bears a prominent tooth at the axial edge (fig. 228). As the specimens are few, and not in a very good condition, I do not name the form from Bougainville I., which should perhaps be regarded as a distinct species or subspecies.

Ceratosolen calopilinae sp. n. (figs. 231—242)

Material.

Series ♀, ♂, ex *Ficus calopilina* Diels (det. E. J. H. CORNER), Wau (Terr. New Guinea), leg. E. J. H. CORNER, 13.IX.1960; coll. no. 538; ♂ (holotype), slide 538a, ♀ (allotype), 538c, ♂, ♀ (paratypes), 538b, d, e.

Description.

Male. Head (fig. 237) little more than twice as long as wide anteriorly, and nearly twice as long (8 : 5) as the maximum width. Eyes absent. Antennal grooves open, not very wide behind. Antenna (fig. 238) slender; the scape (2 : 1) nearly twice as long as the pedicel (3 : 2), the first flagellar segment short, the second (7 : 6) distinctly shorter than half the length of the apical segment (4 : 1). Mandible, fig. 236. Labium and maxillae, fig. 241; maxilla with one lateral hair.

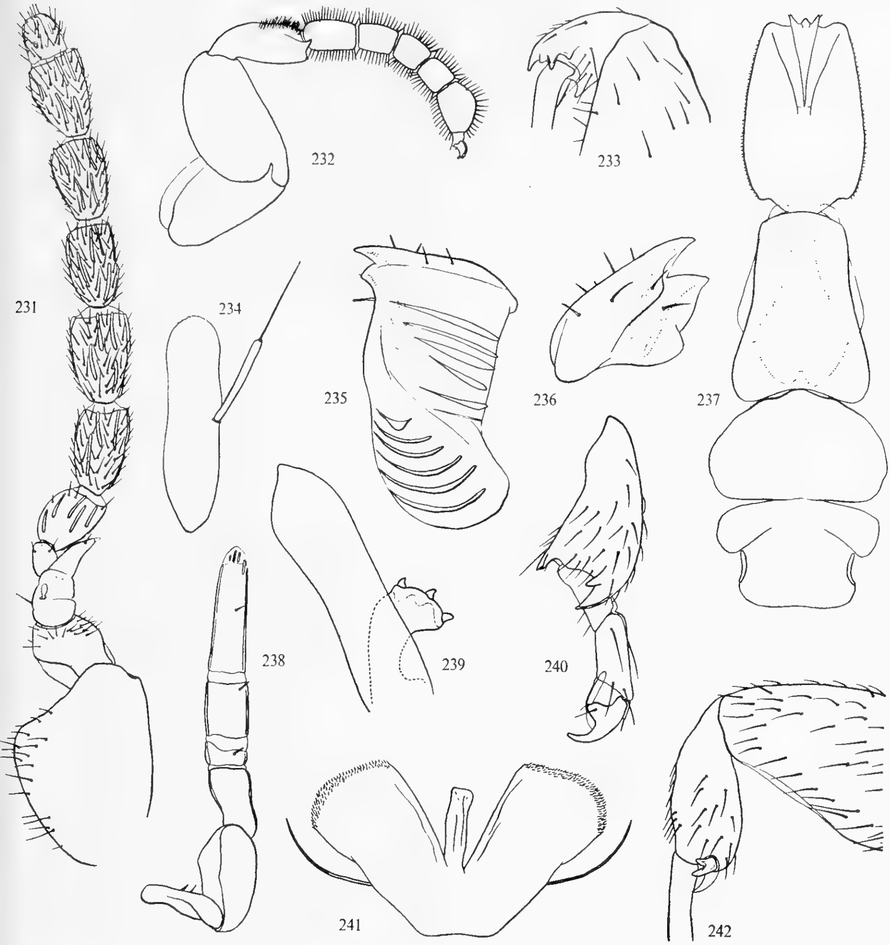
Thorax, fig. 237. Pronotum twice as long as wide anteriorly, and one and a half times as long as wide posteriorly. Mesonotum with a straight posterior margin, tapering anteriorly; the length more than half the maximum width. Metanotum nearly as wide as the mesonotum, incompletely separated from the propodeum, which is approximately one and a half times as long as wide. Fore leg (fig. 240): the tibia nearly half as long as the femur, with three dorsal and three ventro-apical teeth. Tarsus bimerous, distal segment distinctly longer than the proximal one, with long hairs. Coxa and femur of mid leg subequal, approximately as long as the tibia. Tibia subclavate, with long hairs along the dorsal margin and on the axial surface. The apical edge dorsally produced into a stout tooth, ventrally with four smaller teeth. Tarsal segments in ratio 8 : 4 : 4 : 3 : 11. Coxa of the hind leg (fig. 232) little shorter than the femur. Tibia with one apical antaxial tooth, pubescent along the dorsal edge. Tarsus dilated, with pubescence approximately half as long as the width of the segments. There is some variation in the dimensions of the segments, but the relative lengths are rather constant: 11 : 8 : 7 : 6 : 10.

Gaster. Aedeagus slightly dilated at mid length. Cercus of the tenth urite with three claws, paramere with parallel edges (fig. 239).

Length, 1.3 mm. Colour uniformly yellow-brown.

Female. Head slightly shorter than wide across the compound eyes. Longitudinal diameter of the eye longer than the cheek [8 : 7]. Pubescence short. Antenna (fig. 231): scape more than twice as long as the pedicel, which bears approximately twenty axial spines. Third segment not very long, the fourth small, the fifth shorter than the sixth [5 : 6], the seventh longer than the sixth [7 : 6]. Eighth to tenth segments gradually diminishing in length, the tenth as long as the sixth. Eleventh and tenth segments shaped so as to form a club, but not fused. Fifth segment with ten sensilla, sixth to tenth segments with thirteen or fourteen sensilla in two irregular rows; the apical segment with six oblong and two circular sensilla. Mandible (fig. 235), and its appendage, with six ventral ridges. Maxilla (fig. 234): bacilliform process not quite half as long as the maxilla [4 : 9]. Labium without long hairs.

Thorax. Pronotum wide, with long hairs. Scutum one and a half times as long as wide posteriorly, and nearly twice as wide anteriorly; with rows of four hairs along the lateral margins. Scutellum one and a half times as long as wide, with rows of five hairs along the lateral margins, and approximately ten hairs on the disk. Metanotum short, with nine hairs on each side of the mid line. Propodeum with three hairs above, and six beneath the propodeal spiracle. Fore wing (7 : 3), 1.6 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 75 : 17 : 24 : 44. Submarginal vein with three pustules, stigmal vein with five.



Figs. 231—242, *Ceratosolen calopilinae,* New Guinea, 231, female antenna, 232, male hind leg, 233—235, female, 233, detail of fore leg, 234, maxilla, 235, mandible, 236—241, male, 236, mandible, 237, male, 238, antenna, ventral aspect, 239, cercus of tenth urite, and paramere, 240, detail of fore leg, 241, labium and maxillae, 242, detail of female hind leg. Figs. 232, 237, × 50; 231, 233, 240, 242, × 115; 234—236, 238, × 155; 239, 241, × 365

Hind wing (4 : 1), 0.9 mm long. Coxa of the fore leg (fig. 233) more than half as long as the femur, tibia distinctly smaller than the coxa. Tibia with four dorso-apical teeth, and one ventral tooth. Tarsal segments in ratio 13 : 4 : 4 : 5 : 6. Mid leg of the usual slender build, the clavate tibia slightly longer than the femur; tarsal segments in ratio 15 : 7 : 7 : 5 : 9. Coxa of the hind leg (fig. 242) shorter than the femur [4 : 5]. Tibia nearly three quarters the length of the femur, with two ventro-apical teeth, the antaxial one of which is bidentate. Tarsus pubescent, segments in ratio 25 : 10 : 8 : 8 : 11.

Gaster. Ovipositor short, but distinctly projecting beyond the apex of the gaster.

Length, 1.8 mm. Colour dark brown, ventral surface and extremities lighter Nervures of wings light brown.

Remark.

C. calopilinae is very similar to *C. orientalis,* but it differs in the length of the bacilliform process of the female maxilla, the chaetotaxy of the male maxilla, and in the proportions of the male hind leg.

Ceratosolen corneri sp. n. (figs. 243—254)

Material.

Series ♀, ♂, ex *Ficus endothrix*[1]), Mt. Maquiling (Luzon, Philippine Is.), at first creek crossing, leg. F. X. WILLIAMS, 27.VI.1928, no. 3131; coll. HSPA, ♂ (holotype), ♀ (allotype), slide mounted; coll. ML, no. 682: 10 ♀, 10 ♂.

Fragments of several ♂, and 1 ♀, ex *Ficus botryocarpa* Miq. var. *subalbidoramea* (Elmer) Corner (det. E. J. H. CORNER), Mindoro (Philippine Is.), leg. E. D. MERRILL, no. 1813; coll. no. 405; ♂ (paratypes), slide 405a, ♀ (paratype), 405b.

Series ♀, ♂, ex *Ficus barnesii*[2]), Mt. Maquiling (Luzon, Philippine Is.), leg. F. X. WILLIAMS, 28.VI.1928, no. 3131[3]), coll. HSPA.

Description.

Male. Head (fig. 246) more than twice as long as wide anteriorly. Epistomal margin (fig. 247) with four hairs. Eyes very small. Antennal grooves open, narrow behind. Antenna (fig. 248) five-segmented, the scape (5 : 2) four-thirds the length of the pedicel (15 : 7). Pedicel six times as long as the first flagellar segment (5 : 13), the second segment (25 : 14) half as long as the apical segment (4 : 1), and five times as long as the first. Maxillae (fig. 252) for a great part concealed under the hypostomal margin; labium atrophied. Mandible, fig. 251.

Thorax, fig. 246. Pronotum more than twice as long as wide anteriorly, its length one and a half times the maximum width. Mesonotum wider than long (7 : 5). Metanotum incompletely separated from the propodeum, not nearly as wide as the mesonotum [11 : 14]. Propodeum shorter than wide [3 : 4]. Fore leg (fig. 243): the tibia not quite half as long as the femur, with four dorsal and two ventro-apical teeth. Tarsal segments subequal in length. Coxa of the mid leg longer than the femur; the tibia longer than the femur, but not as long as the coxa. Tibia with four sharp apical teeth. Tarsal segments in ratio 22 : 6 : 5 : 4 : 14. Hind leg (fig. 253) very long, all segments with thick pubescence of small hairs. Coxa and femur very long (each about as long as the pronotum), and dilated. Tibia more than half as long as the femur, without any distinct apical armature. Tarsal segments in ratio 15 : 8 : 7 : 6 : 7. Metatarsus distinctly produced dorsally.

Gaster. Cerci of the tenth urite (fig. 249) with three claws.

Length, 1.5 mm. Colour uniformly yellow-brown.

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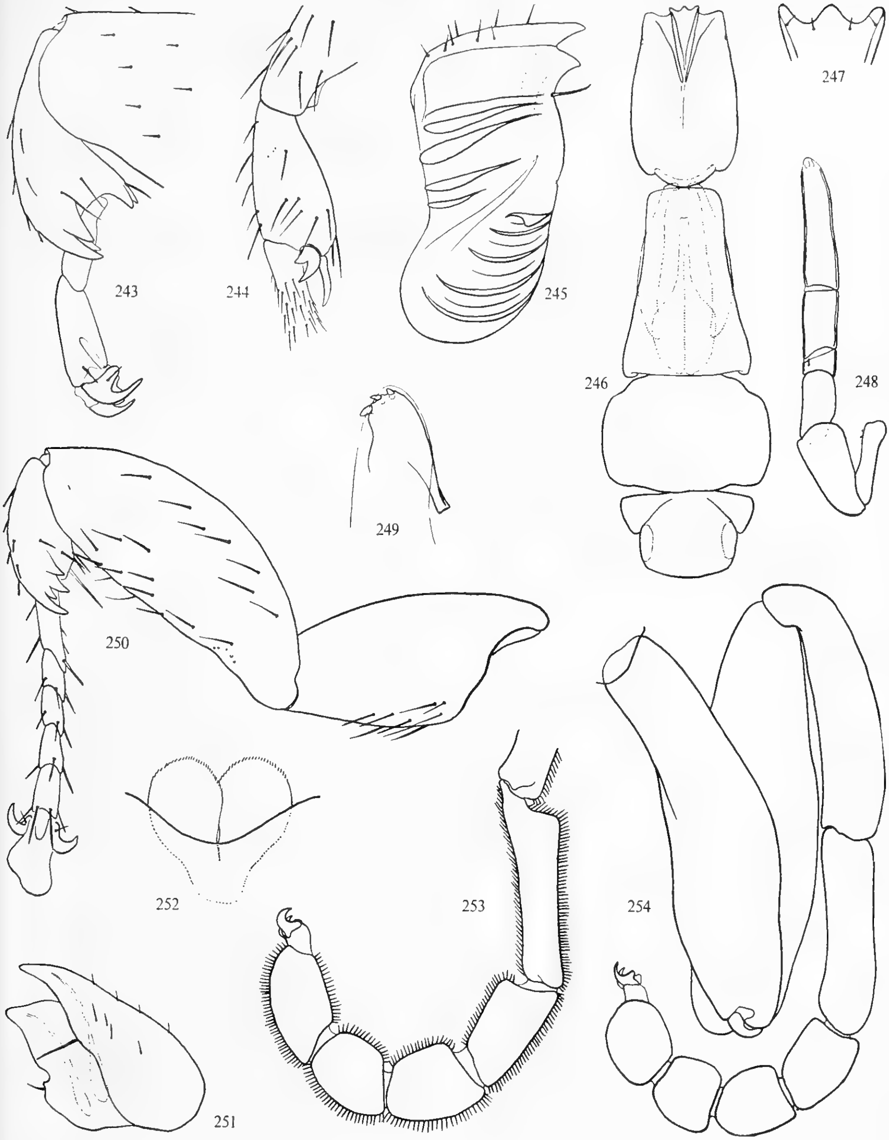
[1]) *Ficus endothrix* Warb. = *F. botryocarpa* Miq.

[2]) *Ficus barnesii* Merr. = *F. botryocarpa* Miq.

[3]) ?, same tree as the first sample (no. 682)?



Figs. 243—254, *Ceratosolen corneri,* Luzon (except 246, 247, 251, 254, specimen from Mindoro), 243, detail of male fore leg, 244, detail of female hind leg, 245, female mandible, 246—249, male, 246, male, 247, epistomal margin, 248, antenna, 249, cercus of tenth urite, and paramere, 250, female fore leg, 251—254, male, 251, mandible, 252, maxillae and hypostomal margin, 253, detail of hind leg, 254, hind leg (specimen from Mindoro). Figs. 246, × 50; 253, 254, × 80; 243, 244, 247, 248, 250, × 155; 245, 251, × 215; 249, 252, × 365

Female. Antenna consisting of eleven segments, the last two of which are joined into a loose club. Scape twice as long as the pedicel, appendage of the third segment robust, the fourth segment small. Length of the fifth segment four-fifths of that of the sixth, two-thirds of that of the seventh, eighth and tenth segments; the ninth as long as the sixth segment. Eleventh segment half as long as the tenth. Funicular segments with one or two rows of long sensilla. Maxilla with one subapical hair, without a bacilliform process. Mandible (fig. 245) with five ventral ridges, its appendage with five large ridges, and smaller ridges in between the larger ones.

Thorax. A few hairs occur along the lateral edges of the scutum, five hairs along the edges of the scutellum. Metanotum with about ten hairs on each side of the mid line. Propodeum with two hairs above, and five beneath the spiracle. Fore wing (5 : 2), 1.4 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 12 : 4 : 3 : 6; the submarginal and stigmal veins with three pustules each. Hind wing (5 : 1), 0.8 mm long. Fore leg (fig. 250): the coxa smaller than the femur [11 : 14], and approximately twice as long as the tibia. Tibial armature consisting of four dorsal teeth. Tarsal segments in ratio 8 : 3 : 3 : 4 : 5. Mid leg slender, the tibia as long as femur and trochanter combined, tarsal segments in ratio 25 : 9 : 9 : 7 : 10. Coxa of hind leg (fig. 244) six-sevenths the length of the femur, tibia slightly longer than half the length of the femur. Tibial armature consisting of a bidentate antaxial, and a long, curved axial tooth. Tarsus fimbriated at the plantar edge, segments in ratio 8 : 3 : 2 : 2 : 3.

Gaster. Projecting part of the ovipositor not quite one quarter the length of the gaster.

Length, 1.4—1.6 mm. Colour brown, ventral surface and extremities lighter. Nervures of the wings light brown.

Remark.

Although the female of this species is in no way aberrant from the normal type, the male is very remarkable. Its very long hind legs distinguish it at once from its congeners; in fact, in none of the other fig wasps have I seen the like.

There are some differences between the samples from Luzon and Mindoro. The specimens from the last mentioned locality are badly damaged, and better series should be studied to be certain of the differences. The males have the tarsus of the hind leg slightly more robust, and the metatarsus without the dorsal protuberance (fig. 254).

I name this species in honour of Mr. E. J. H. CORNER F.R.S., Lecturer in Botany, University of Cambridge.

Ceratosolen solmsi (Mayr) and **C. marchali** Mayr (figs. 255—260, 262—265; map, fig. 261; Table I)

Two forms of *Ceratosolen* were described that are known to live in *Ficus hispida* Linn. f., viz., *C. solmsi* (Mayr) and *C. marchali* Mayr. According to GRANDI (1928c, pp. 174—175), the species differ in the following characters:

♀. Eleventh antennal segment longer than the tenth in *C. solmsi*; shorter in *C. marchali*.

Bacilliform process of the maxilla one quarter the length of the maxilla in *C. solmsi*; one half as long as the maxilla in *C. marchali.*

? Mandibular process with six or seven ridges in *C. solmsi*; with nine ridges in *C. marchali.*

Fore wing hyaline in *C. solmsi*; darker, with striae radiating from the stigmal vein, in *C. marchali.*

♂. Antennal groove narrow behind in *C. solmsi*; wide in *C. marchali.*

Fourth antennal segment slightly longer than the third in *C. solmsi*; distinctly longer in *C. marchali.*

According to GRANDI (1926, p. 358), the male hind tibia is thrice as long as the first tarsal segment in *C. solmsi* from Java; and twice as long in *C. marchali* from Vietnam.

The forms were known from Java and S. Vietnam (*C. solmsi*) and from N. Vietnam and India (*C. marchali*). Moreover, GRANDI (1928c, p. 176) found one slide in MAYR's collection, labelled "Tonkin", and containing *C. solmsi.*

I have seen material from Ceylon, India, Malaya (Selangor and Langkawi Is.), Hongkong, Java, and Queensland (distribution, see map, fig. 261). The data on some of the above mentioned differential characters are arranged in Table 1 (cf. figs. 255—269).

The male mouthparts are identical in the two forms (fig. 264). The genitalia bear cerci (fig. 265), which are clearly visible in the specimens from the Asian continent. In the specimens from Java and Langkawi, however, they are hyaline, and very difficult to be observed: I cannot even find them in all of these specimens, and in none of the sample from Queensland (but this is badly preserved). In general, the specimens from India, Ceylon, and Hongkong are slightly smaller and less slender than those from Malaya, Java, and Queensland.

It seems best to treat *C. solmsi* and *C. marchali* as subspecies. The specimens from Java are distinctly different from those collected in Ceylon, India, and China, but the characters seem to intergrade on the Malayan peninsula. The Australian specimens[1]) are intermediate in some aspects, but they resemble *C. marchali* more closely than they do *C. solmsi.*

Ceratosolen solmsi solmsi (Mayr)

Blastophaga (Ceratosolen) Solmsi Mayr, 1885, pp. 154, 161, 163, 168—169, Pl. IX figs. 4—5 [key ♀, ♂, descr. ♀, ♂, ex *Ficus (Cystogyne) canescens* Kurz[2]) (det. Solms), Bogor (Java), Bot. Gdn., leg. H. Solms-Laubach; type: ♂].

Ceratosolen Solmsi: Mayr, 1906, p. 155 [rectification of original descr., ex *Covellia didyma* Miq.[2]), Bogor (Java), Bot. Gdn., leg. C. Aurivillius, no. 2]; Grandi, 1928c, pp. 173—176 [type specimens of *Blastophaga Solmsi* Mayr studied, = *C ? Marchali:* Grandi; differences from *C. marchali* Mayr].

Ceratosolen ? Marchali: Grandi, 1926, pp. 357—358 [♀, ♂, ex *Ficus hispida* L. (det. J. Beumée; Herb. Bog. no. E. J. 2173), Djakarta (Java), leg. E. Jacobson, IV.1924]; Grandi, 1927b, pp. 174—178, figs. III—IV [descr. ♀, ♂, ex *Ficus* spec., Saigon (S. Vietnam), leg F. Silvestri, 1924].

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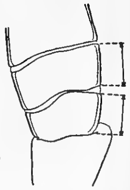
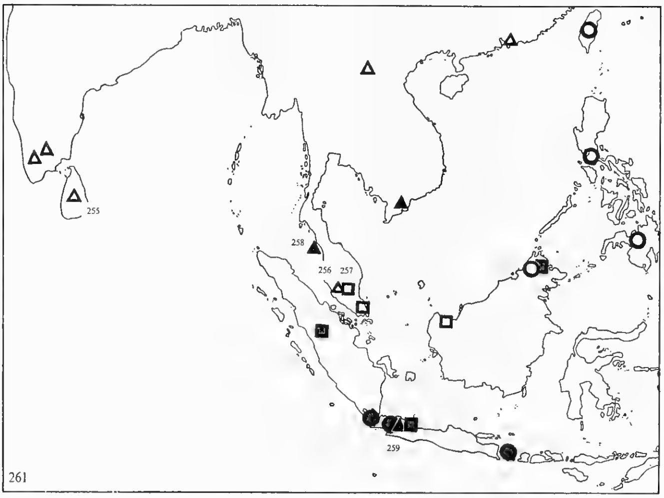
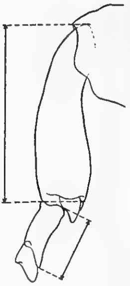
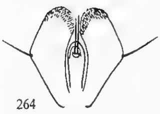
[1]) Series ♀, ♂, ex *Ficus hispida* Linn.f., Hambledon (Queensland), leg. C. E. PEMBERTON, 9.XI.1921; coll. HSPA; coll. ML, no. 590: 20 ♀, 10 ♂.

[2]) For a discussion of the host records, see p. 97.









Figs. 255—260, *Ceratosolen s. solmsi* (255, 256) and *C. s. marchali* (257—260), antennal groove of male, specimens from: 255, Ceylon, 256, 257, Selangor, 258, Langkawi I., 259, Java, 260, Queensland, 261, distribution on the Asian continent, and in the Philippines and Indonesia, of: *C. s. solmsi* (black triangles), *C. s. marchali* (open triangles) — the numbers refer to the figures above —, *C. bisulcatus* (black dots), *C. jucundus* (open circles), *C. constrictus* (black squares), and *C. hewitti* (open squares), 262—264, *C. s. solmsi*, Java, male, 262, detail of right antenna, with the measurements of third and fourth segments, used in Table I, 263, detail of hind leg, with the measurements of tibia and metatarsus, used in Table I, 264, labium and maxillae, 265, *C. s. marchali*, Selangor, male, cercus of tenth urite. Figs. 255—260, 263, × 105; 265, × 140; 264, × 190; 262, × 235

Material.

Series ♀, ♂, ex *Ficus hispida* Linn. f., Bogor (Java), Bot. Gdn, VIII.1954; coll. nos. 9, 10, 11 (205 ♀, 47 ♂, all from one fig), 12; ♂, slide 12a.

One ♀, 1 ♂, Java, no. 186; coll. USNM.

Fragments of 5 ♀, series ♂, ex *Ficus hispida* Linn. f.[1]) (det. E. J. H. CORNER), Langkawi Is. (Malaya), 1941, Sing. F. no. 37889; coll. no. 412; ♀, slide 412a.

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[1]) "This was a rather unusual form of *F. hispida* with completely geocarpic figs (borne on slender twigs rooting in the ground)" (CORNER, 1956, in litt.).

TABLE I. SOME MEASUREMENTS OF *C. s. solmsi* AND *C. s. marchali* FROM DIFFERENT LOCALITIES

Collection number	Locality	♀. Length of: 1) maxilla / bacilliform process	♀. Number of ridges on mandibular appendage. 2)	♀. length of: 1) eleventh / tenth antennal segments.	♂. Length of: 3) fourth / third antennal segments.	♂. Width of antennal groove.4)	♂. Length of: 5) tibia / metatarsus of hind leg.	Number of specimens measured.	Subspecies.
9	Java	3.75 (3.3—4.3)	7 (6—8)	1.7 (1.55—1.76)	1.5 (1.2 —2.0)	1	2.9 (2.7—3.0)	10 ♀, 10 ♂	*C. s. solmsi*
412	Langkawi	2.75	7	broken	1.5 (1.25—1.75)	1	3.0 (2.8—3.2)	1 ♀, 10 ♂	*C. s. solmsi*
618	Selangor	2.2 (2.1—2.4)	6—7	0.8 (0.76—0.85)	2.0 (1.5 —2.5)	1—2	2.6 (2.4—3.3)	10 ♀, 10 ♂	*C s. marchali*
594	Hongkong	2.1	6	0.67	3.5	3	2.4	1 ♀, 1 ♂	*C s. marchali*
564	India	2.3 (2.1—2.5)	8 (8—9)	0.75 (0.7 —08)	4.0 (3.3 —4.7)	3	2.2 (2.0—2.4)	5 ♀, 5 ♂	*C s. marchali*
378 382	Ceylon	2.4	9	broken	3.5	3	3.0	1 ♀, 2 ♂	*C s. marchali*
590	Queensland	2.9 (2.5—3.3)	6	0.66 (0.62—0.76)	1.25 (1.0—1.6)	2	3.75 (3.5—4.0)	10 ♀, 5 ♂	*C. s.* cf. *marchali*

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1) Unit of measure, 4.5 μ.

2) Ridges only, distal edge not counted

3) Measured along the antaxial margin, in dorsal view (fig. 262). Unit of measure, 4.5 μ.

4) A grade from narrow to wide is indicated by the numbers 1—3 (see figs. 255—260).

5) Metatarsus measured along the plantar edge, tibia without the apical teeth (fig. 263). Unit of measure, 15 μ.

Ceratosolen solmsi marchali Mayr

Ceratosolen Marchali Mayr, 1906, pp. 155—156 [descr. ♀, ♂, ex *Ficus* spec., Tonkin (N. Vietnam) leg. P. Marchal, no. 20a]; Grandi, 1928c, pp. 173—175 [type specimens of *C. Marchali* Mayr studied, = *C. Berlandi* Grandi; differences from *C. solmsi* (Mayr)]; Joseph, 1953c, p. 282 [♀, ♂, ex *Ficus hispida* L., Kottayam (Travancore, India), leg. K. J. Joseph, 26.VI.1951].

Ceratosolen Berlandi Grandi, 1928a, pp. 74—79, fig. II [descr. ♀, ♂, ex *Ficus hispida* L., Chambaganour (Pulneys, India)¹), 5000 ft. alt., leg. E. Gombert, 14.IV.1914].

Material.

Series ♀, ♂, India, ex coll. JOSEPH; coll. ML, no. 564.

Ten ♂, 5 ♀, Calcutta (India), leg. ROTHNEY, VIII.1885; coll. OUM.

Series ♀, ♂, ex *Ficus hispida* Linn. f., Hongkong (China), leg. GREEN, issued at Honolulu, 29.VIII—1.IX.1921; coll. HSPA; coll. ML, no. 594: 1 ♀, 1 ♂.

Series ♀, ♂, ex *Ficus hispida* Linn. f., Hongkong (China), leg. D. T. FULLAWAY, 16.I.1921; coll. HSPA.

Series ♀, ♂, ex *Ficus hispida* Linn. f. (det. E. J. H. CORNER), Sungei Gombah (Selangor, Malaya), leg. E. J. H. CORNER, 4.X.1961; coll. no. 618; ♀, slide 618a, ♂, 618b, c.

Ten ♀, 2 ♂, ex *Ficus hispida* Linn. f., Peradeniya (Ceylon), Bot. Gdn., leg F. KEISER, 25.II.1954; coll. NMB; coll. ML, no. 378: 1 ♀.

Three ♀, series ♂, ex *Ficus hispida* Linn. f., Peradeniya (Ceylon), Bot. Gdn., leg. F. KEISER; coll. NMB; coll. ML, no. 382: 3 ♂.

Ceratosolen brongersmai sp. n. (figs. 266—277)

Material.

Series ♀, ♂, ex *Ficus treubii* King (det. E. J. H. CORNER), Sungei Mesilau (N. Borneo), 5500 ft. alt., leg. E. J. H. CORNER, VIII.1961; coll. no. 604; ♂ (holotype), slide 604a, ♀ (allotype), 604c, ♂, ♀ (paratypes), 604b, d.

Series ♀, ♂, ex *Ficus treubii* King (det. E. J. H. CORNER), Sungei Bembangan (N. Borneo), 5500 ft. alt., leg. E. J. H. CORNER, VIII.1961, RSNB no. 1891; coll. no. 612; ♂, slide 612a, ♀, ♂, 612b.

Description.

Male. Maximum width of the head (fig. 269) three quarters of the length, the head slightly narrower anteriorly and posteriorly. Pubescence short and sparse. Eyes absent. Antennal grooves open, wide behind. Antenna (fig. 270) five-segmented: the scape (7 : 4) one and a half times as long as the pedicel (2 : 1); the first flagellar segment annuliform, the second (1 : 2) less than one fifth the length of the third (3 : 1). Labium and maxillae (fig. 277) large, the labium bilobate, the lobes not equal; maxilla with a lateral expansion bearing one long hair. Mandible, fig. 266.

Thorax, fig. 269. Pronotum nearly twice as long as wide anteriorly, the posterior width one and a half times the anterior width. Maximum width of the

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[1] ? = Shembaganur, Palni Hills, S. India?

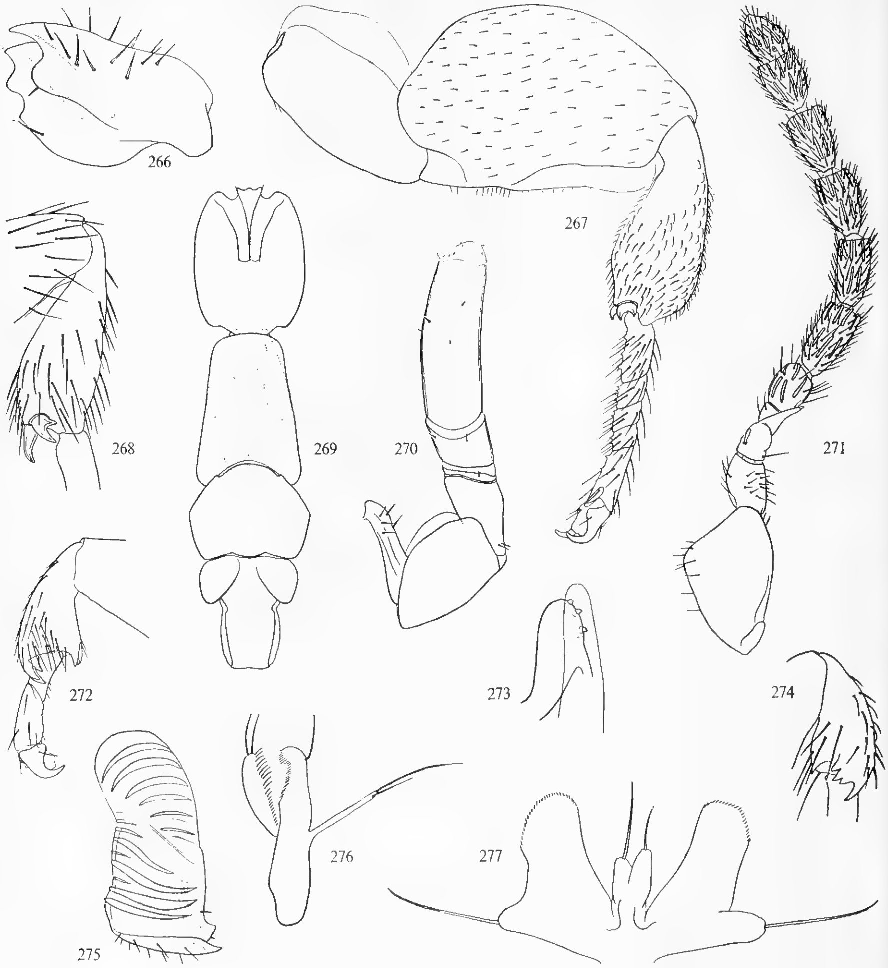
mesonotum, across the lateral angles, distinctly longer than the length [13 : 10]. Metanotum narrower than the mesonotum, incompletely separated from the propodeum. Propodeum long and rather narrow, with large peritremata. Metasternum glabrous. Femur of the fore leg (fig. 272) twice as long as the tibia. Tibia apically with four dorsal teeth (three large and one smaller), and three ventral teeth. Tarsus bimerous, segments in ratio 5 : 6. Mid leg slender, the coxa nearly as long as the femur, the tibia distinctly longer [3 : 2]. Tibia with the ventro-apical edge produced into two teeth. Tarsus pentamerous, the segments in ratio 7 : 2 : 2 : 2 : 7. Hind leg, fig. 267. Coxa large, with a hyaline border along the dorsal margin as in the species with dilated hind feet, pubescent axially, glabrous antaxially. Femur with a hyaline part along the distal ventral border; antaxial surface with small hairs, axially with many long stout hairs. Tibia two-thirds the length of the femur; ventral apex with two articulating teeth: the axial one curved, the antaxial one deeply bidentate. Tarsus with small protuberances along the ventral margin; the five segments in ratio 16 : 6 : 5 : 5 : 14.

Gaster. Cerci of the tenth urite with three claws, parameres straight and narrow (fig. 273).

Length, 1.7 mm. Colour uniformly olive-brown, the pubescent parts of the hind legs darker.

Female. Head as long as wide across the eyes. Longitudinal diameter of the eye longer than the cheek [7 : 5]. Pubescence long. Antenna (fig. 271): scape not very long, but wide; the pedicel not quite half as long as the scape, with approximately thirty-five spines at the axial surface. Appendix of the third segment long and slender; the fourth segment small. Fifth segment wide, with twelve long sensilla. Sixth segment longer than the following [8 : 7], seventh to ninth segments subequal, and longer than the tenth [7 : 6], which is a little longer than the apical segment. Sixth to tenth segments with two irregular rows of ten long sensilla each; the eleventh segment with ten long and two circular sensilla. Labium and maxillae (fig. 276): labium with two hairs, maxilla with one apical hair; maxilla moreover with a bacilliform process, which is nearly half as long as the maxilla. The process bears two hairs. Mandible (fig. 275) with four large and four smaller ventral ridges, the appendage with six or seven ventral ridges.

Thorax. Pronotum not very large, pubescent. Scutum nearly as long as its maximum width, a little narrower behind; with approximately twenty long hairs. Scutellum one and a half times as long as wide, with eight hairs along each lateral edge. Metanotum with a row of nine or ten hairs on each side of the mid line. Propodeum large, with two hairs above, and fifteen beneath the peritremata. Fore wing (2 : 1), 2.0 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 7 : 3 : 3 : 4; the stigma with four pustules, the submarginal vein with three. Hind wing (4 : 1), 1.2 mm long. Fore leg (fig. 274): the coxa two-thirds the length of the femur, which is more than twice as long as the tibia. Apical tibial comb consisting of four sharp teeth. Tarsus pentamerous, the segments in ratio 18 : 8 : 7 : 7 : 8. Mid leg slender, with long hairs. Tibia nearly as long as femur and trochanter combined, with a long, slightly curved ventral spur. Tarsal segments in ratio 17 : 8 : 8 : 8 : 11. Coxa of the hind leg (fig. 268) large;



Figs. 266—277, *Ceratosolen brongersmai,* Borneo, 266, male mandible, 267, male hind leg, 268, detail of female hind leg, 269, male, 270, male antenna, 271, female antenna, 272, detail of male fore leg, 273, male, cercus of tenth urite, and paramere, 274—276, female, 274, fore tibia, 275, mandible, 276, labium (lateral aspect), and maxilla, 277, male labium and maxillae. Figs. 269, × 40; 272, × 90; 267, 268, 271, 274—276, × 115; 266, 270, × 160; 273, 277, × 275

the femur long but not very wide, with long hairs; the tibia as long as the coxa, and nearly two-thirds the length of the femur. Tibia with two ventral teeth: the axial one rather long and curved, the antaxial one bidentate. Tarsus pubescent, especially along the plantar edge; segments in ratio 15 : 6 : 6 : 4 : 8.

Gaster. Projecting part of the ovipositor about one tenth the length of the gaster.

Length, 2.0 mm. Colour brown, the extremities and ventral surface lighter. Nervures of the wings brown, light brown striae radiate from the stigma.

Remark.

In some aspects, this species is close to *C. humatus* and *C. albulus* (see below), notably in the shape of the male trophi. The female, however, has a different tibial armature in the fore leg, and the male hind tarsi are not dilated. The other connection is that with *C. solmsi*, which, however, has different male mouthparts. For further remarks on the classification of *C. brongersmai* and *C. solmsi*, see p. 87.

I name this remarkable species in honour of Dr. L. D. BRONGERSMA, Director of the Rijksmuseum van Natuurlijke Historie, Leiden.

Ceratosolen pilipes sp. n. (figs. 278—285; 287—292)

Material.

Series ♀, ♂, ex *Ficus cereicarpa* Corner (det. E. J. H. CORNER), Mt. Kinabalu East (N. Borneo), 2000 ft. alt., leg. E. J. H. CORNER, VI.1961; coll. no. 636; ♂ (holotype), slide 636a, ♀ (allotype), 636e, ♂, ♀ (paratypes), 636b, c, d, f.

Description.

Male. Head (fig. 279) nearly twice as long as wide anteriorly; the maximum width two-thirds of the length. Dorsal surface, especially along each side of the antennal grooves, with rather long hairs. Eyes present. Antennal grooves open, wide behind. Antenna (fig. 281) five-segmented; the scape (17 : 10) nearly twice as long as the pedicel (9 : 5); the first flagellar segment annuliform, the second (1 : 1, longer antaxially than axially) one third the length of the apical segment (9 : 4). Labium and maxillae, fig. 288. Labium with two subapical hairs, and sometimes with a pair of basal hairs, which, however, more often than not are absent. Maxilla expanded laterally, with two lateral hairs. Mandible, fig. 278.

Thorax, fig. 279. Pronotum not quite twice as long as wide anteriorly, and nearly as long as wide posteriorly. Mesonotum large, little wider than long. Metanotum incompletely separated from the propodeum; propodeum long and rather narrow, with large peritremata. The metasternum, and to a lesser extent also the mesosternum, with a rather long and heavy pubescence (fig. 289). Fore leg (fig. 292): the coxa large, the femur twice as long as the tibia including the large dorsal teeth. Tibia with a comb of four closely joined large teeth at the dorsal edge, and three ventral teeth. Tarsus bimerous, but with an indication of a trimerous condition; the two free segments subequal in length. Coxa of the mid leg little shorter than the femur; the tibia as long as femur and trochanter combined, with heavy pubescence apically, the ventral edge produced into two teeth. Tarsus pentamerous; the segments in ratio 23 : 7 : 9 : 8 : 23. Hind leg (fig. 287) with heavy pubescence on all segments. Coxa wide, but shorter than the femur. Tibia two-thirds the length of the femur; the dorso-apical edge produced; ventrally with a bidentate tooth. Tarsal segments in ratio 12 : 6 : 6 : 5 : 9, the length of the pubescence approximately two-thirds the width of the segments.

Gaster partly sclerotized. Cerci of the tenth urite (fig. 284) with five or six short claws, the parameres curved axially.

Length, 2.3—2.4 mm. Colour yellow-brown, the head a trifle darker. Hind legs, especially the femora, dark brown.

Female. Head longer than wide across the eyes [10 : 9]; pubescent. Longitudinal diameter of the eye three quarters the length of the cheek. Antenna (fig. 283): the scape large; the pedicel with several hundreds of small spines (fig. 285) at the axial surface; the third segment rather robust, its appendage strongly curved. Fourth segment small. Fifth segment almost glabrous, with ten oblong sensilla. Sixth to ninth segments long, about twice the length of the fifth segment. Tenth segment shorter; the apical segment but little longer than the fifth. Sixth to eleventh segments with several irregular rows of sensilla. Labium with two subapical hairs. Maxilla (fig. 291) with one subapical lateral hair, and a bacilliform process, which is nearly half as long as the maxilla itself. The process bears one apical hair, and a lateral hair at four-fifths of the length. The mandible (fig. 290) bears nine ventral ridges, its appendage seven.

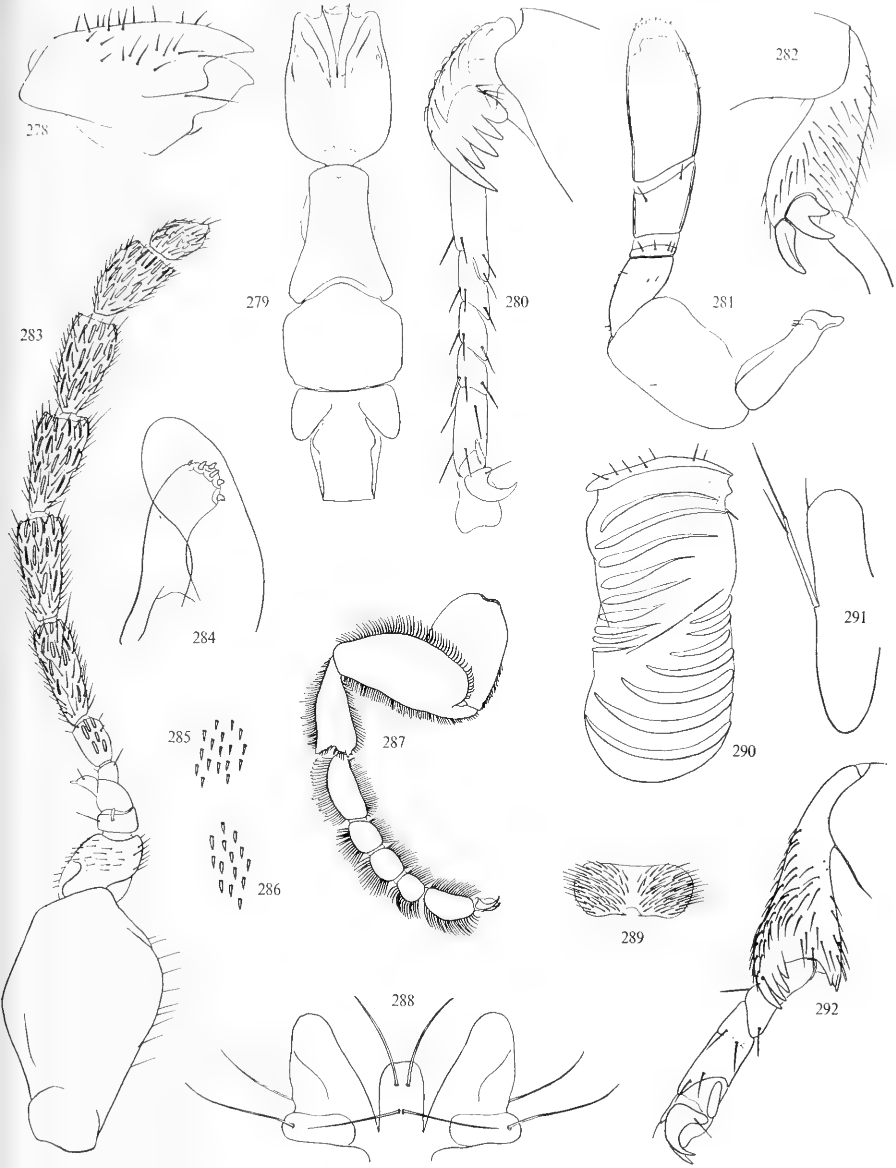
Thorax. Pronotum rather long, with long hairs. Scutum about as long as its maximal width; its lateral and ventral edges with about ten long hairs. Anterior width of the scutellum five-sevenths of its length; the scutellum bears approximately forty long hairs. Metanotum with rows of fifteen hairs on each side of the mid line. Propodeum long, with tufts of seven hairs above, and nearly fifty hairs beneath and next to the spiracular peritremata. Fore wing (11 : 5), 3.0 mm long. Submarginal, marginal, stigmal, and postmarginal veins approximately in ratio 16 : 5 : 4 : 11; the stigma distally produced, with two pairs of pustules; the submarginal vein with three pustules. Hind wing (4 : 1), 1.85 mm long. Fore leg (fig. 280): the coxa two-thirds, the tibia (including the dorsal armature) one half the length of the femur. Tibia with a dorso-apical comb of four sharp and one blunt teeth; ventrally with a blunt protuberance, which bears several long hairs. Axially, the tibia and the tarsus bear several long, stout spine-like hairs. Tarsal segments in ratio 18 : 5 : 5 : 4 : 8. Mid leg slender; the coxa semiglobular, the trochanter short, but rather wide, the subclavate tibia nearly as long as trochanter and femur combined, with one long ventral spur; tarsal segments in ratio 10 : 4 : 4 : 3 : 6. Hind leg (fig. 282): the coxa as wide as the femur, but shorter [4 : 5]; the femur pubescent, with a distinct ventral groove for the reception of the tibia. Tibia with two ventro-apical teeth, the antaxial one of which is bidentate. Tarsus with spines and many hairs, especially along the plantar edge, the segments in ratio 16 : 7 : 7 : 4 : 8.

Gaster. Ovipositor short, approximately one tenth the length of the gaster.

Length, 3.2—3.4 mm. Colour of head and dorsal surfaces of thorax and gaster black-brown, lighter ventrally. Nervures of wings brown, with dark striae radiating from the stigma.

Remark.

C. pilipes is remarkable in having the dorso-apical edge of the male hind tibia produced, and the parameres strongly curved. The dorsal armature of the female fore tibia — and this holds for several other species in the relationship of *C. pilipes* — reminds one of the tibial comb in *C. armipes* and relatives.



Figs. 278—292, *Ceratosolen pilipes* (286, *C. josephi*), Borneo, 278, male mandible, 279, male, 280, detail of female fore leg, 281, male antenna, 282, detail of female hind leg, 283, female antenna, 284, male, cercus of tenth urite, and paramere, 285, female, axial spines of pedicel, 286, do., of *C. josephi*, 287—289, male, 287, hind leg, 288, labium and maxillae, 289, metasternum, 290, female mandible, 291, female maxilla, 292, male fore leg. Figs. 279, 287, 289, × 40; 280, 282, 283, 290—292, × 90; 278, 281, × 115; 285, 286, 288, × 200; 284, × 275

Ceratosolen josephi sp. n. (figs. 286, 293—303)

Material.

Series ♀, ♂, ex *Ficus francisci* Winkler (det. E. J. H. Corner), Sungei Mamut (N. Borneo), 3000 ft. alt., leg. E. J. H. Corner, VIII.1961; coll. no. 621; ♂ (holotype), slide 621a, ♀ (allotype), 621c, ♂, ♀ (paratypes), 621b, d-g.

Description.

Male. Head (fig. 296) twice as long as wide anteriorly. The maximum width is but little longer than the anterior width [5 : 4]. Pubescence short, especially occurring along the antaxial edges of the antennal grooves. Eyes present. Antennal grooves open, wide behind. Antenna (fig. 294) five-segmented; the scape, not nearly twice as long as wide apically, twice as long as the pedicel (3 : 2); the first flagellar segment annuliform, the apical segment (7 : 3) thrice as long as the second flagellar segment (9 : 7). Mouthparts, fig. 301. Labium with a pair of subapical hairs; maxilla expanded laterally, with two lateral hairs. Mandible, fig. 298.

Thorax, fig. 296. Pronotum twice as long as wide anteriorly, and distinctly longer than wide posteriorly [6 : 5]. Maximum width of the mesonotum four-fifths of its length. Metanotum incompletely separated from the propodeum, which is but little longer than its maximum width. Metasternum with heavy pubescence, mesosternum with less hairs. Fore leg (fig. 303): the femur more than twice as long as the tibia [11 : 5]; the four dorsal teeth of the tibia not so close together as in *C. pilipes.* Tibia with three ventral apical teeth. Tarsus bimerous, with notches indicating the presence of a third intermediate segment; the two free segments subequal. Mid leg: the coxa smaller than the femur; the tibia smaller than femur and trochanter combined. Tibia with long dorsal and ventral hairs, the ventral edge produced into two apical teeth. Tarsus with long hairs, the segments in ratio 9 : 4 : 4 : 4 : 8. Hind leg (fig. 299) with heavy pubescence on all segments. Coxa rather narrow, shorter than the femur, the tibia two-thirds the length of the femur. Dorso-apical edge of the tibia produced; ventrally, the apical edge bears a bidentate tooth, and a sharp tooth at the outermost corner. Tarsal segments in ratio 9 : 7 : 6 : 4 : 7; pubescence nearly as long as the width of the segments.

Gaster partly sclerotized. Cerci of the tenth urite with three short claws, parameres almost straight (fig. 297).

Length, 2.0—2.2 mm. Colour light brown, with darker hind legs.

Female. Head as long as wide across the compound eyes; with rather long hairs. Longitudinal diameter of the eye four-fifths of the length of the cheek. Antenna (fig. 293): scape not very large relative to the large pedicel, which bears approximately one hundred and fifty spines. Compared with those of *C. pilipes*, these spines are rather large (fig. 286). Fifth segment with ten oblong sensilla. Sixth to eighth segments longer than the ninth [11 : 10], which is twice as long as the fifth. Tenth segment smaller than the ninth, the apical segment slightly longer than the fifth. Sixth to eleventh segments bear several irregular rows of sensilla. Labium and maxillae (fig. 302): the labium bears two subapical hairs; the maxilla bears one subapical hair and a bacilliform process, which is half as long as the maxilla. The apical hair of the bacilliform process is visible in all specimens. The presence of a lateral hair is indicated by a small pit, at four-fifths of the length; I cannot find any specimens in which the hair is actually present. Mandible (fig. 300) with eight ventral ridges, the appendage with seven.

Thorax. Relative proportions much as in *C. pilipes*, but some parts are distinctly less pubescent: scutellum with four hairs along each lateral edge; metanotum with rows of four to five hairs on each side of the mid line; propodeum with about twenty-five hairs below the peritremata. Fore wing (21 : 10), 2.55 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 20 : 7 : 8 : 15. Stigma rather blunt distally, with three pustules; submarginal vein with three pustules. Hind wing (4 : 1), 1.6 mm long. Fore leg (fig. 295): the coxa nearly two-thirds the length of the femur, which is more than twice as long as the tibia including the dorsal armature. Dorsal comb of the tibia consisting of four sharp and one blunt teeth; ventrally, the tibia bears a protuberance with long hairs. Axial surfaces of tibia and tarsus with several stout hairs. Tarsal segments in ratio 22 : 7 : 8 : 7 : 14. Mid leg as in *C. pilipes*. Femur of the hind leg rather pubescent, twice as long as the tibia, which bears the usual axial, and bidentate antaxial teeth. Tarsus rather wide, pubescent along the plantar edge; segments in ratio 30 : 13 : 11 : 10 : 16.

Gaster. Ovipositor distinctly projecting, one seventh the length of the gaster.

Length, 2.5—2.7 mm. Colour dark brown dorsally, lighter ventrally. Fore wings with brown nervures and dark striae.

Remark.

This species is close to *C. pilipes*, yet it is easily recognized by its smaller size, and by several characters in the female antenna and thorax, and in the male mouthparts and legs.

I name the species after Dr. K. J. JOSEPH, Head, Department of Zoology, Karnatak University, Dharwar (India), in recognition of his contributions to the knowledge of Indian fig insects.

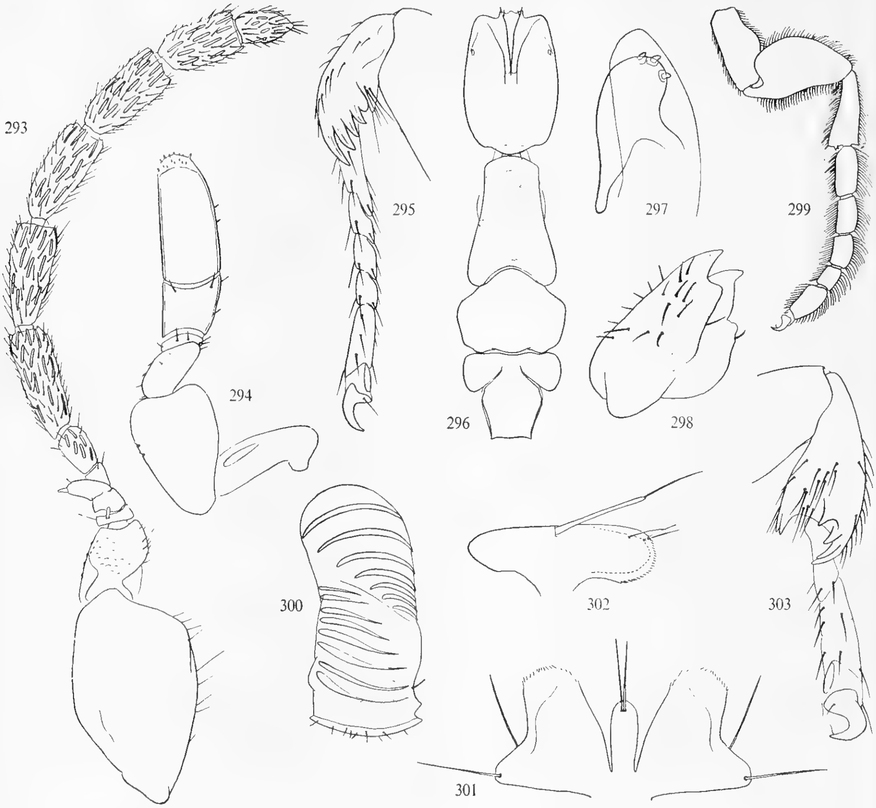
Ceratosolen albulus sp. n. (figs. 304—316)

Material.

Series ♀, ♂, ex *Ficus uncinata* Becc. var. *strigosa* Corner (det. E. J. H. CORNER), Mt. Kinabalu East (N. Borneo), 3500 ft. alt., leg. E. J. H. CORNER, VI.1961, RSNB no. 666; coll. no. 603; ♂ (holotype), slide 603a, ♀ (allotype), 603b, ♀, ♂ (paratypes), 603c, d.

Description.

Male. Head (fig. 305) longer than its maximal width [5 : 4], the anterior width three-fifths of the length. Pubescence short and sparse. Eyes absent. Antennal grooves open, wide behind. Antenna (fig. 306) five-segmented; the scape (3 : 2) but little longer than the pedicel (4 : 1). First flagellar segment (1 : 2) one sixth the length of the pedicel; the second segment nearly thrice as long as the first, and one third the length of the apical segment (3 : 1). Labium and maxilla (fig. 316)



Figs. 293—303, *Ceratosolen josephi*, Borneo, 293, female antenna, 294, male antenna, 295, detail of female fore leg, 296—299, male, 296, male, 297, cercus of tenth urite, and paramere, 298, mandible, 299, hind leg, 300, female mandible, 301, male labium and maxillae, 302, female labium and maxilla, lateral aspect, 303, detail of male fore leg. Figs. 296, 299, × 40; 293, 295, 300—303, × 90; 294, 298, × 115; 297, × 275

wide, with one lateral hair on the maxilla; labium bilobate. Mandible, fig. 315.

Thorax, fig. 305. Pronotum as long as wide posteriorly, the anterior width two-thirds of the length. Mesonotum distinctly wider than long [17 : 14], the lateral edges with a stricture at mid length. Metanotum rather large, incompletely separated from the propodeum; the latter longer than wide [5 : 4], with straight lateral margins. Fore leg (fig. 304): the coxa two-thirds the length of the femur, which is twice as long as the tibia. Dorso-apical comb of the tibia consisting of three large and two smaller teeth; there are several ventral teeth. Tarsus bimerous, segments approximately in ratio 2 : 3. Femur of the mid leg as long as coxa and trochanter combined; the tibia slightly longer than femur and trochanter combined. Ventral tibial edge produced into two apical teeth. Tarsal segments in ratio 17 : 5 : 6 : 6 : 20. Femur of the hind leg (fig. 307) not much longer than coxa and trochanter combined; the tibia distinctly shorter [4 : 5]. The coxa with a small hyaline dorsal ridge, and many hairs on the axial surface; the femur and tibia, as well as the tarsus, pubescent. Tibial armature consisting of two ventro-apical teeth (fig. 308), the antaxial one of which is bidentate. Tarsus dilated, the segments in ratio 45 : 22 : 23 : 20 : 40. Length of the pubescence one half to three quarters the width of the segments.

Gaster. Cerci of the tenth urite with six claws; in many specimens, the parameres are folded longitudinally (fig. 309).

Length, 2.2—2.3 mm. Colour yellowish; the thoracic terga ivory-whitish.

Female. Head slightly shorter than wide across the eyes [17 : 18]. Pubescence long. Longitudinal diameter of the eye longer than the cheek [5 : 3]. Antenna, fig. 310. Scape two and a half times as long as the pedicel, which bears approximately fifty spines at the axial surface. Third segment small, not half as long as the fifth; the latter two-thirds the length of the sixth; seventh to eleventh segments gradually diminishing in size, the eleventh about as long as the fifth, but narrower. Sensilla rather long and narrow; fifth to tenth segments with about twenty to twenty-five, the apical segment with fifteen sensilla. Labium and maxilla (fig. 311): the labium with two hairs; the maxilla with a bacilliform process (half as long as the maxilla) and a subapical, lateral hair. Mandible (fig. 312) with seven ridges, the appendage with eleven ridges, the proximal two of which are very small and not always distinctly visible.

Thorax. Pronotum with rather short hairs. Scutum anteriorly one and a half times as wide as long, the posterior width half the anterior width; with five long hairs along each lateral margin. Posterior width of the scutellum nearly equal to its length, anterior width four-fifths of the length. Lateral margins with five hairs. Metanotum rather long, with fourteen hairs on each side of the mid line. Propodeum with two hairs above, and nine hairs beneath the peritremata. Fore wing (2 : 1), 2.5 mm long. Submarginal, marginal, stigmal, and postmarginal veins in ratio 39 : 21 : 20 : 25; submarginal vein with three pustules, stigma with four. Hind wing (5 : 1), 1.6 mm long. Fore leg (fig. 314): the coxa more than half as long as the femur [5 : 8], which bears long hairs. Tibia, not nearly half as long as the femur [3 : 8], with a dorso-apical comb of six teeth, the first of which is blunt. Ventrally, the tibia bears a blunt tooth and a long spur. Antaxial surface with long hairs, especially in the ventral part; axial surface with ten stout spine-like hairs. Tarsal segments in ratio 13 : 5 : 5 : 6 : 7; axial surfaces of the segments with stout spines, except for the fifth, which has hairs instead. Mid leg slender, the tibia nearly as long as trochanter and femur combined; tarsal segments in ratio 23 : 11 : 13 : 12 : 15. Hind leg (fig. 313); the femur slender, one and a half times as long as the tibia. Tibia with long hairs and two ventral teeth, the antaxial one of which is bidentate. Tarsus pubescent, segments in ratio 23 : 9 : 7 : 8 : 11.

Gaster. Ovipositor short, but distinctly protruding behind the gaster.

Length, 2.3—3.0 mm. Colour brown, pronotum and head darker, ventral surface and extremities lighter. Fore wing with two dark striae radiating from the stigma

Remark.

C. albulus is close to *C. humatus,* but it differs in its dimensions, the dentation of the male fore tibia, the length of the pedicel of the male antenna, etc.

Ceratosolen humatus sp. n. (figs. 317—329)

Material.

Series ♀, ♂, ex *Ficus beccarii* King var. *latifolia* Corner (det. E. J. H. CORNER), Kundasan (N. Borneo), 4000 ft. alt., leg. E. J. H. CORNER, 24.VIII.1961; coll. no. 608; ♂ (holotype), slide 608a, ♀ (allotype), 608c, ♂ (paratype), 608b.

Series ♀, ♂, ex *Ficus beccarii* King var. *latifolia* Corner (det. E. J. H. CORNER), Mt. Kinabalu East (N. Borneo), 6500 ft. alt., leg. E. J. H. CORNER, 7.VIII.1961, RSNB no. 709; coll. no. 611; ♀, ♂ (paratypes), slides 611a, b.

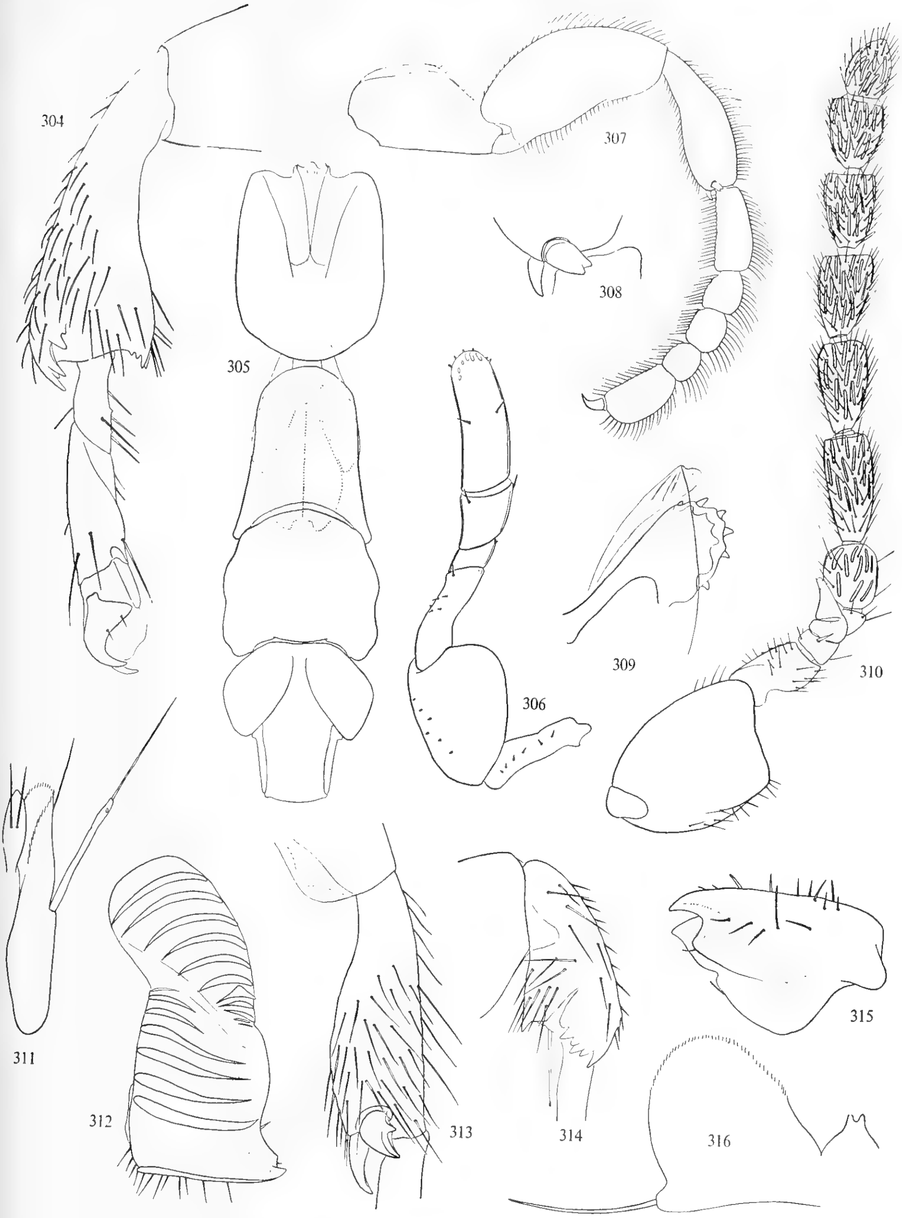
Series ♀, ♂, ex *Ficus beccarii* King var. *latifolia* Corner (det. E. J. H. CORNER), Mt. Kinabalu East (N. Borneo), 3500 ft. alt., leg. E. J. H. CORNER, VI.1961, RSNB no. 665; coll. no. 614; ♀, ♂ (paratypes), slides 614a, b.

Series ♀, ♂, ex *Ficus subterranea* Corner (det. E. J. H. CORNER), Tenompok (N. Borneo), 4500 ft. alt., leg. E. J. H. CORNER, VIII.1961, RSNB no. 1987; coll. no. 607; ♂, slides 607a, b, ♀, 607c, d.

Description.

Male. Head (fig. 326) one and a half times as long as wide anteriorly, and distinctly longer than its maximum width [9 : 7]. Pubescence short and sparse. Eyes absent. Antennal grooves open, wide behind. Antenna (fig. 323) five-segmented: the scape (12 : 7) twice as long as the pedicel (2 : 1); the first flagellar segment (3 : 7) one third the length of the pedicel, the second segment (2 : 3) twice, the apical segment (3 : 1) seven times as long as the first. Labium and maxillae, fig. 319. Labium bilobate at apex, each lobe with an apical hair, and sometimes with an extra hair at the axial surface; maxilla with two lateral hairs as in the figure. Mandible, fig. 324.

Thorax, fig. 326. Pronotum short, as long as wide at mid length, slightly narrower in front, and much wider behind. Mesonotum large, nearly as long as wide posteriorly, narrower anteriorly. Metanotum incompletely separated from the propodeum, the free part of which is about as long as wide. Coxa of fore leg (fig. 325) large, more than half as long as the femur; the femur twice as long as the tibia. Apical armature of the tibia consisting of a series of dorsal teeth, and three ventral teeth. Tibia axially as well as antaxially with stout hairs. Tarsus bimerous, although a dorsal notch in the distal segment indicates an original trimerous condition; the free segments subequal in length. Mid leg slender, the coxa slightly longer than the femur, but shorter than the clavate tibia. Tibia with long hairs; its ventro-apical edge produced into two teeth. Tarsal segments in ratio 14 : 5 : 5 : 4 : 14. Hind leg (fig. 321): the coxa but little shorter than the femur, glabrous antaxially, strongly pubescent axially, with a dorsal hyaline ridge. Femur antaxially with few short hairs, pubescent axially. Tibia three quarters the length of the femur, pubescent; the ventral armature consisting of a bidentate antaxial, and an axial tooth, which is slightly curved. Tarsus dilated, the pubescence approximately one half to five-sevenths the width of the segments. Tarsal segments in ratio 23 : 11 : 11 : 11 : 18, or the first segment slightly shorter and the tarsus wider, or the first segment slightly longer and the tarsus longer, in some specimens.



Figs. 304—316, *Ceratosolen albulus*, Borneo, 304—309, male, 304, detail of fore leg, 305, male, 306, antenna, 307, hind leg, 308, apex of hind tibia, 309, cercus of tenth urite, and paramere, 310—314, female, 310, antenna, 311, labium and maxilla, 312, mandible, 313, detail of hind leg, 314, detail of fore leg, 315, male mandible, 316, male labium and maxilla. Figs. 305, 307, × 40; 310, × 90; 304, 306, 308, 311—314, × 115; 315, × 160; 309, 316, × 275

Gaster. Cercus and paramere, fig. 322; the cercus apically with four claws. Apodemae aedeagales rather darkly sclerotized.

Length, 1.5—1.9 mm. Colour uniformly whitish yellow, darker in older specimens.

Female. Head short, not quite as long as wide across the eyes [23 : 24]. Pubescence long. Longitudinal diameter of the eye twice as long as the cheek. Antenna (fig. 318): the scape thrice as long as the pedicel, which bears approximately forty spines. Appendage of the third segment slender, rather long; the fourth segment small. Fifth segment twice as long as the fourth, with twelve long sensilla. Sixth and seventh segments one and a half times as long as the fifth, but narrower; eighth to eleventh segments gradually diminishing in size. Sixth to tenth segments with irregular, alternating rows of long sensilla: approximately twenty sensilla per segment; apical segment with twelve long and two circular sensilla. Labium with two subapical hairs. Maxilla (fig. 317) with one subapical lateral hair, and a bacilliform process, which is more than half as long as the maxilla. Mandible (fig. 320) with six ventral ridges, its appendage with nine.

Thorax. Pubescence of pronotum long. Scutum shorter than its maximal width, with six hairs along each lateral margin. Scutellum one and a half times as long as wide, its sides (except posteriorly) subparallel, with five or six hairs along each lateral edge. Metanotum with eleven hairs on each side of the mid line; propodeum with three hairs above, and about ten beneath the large peritremata. Fore wing (2 : 1), 2.1 mm long; submarginal, marginal, stigmal, and postmarginal veins in ratio 8 : 4 : 3 : 5; submarginal vein with two pustules, stigma with four. Hind wing (5 : 1), 1.4 mm long. Fore leg (figs. 327—328): the coxa two-thirds the length of the femur; the tibia not quite half as long as the femur. Tibial armature consisting of a dorsal comb of six teeth (the first blunt), and one ventral tooth. Axially, the tibia is provided with several stout hairs. Tarsal segments in ratio 11 : 5 : 5 : 5 : 7. Mid leg slender, the coxa semiglobular; the tibia not quite as long as femur and trochanter combined. Ventral edge of the tibia produced apically. Tarsal segments in ratio 25 : 10 : 9 : 8 : 12. Coxa of the hind leg (fig. 329) shorter than the femur, but wider; the femur narrow; the tibia slender, two-thirds the length of the femur. Tibial apex axially with a curved tooth, antaxially with a bidentate tooth. Tarsus pubescent, the segments in ratio 25 : 11 : 11 : 9 : 10.

Gaster. Ovipositor scarcely projecting beyond the apex of the gaster.

Length, 2.2 mm. Colour blackish brown dorsally, lighter ventrally. Extremities light yellow-brown. Old specimens are darker; young specimens sometimes have the last two or three antennal segments of an ivory-white colour. Fore wings with two dark striae radiating from the stigma.

Remark.

C. humatus is evidently related to *C. pilipes* and *C. josephi*, but the male metasternum is glabrous, and the hind tibia is not produced dorsally; the female tibial comb consists of six teeth.

I cannot find distinct constant differences between the wasps from *Ficus bec-*

carii and *F. subterranea.* Although the specimens from coll. no. 608 have the male hind legs slightly more slender than those of coll. no. 607, this differential character is bridged by the males from coll. no. 611. Consequently, I refer the specimens from *F. subterranea* to *C. humatus.*

Ceratosolen bisulcatus (Mayr) and **C. jucundus** Grandi (figs. 152, 153; map, fig. 261)

C. bisulcatus (Mayr) and *C. jucundus* Grandi are so similar that it is questionable whether the two should be maintained as separate species. Some differences between *C. bisulcatus* from Java and Bali, and *C. jucundus* from Luzon, are:

♀. Maxilla with a bacilliform process in *C. jucundus,* without such a process in *C. bisulcatus* (fig. 153).

♂. The head is slender in *C. bisulcatus* (one and a half times as long as wide), and bears small eyes. In *C. jucundus* the head is relatively shorter, and the form is anophthalmous.

Specimens from New Guinea are slightly longer than those from Java and Bali, and the females are darker. Specimens from Borneo are of the general facies of *C. jucundus* from Luzon, but the female maxilla does not bear a bacilliform process, or, at most, it has a small protuberance instead (in this it is similar to the form recorded from Formosa, of which I did not see examples). Distribution, see map, fig. 261. The male mouthparts (fig. 152) and genitalia (cercus of the tenth urite with two claws) are similar in the two species, and both show the oligomery in the male mid tarsi (but these are pentamerous in the specimens from Formosa, and heteromerous in those from Borneo). *C. bisulcatus* males have heteromerous hind tarsi, which I do not find in *C. jucundus.*

Ceratosolen bisulcatus (Mayr)

Blastophaga (Ceratosolen) bisulcata Mayr, 1885, pp. 154, 161, 163, 170—171 [key ♀, ♂, descr. ♀, ♂, ex *Ficus (Cystogyne) lepicarpa* Bl. (det. Solms)[1]), Bogor (Java), Bot. Gdn.; type: ♂].

Ceratosolen bisulcatus: Karny, 1923, figs. 5—6 [♀, ♂, Krakatau, leg. K. W. Dammerman]; Grandi, 1928c, pp. 180—184, figs. XXIX—XXX [redescr. ♀, ♂, type specimens of *B. bisulcata* Mayr]; Dammerman, 1948, pp. 381—382, fig. 21 [♀, ♂, Krakatau, and Verlaten Island, IX.1920, 1933].

Material.

Series ♀, ♂, ex *Ficus septica* Burm. f., Bogor (Java), Baranangsiang, 24.X. 1954; coll. no. 75.

Series ♀, ♂, ex *Ficus septica* Burm. f. (det. E. J. H. CORNER), Lae (Terr. New Guinea), Erap, leg. E. J. H. CORNER, 7.IX.1960; coll. no. 544; ♂, slide 544a, ♀, 544b.

Series ♀, ♂, ex *Ficus septica* Burm. f., Sudadji (Bali, distr. Sawahan, 16 km SE of Singaradja), leg. NJOMAN TOJA; coll. no. 58; ♂, slide 58a.

Series ♀, ♂, ex *Ficus* spec., Java, leg. A. HOOGERWERF, XI.1954, no. 9; coll. no. 283.

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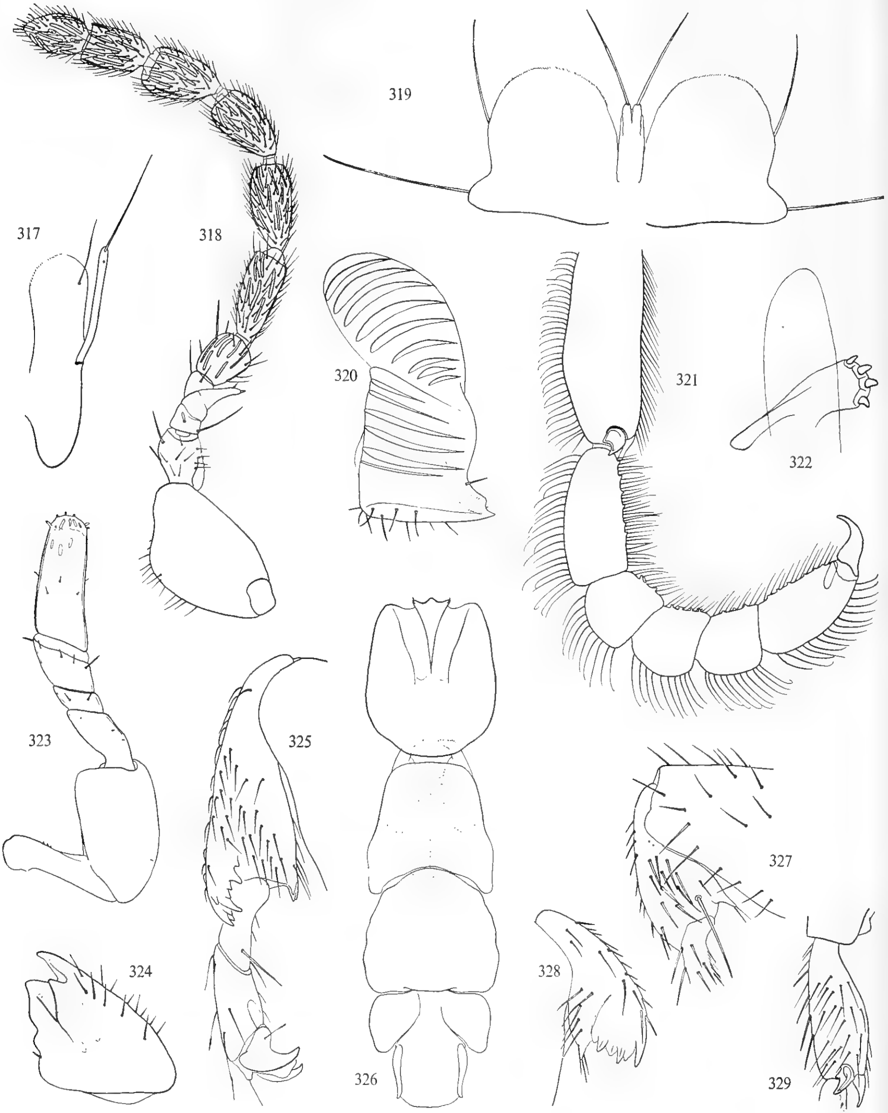
[1]) SOLMS evidently confused *F. septica* with *F. lepicarpa*; see p. 98.



Figs. 317—329, *Ceratosolen humatus*, Borneo, 317, female maxilla, 318, female antenna, 319, male labium and maxillae, 320, female mandible, 321—326, male, 321, detail of hind leg, 322, cercus of tenth urite, and paramere, 323, antenna, 324, mandible, 325, detail of fore leg, 326, male, 327—329, female, 327, detail of fore leg, axial aspect, 328, fore tibia, 329, detail of hind leg. Figs. 326, × 40; 318, 321, 329, × 90; 317, 320, 323—325, 327, 328, × 115; 319, 322, × 275

Series ♀, ♂, ex *Ficus septica* Burm. f., Udjung Kulon (Java), leg. A. Hoogerwerf, XI.1954, no. 11; coll. no. 273; ♀, ♂, slide 273a, immature specimens, 273b.

Series ♀, ♂, ex *Ficus septica* Burm. f., Udjung Kulon (Java), leg. A. Hoogerwerf, XI.1954, no. 16; coll. no. 287; ♀, slide 287a, ♂, 287b.

Ceratosolen jucundus Grandi

Ceratosolen jucundus Grandi, 1927a, pp. 320—323, Pl. 5 figs. 67—76, Pl. 6 figs. 77—83 [descr. ♀, ♂, ex *Ficus hauili* Blanco[1]), Mt. Maquiling (Luzon, Philippine Is.), leg. C. F. Baker]; Grandi, 1927b, pp. 178—179 [descr. ♀, ♂, *C. ? jucundus,* Taihoku (Formosa), leg. F. Silvestri, 21.XI.1954].

Material.

Three ♀, 3 ♂, ex *Ficus hauili* Blanco[1]), Mt. Maquiling (Luzon, Philippine Is.), ex coll. Grandi; coll. ML, no. 507.

Series ♀, ♂, Mt. Maquiling (Luzon, Philippine Is.); coll. USNM.

Series ♀, ♂, ex *Ficus hauili* Blanco[1]), Los Baños (Luzon, Philippine Is.), Coll. Agric., leg. F. X. Williams, 6.II, 21.V, and 19.VI.1921; coll. HSPA.

Series ♀, ♂, ex *Ficus hauli* Blanco[1]), Lake Lanao (Mindanao, Philippine Is.), leg. F. X. Williams, 2.XI.1921; coll. HSPA; coll. ML, no. 587; ♀, slide 587a, ♂, 587b.

Series ♀, ♂, ex *Ficus septica* Burm. f., (det. E. J. H. Corner), Ranau (N. Borneo), 1800 ft. alt., leg. E. J. H. Corner, 3.VI.1961; coll. no. 616.

Series ♀, ♂, ex *Ficus septica* Burm. f. (det. E. J. H. Corner), Kundasan (N. Borneo), 4000 ft. alt., leg. E. J. H. Corner, IX.1961; coll. no. 634.

Species incertae sedis

Ceratosolen spec.

Material.

Immature ♀, ♂, ex *Ficus microdictya* Diels (det. E. J. H. Corner), Papua, leg. C. E. Carr, 14.XII.1935, no. 13785; coll. no. 449.

Remark.

From *Ficus microdictya*, I saw some immature wasps only, which I prefer not to describe. They seem to be close to *C. armipes* and allied species.

Ceratosolen spec.

Ceratosolen ? crassitarsus: Grandi, 1923a, p. 299 [descr. note on ♀, ♂, ex *Ficus roxburghi*[2]), Singapore, leg. H. N. Ridley]; 1927b, p. 174 [note on host record].

Material.

One ♀, 5 ♂, ex *Ficus Roxburghii*[2]), Singapore, H. N. Ridley, 89—38; coll. BM: 5 slides.

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[1]) = *Ficus septica* Burm. f.

[2]) Synonym of *Ficus auriculata* Lour., but the record is probably incorrect.

Remark.

In my opinion these specimens should be referred to a form of *Ceratosolen vechti,* rather than to *C. crassitarsus*; but the description has to wait until more and better material becomes available.

Ceratosolen spec.

Material.

Fragments of 3 ♀, ex *Ficus stolonifera* King (det. E. J. H. CORNER), Sarawak (Borneo), leg. M. JACOBS, no. 5257; coll. no. 503.

Remark.

These specimens, taken from dried figs in the Leiden Herbarium, are too fragmentary for specific identification, but they can be recognized as belonging to a species of *Ceratosolen.* The dorsal comb of the female fore tibia consists of four sharp teeth, and it does not show the blunt tooth found in other *Ceratosolen* from geocarpic figs.

Provisionally excluded

Ceratosolen megarhopalus Grandi, 1923b, pp. 103—104 [descr. ♀, at light, Fort de Kock (Sumatra), leg. E. JACOBSON, XI.1920, I.1923].

Ceratosolen elisabethae Grandi, 1923b, pp. 104—105 [descr. ♀, at light, Fort de Kock (Sumatra), leg. E. JACOBSON, XI.1920, I. 1923].

These two species, which are known in the female sex only, are characterized by the peculiar antennae, and the large eyes.

In the collection made by Dr. F. X. WILLIAMS in the Philippine Islands, I find a sample of females and males ex *Ficus ? longipedunculata,* Mt. Maquiling (Luzon), 23/24.VI.1921; coll. HSPA, which evidently belong to a species close to *C. megarhopalus* Grandi. The males have a very distinct *Blastophaga* facies, and this is the reason why I exclude the species of this group from the present revision of *Ceratosolen.*

Other samples ex "*Ficus longipedunculata*" (without the query; *F. longipedunculata* (Merril) Elmer = *F. chrysolepis* Miq., subgenus *Urostigma*) consist of a different species of Agaonidae.

CLASSIFICATION AND KEY TO THE SPECIES

In this chapter an attempt is made to classify the species in groups. I am well aware that these groups must be considered provisional divisions, which show some overlapping.

It is difficult to arrive at a satisfactory conclusion as to the status of some taxa. In one instance *(C. solmsi* and *C. marchali,* cf. p. 64, Table I) it is evident that the two forms should be regarded as subspecies. In other instances this evidence is lacking or non-conclusive, due to the scantiness of the material. For the time being, pending the examination of more material from more localities, I treat the following forms: *C. constrictus* and *C. hewitti*; *C. notus, C. orientalis*, and *C. calopilinae*; *C. bisulcatus* and *C. jucundus,* as full species.

I. *C. pygmaeus* group.

In this group I place *C. pygmaeus*, *C. marshalli*, and *C. nanus*, which all have the antennal grooves in the male head half closed, the labium and the maxillae atrophied, the lateral edges of the propodeum more or less rounded, the female maxillae without a bacilliform process, and the fore tibia with no more than three teeth in the dorsal comb and without the ventral spur.

C. nanus is aberrant in some aspects (male antenna consisting of five segments, genitalia without cerci, female antenna of a peculiar shape, its segments with few sensilla), but the trimerous mid and hind tarsi in the male, and the tetramerous fore and mid tarsi in the female, next to the general facies, connect the species with *C. pygmaeus.*

C. gravelyi, although evidently related to the species of this group (facies, male tibia without spines on the disk), seems to show more connections with the *C. appendiculatus* group.

I have long hesitated about the classification of *C. constrictus* and *C. hewitti*, which show some relationships with the *C. pygmaeus* group in the general facies, the oligomery of the mid and hind tarsi, and in the absence of the ventral spur from the female fore tibia. On the other hand, they have four teeth in the combs of the male and female fore tibiae (except for the sample from N. Borneo), as in some other groups. Tentatively I place *C. constrictus* and *C. hewitti* in this *C. pygmaeus* group.

Species of the *C. pygmaeus* group:

C. pygmaeus Grandi,
C. marshalli Grandi,
C. nanus Wiebes,
C. constrictus (Mayr),
C. hewitti Waterston.

II. *C. appendiculatus* group.

The species of this group have the antennal grooves in the male head half closed; as a rule the mid and hind legs bear spines on the disks, and the shape of the propodeum is rather uniform. The female fore tibia bears a simple ventral spur, and the dorsal dentation consists of four sharp teeth.

C. *gravelyi* connects the *C. pygmaeus* group with *C. emarginatus,* which at its turn resembles *C. fusciceps* and *C. appendiculatus.* Apparently *C. appendiculatus* and *C. grandii* are closely related: both species have the male genitalia without cerci and the club of the female antenna is composed of the united apical three segments.

Species of the *C. appendiculatus* group:

C. gravelyi Grandi,
C. emarginatus Mayr,
C. fusciceps (Mayr),
C. appendiculatus (Mayr),
C. grandii Wiebes.

Judging from the descriptions, the African species of *Ceratosolen* belong in this group.

III. *C. armipes* group.

C. armipes, C. bianchii, C. boschmai, and *C. sordidus* have in common the half closed antennal groove, the spines on the disk of the mid tibia, and the aberrant shape of the propodeum of the male, the dentation of the comb of the female fore tibia, and to some extent the general facies.

The group in which these species are united shows a rather great variation, e.g., in the shape of the male propodeum. In a way, the species resemble *C. pilipes* and its relatives, notably in the dentation of the female fore tibia.

Species of the *C. armipes* group:

C. boschmai Wiebes,
C. bianchii Wiebes,
C. armipes Wiebes,
C. sordidus Wiebes.

IV. *C. bakeri* group.

Some characters connect *C. bakeri* with the *C. armipes* group (male antenna resembling that of *C. boschmai,* male propodeum, dentation of female hind tibia), but the species has open antennal grooves and a three-segmented fore tarsus in the male.

Species of the *C. bakeri* group:

C. bakeri Grandi.

V. *C. abnormis* group.

C. abnormis, though evidently related to the species of the *C. armipes* group in some aspects (male antennal grooves half closed, segments of the fore tarsus incompletely separated, dentation of the female hind tibia), is aberrant in the male genitalia and in the armature of the female fore tibia.

It is classified here as a separate group:

C. abnormis Wiebes.

VI. *C. crassitarsus* group.

Characterized by the dilated hind feet of the male, the normal mouthparts — without large lateral expansions on the maxillae — and the dentation (four sharp teeth) of the comb of the female fore tibia. In some species (*C. notus*, *C. moderatus*, etc.) the male maxillae bear small lateral expansions, thus connecting the group with the *C. pilipes* group. Some other species are aberrant in the dentation of the male hind tibia, e.g., *C. nugatorius* and *C. dentifer* have a large motile spur on the disk of the hind tibia; *C. corneri* is aberrant in having very long hind feet in the male sex. Otherwise, the species of this group are very similar, and it is difficult to distinguish between the females of the various subgroups.

Species of the *C. crassitarsus* group:

C. crassitarsus (Mayr),
C. gracilis Wiebes,
C. hooglandi Wiebes,
C. vechti Wiebes,
C. nugatorius Grandi,
C. dentifer Wiebes,
C. moderatus Wiebes,
C. praestans Wiebes,
C. iodotrichae Wiebes,
C. notus (Baker),
C. orientalis Wiebes,
C. calopilinae Wiebes,
C. corneri Wiebes.

VII. *C. solmsi* group.

Two species with normal hind feet in the male (others with the same character, viz., *C. bisulcatus* and *C. jucundus* are aberrant in other features too and are joined to represent a distinct group IX) are difficult to be classified.

C. solmsi is evidently related to species with dilated hind feet, notably the *C. crassitarsus* group. In some characters, however, it is close to *C. brongersmai* (e.g., in the dentation of the male hind tibia) and in the dentation of the female fore tibia it differs from both the *C. crassitarsus* group and *C. brongersmai.*

C. brongersmai seems to be close to *C. albulus* and *C. humatus,* although it has the hind feet of the male not dilated and the comb of the female fore tibia is of normal constitution.

For convenience' sake the two species are here taken together in one group, which connects the *C. crassitarsus* group with the *C. pilipes* group.

The occurrence of *C. brongersmai* and *C. solmsi* among the species with dilated hind feet in the male makes it plausible that the character "dilated hind feet" may have been more than once acquired, or secondarily lost, in the evolution of the group.

Species of the *C. solmsi* group:
C. solmsi (Mayr), and subspec. *marchali* Mayr,
C. brongersmai Wiebes.

VIII. *C. pilipes* group.

Some species have the male maxilla with a very large, lateral expansion, and the female fore tibia with a blunt first tooth in the dorsal comb. *C. pilipes* and *C. josephi* have the metasternum of the male hirsute, and the apical edge of the hind tibia produced dorsally; the fore tarsus shows three incompletely separated segments. The tibial comb of the female fore leg consists of five teeth.

C. albulus and *C. humatus* have a glabrous metasternum, and the male hind tibia is not produced. The combs of the fore tibiae consist of six teeth in the females, and of five and nine teeth in the males of *C. albulus* and *C. humatus*, respectively.

Species of the *C. pilipes* group:
C. pilipes Wiebes,
C. josephi Wiebes,
C. albulus Wiebes,
C. humatus Wiebes.

IX. *C. bisulcatus* group.

C. bisulcatus and *C. jucundus* cannot easily find a place in any of the other groups. Apparently they are close to the species of the *C. crassitarsus* group; but they differ from all other species of *Ceratosolen* in the bilobate epistomal margin of the male.

Species of *C. bisulcatus* group:
C. bisulcatus (Mayr),
C. jucundus Grandi.

Key to the species.

But for *C. gravelyi,* which is intermediate between the *C. appendiculatus* group and the *C. pygmaeus* group, and keys out with the latter although classified in the former, all species groups can be identified by using the key, provided male specimens are available.

The following remarks may be helpful for identifying female specimens. Each alternative excludes the preceding one(s).

1. If the fore tibia is without a ventral spur, try no. 4 (*C. pygmaeus* group), and compare *C. abnormis* and *C. bakeri.*

2. If the comb of the fore tibia consists of more than four teeth, the first of which is blunt, try nos. 13 (*C. armipes* group) and 34 (*C. pilipes* group).

3. If the apical segments of the antenna are united (i.e., the antenna consists of less than eleven segments), try no. 10 (some species of the *C. appendiculatus* group).

4. If the apical three segments of the antenna are shaped so as to form together a club, compare *C. gravelyi* and *C. emarginatus.*

5. If the apical two segments of the antenna are shaped so as to form together a (sometimes very loose) club, try no. 18 (*C. bisulcatus* and *C. solmsi* groups), and compare the species of the *C. crassitarsus* group. The latter are not keyed out; it will be possible to arrive at a satisfactory identification only after careful comparison with the descriptions.

1. ♂. Antennal grooves half closed (example, fig. 20) 2
— ♂. Antennal grooves open (example, fig. 180) 16
2. ♂. Propodeum with comparatively small spiracular peritremata. ♀. Fore tibia with two to four sharp teeth in the dorsal comb 3
— ♂. Peritremata of the propodeum large. ♀. Fore tibia with five to ten teeth in the dorsal comb 12
3. ♂. Mid and hind tibiae without spines on the disks (*C. pygmaeus* group, and *C. gravelyi*) 4
— ♂. Mid tibia, and mostly the hind tibia also, with many spines on the disk (*C. appendiculatus* group except *C. gravelyi*) 9
4. ♂. Genitalia without cerci. ♀. Antenna aberrant (fig. 16), with few sensilla . . . . *C. nanus*
— ♂. Genitalia with cerci. ♀. Antenna normal, funicular segments with one or two rows of sensilla 5
5. ♂. Antenna consisting of four segments. Labium and maxillae atrophied. ♀. Fore tibia with three teeth in the dorsal comb 6
— ♂. Antenna consisting of five segments, one of which may be annuliform. Mouthparts present. ♀. Fore tibia with two or four teeth in the dorsal comb 7
6. ♂. Propodeum with distinctly rounded edges. Cerci of the tenth urite with one claw. ♀. Mandible with ten ventral ridges, its appendage with nine ridges . . . . *C. pygmaeus*
— ♂. Propodeum more angular behind (fig. 10). Cerci with three claws. ♀. Mandible, and its appendage, with four or five ventral ridges . *C. marshalli*
7. ♂. Thorax constricted (figs. 1, 2). ♀. Funicular segments with two to three rows of sensilla. Maxilla without a bacilliform process. Fore tibia without a ventral spur 8

— ♂. Thorax not as above. ♀. Funicular segments with one row of sensilla. Maxilla with a bacilliform process. Fore tibia with a ventral spur . . . . *C. gravelyi*

8. ♂. Head and thorax rather short, robust (fig. 2). ♀. Sixth antennal segment as long as the seventh, with three rows of short sensilla; the tenth segment approximately as long as the eleventh . . . . *C. constrictus*

— ♂. Head and thorax more slender (fig. 1). ♀. Sixth antennal segment two-thirds the length of the seventh, with two irregular rows of longer sensilla; the tenth segment approximately one and a half times as long as the eleventh . . . . *C. hewitti*

9. ♂. Mid and hind tibiae with spines or protuberances on the disks. ♀. Apical two or three antennal segments united. Maxilla without a bacilliform process 10

— ♂. Hind tibia without spines on the disk. ♀. Antennal segments free, but the apical three segments shaped so as to form together a distinct club. Maxilla with a bacilliform process . . . . *C. emarginatus*

10. ♂. Antenna consisting of five segments. Labium and maxillae atrophied. ♀. Funicular segments with two rows of sensilla . . . *C. appendiculatus*

— ♂. Antenna consisting of four segments. Mouthparts present. ♀. Funicular segments with one row of sensilla 11

11. ♂. Tarsal segments of the fore leg incompletely separated. Genitalia without cerci. ♀. Apical three antennal segments united . . . . . . *C. grandii*

— ♂. Tarsal segments of the fore leg free. Genitalia with cerci. ♀. Apical two antennal segments united . . . . *C. fusciceps*

12. ♂. Tibiae without spines on the disks. Genitalia with parameres only (fig. 81). ♀. Antenna with very few sensilla. Comb of the fore tibia consisting of eight to ten sharp teeth . . . . *C. abnormis*

— ♂. Mid and hind tibiae with spines or stout hairs on the disks. Genitalia not as above. ♀. Funicular segments with one to three rows of sensilla (unknown in one species). Comb of the fore tibia consisting of five or six teeth, the first of which is blunt (*C. armipes* group) 13

13. ♂. Antenna consisting of four segments. Fore tibia with three dorso-apical teeth. ♀. Apical two antennal segments united . . . . . . *C. armipes*

— ♂. Antenna consisting of five segments, one of which may be annuliform, or incompletely separated. Fore tibia with four dorso-apical teeth. ♀. Antennal segments free, although the apical three shaped so as to form a club . . 14

14. ♂. Tarsal segments of the fore leg free. ♀. Comb of the fore tibia consisting of six teeth . . . . *C. sordidus*

— ♂. Segments of the fore tarsus incompletely separated. ♀. Fore tibia with five teeth in the dorsal comb 15

15. ♂. Genitalia with cerci. ♀. Funicular segments with one row of sensilla Antaxial apical tooth of the hind tibia bidentate . . . . . *C. boschmai*

— ♂. Genitalia without cerci. ♀. Funicular segments with two rows of sensilla. Antaxial apical tooth of the hind tibia tridentate . . . *C. bianchii*

16. ♂. Hind feet normal, not dilated 17

— ♂. Hind feet dilated and hirsute 21

17. ♂. Antenna consisting of six segments, one of which is annuliform. Fore leg with three tarsal segments. ♀. Antaxial apical tooth of the hind tibia tridentate . . . . *C. bakeri*
— ♂. Antenna consisting of five segments, one of which may be annuliform. Tarsus of the fore leg consisting of two free segments. ♀. Antaxial apical tooth of the hind tibia bidentate 18
18. ♂. Epistomal margin bilobate. ♀. Funicular segments with one row of sensilla (*C. bisulcatus* group) 19
— ♂. Epistomal margin trilobate. ♀. Funicular segments with two or three rows of sensilla (*C. solmsi* group) 20
19. ♂. Head one and a half times as long as wide. Eyes present. ♀. Maxilla without a bacilliform process . . . . *C. bisulcatus*
— ♂. Head relatively shorter, the length not more than four thirds of the maximum width. Eyes absent. ♀. Maxilla mostly with a long bacilliform process, or with a small protuberance instead . . . . . . *C. jucundus*
20. ♂. Maxillae with lateral expansions. ♀. Fore tibia with four teeth in the dorsal comb . . . . *C. brongersmai*
— ♂. Maxillae without lateral expansions. ♀. Fore tibia with five teeth in the dorsal comb . . . . *C. solmsi*
21. ♂. Propodeum wider than long, or subquadrate, the posterior angles rounded. ♀. Comb of the fore tibia consisting of four sharp teeth (*C. crassitarsus* group) 22
— ♂. Propodeum longer than wide, the posterior angles slightly produced laterally. ♀. Comb of the fore tibia consisting of five or six teeth, the first of which is blunt (*C. pilipes* group) 34
22. ♂. Hind leg very long, as in fig. 254 . . . . *C. corneri*
— ♂. Hind leg not very long 23
23. ♂. Hind tibia with a large dark spur (figs. 144, 157) 24
— ♂. Hind tibia with the normal apical armature only 25
24. ♂. The spur on the hind tibia is situated apically. ♀. Funicular segments with one row of very long sensilla. Maxilla with a bacilliform process . . . . *C. dentifer*
— ♂. The spur is situated more proximally, on the disk. ♀. Funicular segments with two rows of normal sensilla. Maxilla without a bacilliform process . . . . *C. nugatorius*
25. ♂. Hind tibia approximately twice as long as the metatarsus 26
— ♂. Hind tibia distinctly less than twice as long as the metatarsus . . . 27
26. ♂. Maxillae with nearly straight lateral edges, without any lateral expansions. Length of male and female, approximately 1 and 1.5 mm, respectively . . . . *C. crassitarsus*
— ♂. Maxillae large, with lateral expansions. Length of male and female, approximately 1.5 and 2 mm, respectively . . . . *C. notus*
27. ♂. Hind tibia as long as or up to one and a half times as long as the metatarsus 28
— ♂. Hind tibia approximately one and three quarters the length of the metatarsus 32

28. ♂. Length of the apical antennal segment one and a half to one and three quarters the length of the subapical segment 29

— ♂. Apical segment of the antenna approximately two and a half times as long as the subapical one, or longer 30

29. ♂. Maxilla with a lateral expansion. Cerci of the tenth urite with five claws . . . . *C. moderatus*

— ♂. Maxilla without lateral expansions. Cerci of the tenth urite with two claws . . . . *C. gracilis*

30. ♂. Cerci of the tenth urite with seven claws. ♀. Bacilliform process one fifth the length of the maxilla . . . . *C. praestans*

— ♂. Cerci of the tenth urite with three to five claws. ♀. Bacilliform process nearly half as long as the maxilla 31

31. ♂. Apical segment of the antenna two and a half times as long as the subapical segment . . . . *C. hooglandi*

— ♂. Apical segment of the antenna six times as long as the subapical segment . . . . *C. iodotrichae*

32. ♂. Apical segment of the antenna less than twice as long as the subapical segment. ♀. Bacilliform process one third the length of the maxilla . . . . *C. vechti*

— ♂. Apical segment of the antenna approximately two and a half times as long as the subapical segment. ♀. Bacilliform process two-fifths the length of the maxilla, or longer 33

33. ♂. Maxilla with two lateral hairs. Hind leg long and slender. ♀. Maxilla not quite twice as long as its bacilliform process . . . . . . *C. orientalis*

— ♂. Maxilla with one lateral hair. Hind leg shorter, more robust. ♀. Maxilla approximately two and a half times as long as the bacilliform process . . . . *C. calopilinae*

34. ♂. Fore tarsus consisting of three segments, the distal two of which are incompletely separated. Dorsal edge of the hind tibia produced apically. Metasternum hirsute. ♀. Comb of the fore tibia consisting of five teeth . 35

— ♂. Fore tarsus consisting of two free segments. Dorsal edge of the hind tibia not produced apically. Metasternum not hirsute. ♀. Comb of the fore tibia consisting of six teeth 36

35. ♂. Cerci of the tenth urite with five or six claws, parameres curved. ♀. Pedicel of the antenna with several hundreds of small spines . . *C. pilipes*

— ♂. Cerci of the tenth urite with three claws, parameres straight. ♀. Pedicel of the antenna with approximately one hundred and fifty spines. . *C. josephi*

36. ♂. Fore tibia with a dorsal comb of five teeth. Pedicel of the antenna nearly as long as the scape. Cerci of the tenth urite with six claws. ♀. Mandibular appendage with nine to eleven ventral ridges . . . . *C. albulus*

— ♂. Fore tibia with nine teeth in the dorsal comb. Pedicel of the antenna about half as long as the scape. Cerci of the tenth urite with four claws. ♀. Mandibular appendage with nine ventral ridges . . . . *C. humatus*

THE HOST PREFERENCES OF THE AGAONIDAE[1])

> "Supremus Genitor Ficui propriam assignavit cupidinem"
>
> (Hegardt, 1749, p. 41)

Specificity of the relation between figs and fig wasps

Theories on the evolution of the symbiosis between figs and fig wasps are necessarily highly speculative. Fossil data do not provide any clue to the problem, although a fossil fig wasp (*Tetrapus mayri* Brues, 1910, p. 16) was described from the Tertiary (Miocene)[2]) of Florissant, Colorado, and the presence of fossil fig leaves is known from the Cretaceous.

Presumably, the fig wasps have descended from gall-forming Chalcidoidea, or from parasitic Chalcidoidea living on other insects in the flowers or seeds of the pre-*Ficus*. The assumption that the interaction of figs and wasps secondarily became synagonistic — gradually acquiring mutual value and evolutionary significance for both participants (Leppik, 1957, p. 479) — is not new. Although Müller (1886b, p. 63) already stated: "die Feigen (haben) einen ursprünglich einfach ihre Früchte zerstörenden Schmarotzer für ihre Kreuzung sich immer volkommener dienstbar gemacht", all subsequent theoretical considerations deal almost exclusively with morphological features of the fig wasps (Grandi, many papers, see 1955c; english summary in 1961). Müller, for that matter, did not elaborate on his thesis either. Moreover, he was of the opinion that also parasitic and inquiline wasps could pollinate the fig flowers, especially those of isolated trees (Müller, 1883, p. 312). The flight capacity of *Blastophaga*, and consequently its dispersal, was supposed to be very weak.

Probably, only the Agaonidae serve as pollinators, every species to its peculiar species of *Ficus*. The dispersal of the fig wasps does not seem to be such a problem as might be presumed: Pemberton (1934, p. 379) stated that both *Pleistodontes imperialis* Saunders and *P. froggatti* Mayr reached Kauai from Mahu (Hawaiian Islands) without human assistance[3]). The width of the Kauai Channel is about one hundred kilometers!

As incidentally remarked above, the relation between figs and fig wasps is supposed to be highly specific, and it seems to represent a strict one-to-one relationship. Some evidence of this supposition may be found in the systematic part of this paper. More arguments, and reputed contra-evidence, objections and related considerations are discussed below.

Some authors (Van der Pijl, 1960, p. 415; Baker, 1961, p. 378) pointed out the evolutionary dangers with which every narrow specialist must cope. Van der

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[1]) "Agaonidae" and "fig wasps" are used here in the restricted sense (Wiebes, 1961b), without including the Sycophaginae, and thus coincide with Agaoninae auctt., and Agaonini auctt.

[2]) Lower to Middle Oligocene, according to Mac Ginitie as cited by Axelrod (1954).

[3]) A similar phenomenon was recorded by Corner (1958, p. 18) for the wasps from *Ficus fistulosa* Reinw. and *F. grossularioides* Burm.

PIJL is surprised to find the genus *Ficus*, each species with its own gall wasp, still flourishing; BAKER, however, seems to change his surprise to disbelief and does not accept the specificity until more data are available (BAKER, l.c., and in litt.). Yet, I think that the evidences in favour of a specific relation are fairly sound as far as any extrapolation in biology goes. Moreover, in my opinion, the "evolutionary dangers" are not correctly understood. Admittedly a narrow specialism may endanger evolution to the extent of making the development of new major types well nigh impossible, but there is no reason why it should hamper evolution at the specific level. The great variety of related forms within the genus *Ficus*, which all are bound to the same mode of pollination, and the relatively uniform family Agaonidae, all species of which live and must develop in the gall receptacles of *Ficus*; in short: many species without any clear-cut generic intersections, are what should be expected as the result of a narrowly specialized and obligate symbiosis, where other features, as fecundity and dispersal, do not retard evolution.

The experiments on the cross pollination of *Ficus carica* Linn. and *F. pumila* Linn., which showed the perfect compatibility of these species — and which led BAKER (l.c., p. 379) to the suggestion that many hybrids might occur that are not recognized as such — are not conclusive. These experiments only show that the "choice" of the pollinating agent may be the only isolating mechanism between the fig species (which in this case, however, do not even occur sympatrically).

WILLIAMS (1928, pp. 9, 10) induced *Eupristina bakeri* Grandi, the wasp from *Ficus forstenii* Miq., to crawl into the small figs of *F. retusa* Linn. (= *F. microcarpa* Linn.f.), the normal inhabitant of which in the Philippines is *E. verticillata* Waterston:[1])

"A *F. retusa* fruit was placed in a test tube containing some of the wasp pollinators belonging to *F. forstenii*, and while these wasps were not constantly watched, soon a pair of wings was observed protruding from the *F. retusa* ostiole, where the wasp's body had not altogether disappeared within, the ovipositor being flattened into some drying liquid discharged from the abdomen. This comparatively immense *E. bakeri* wasp finally worked her way within. She did nothing in the receptacle save walk about prying here and there with her head, using the now stubby antennae as a wedge apparently in an endeavor to force apart the flowers. Another similar experiment was unsuccessful."

Similar experiments were also done with *Ceratosolen notus* (Baker) — from *F. nota* (Blanco) Merrill — in *F. barnesii* Merrill (= *F. botryocarpa* Miq.), the normal pollinator of which is *C. corneri* Wiebes:

"... several wasps had succeeded in gaining complete entrance and stood free on the inner scales, their abdomen compressed and with sharp lateral angles greatly suggesting an expulsion of body fluid, and the ovipositor still projecting needle-like behind. Now to be in readiness for oviposition an effort was made to pull the ovipositor from its sheath so that it points downwards beneath the forepart of the abdomen; in this some are immediately successful, curving the abdomen, jabbing the ovipositor into the funnel-like stigma of a gall flower and then in

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[1]) I give these and other citations at some length, because they describe the only experiments of this sort; experiments worth while to repeat with more species.

bringing the abdomen back to the natural, more or less horizontal position the ovipositor is swung forward out of its sheath; in other cases the wasp has great difficulty or even fails — possible due to abnormal conditions — in unsheathing her egg-laying apparatus, bending down the tip of her abdomen and endeavoring to hook her claws into the ovipositor and draw it out."

and further:

"it seemed that very few ovipositions (?) occurred, and such as they were — for the conditions seemed unsuitable — occupied in one case about a minute."

WILLIAMS stated that his experiments showed that it is possible to induce fig wasps to enter other than their own particular species of fig, although this would be expected to take place but rarely in nature. In view of the large number of species of wild figs that may occur in a single habitat, it is, according to WILLIAMS, not unreasonable to suppose that hybridization might have taken place there. In addition to this conclusion I may remark that in the experiments the figs were presented in closer proximity to the wasps than I presume any wasp — with the possible exception of the inhabitants of strangler figs and their victims — ever to come near a "foreign" fig receptacle. Probably, the wasps are attracted by the scent of their own *Ficus*; this scent may be produced by glands on young leaves and petioles¹).

A questionable point to some authors is whether the wasps carry enough pollen from a ripe to a young fig for the development of the thousands of ovaries that may be present in one receptacle, and whether or not the pollen is used at all by the fig. In a nearly mature female receptacle of *F. roxburghii* Wall. (= *F. auriculata* Lour.), with general enlargement of the ovaries, CUNNINGHAM (1889, p. 42) found three insects with only one or two shrunken pollen-grains adhering to them. Contrarily, PEMBERTON (1921, p. 306) stated for *Pleistodontes froggatti* Mayr in *F. macrophylla* Desf. that sufficient pollen is carried over to secure ample pollination for a great many flowers in each fig. TREUB (1902, p. 137) found the pollen grains in the female receptacles in *F. hirta* Vahl: "assez nombreux pour effectuer la fécondation, sinon de toutes, en tout cas de la grande majorité de fleurs". BAKER (1913, p. 68) described the habits of the female *Ceratosolen notus* (Baker) in the young fertile figs of *F. nota* (Blanco) Merr. as: "distributing to the stigmas the pollen with which her body was thoroughly dusted".

CUNNINGHAM concluded from his observations that the seeds develop by adventitious embryony from the nucellus. This agamospermic reproduction needed the action of the female fig wasp, but it was independent of pollination²). Similar observations were made by TREUB. He concluded from his cytological investigations that *F. hirta* reproduces parthenogenetically. The embryogenesis presumably needed the action of the insect as a stimulus, but the embryo started its development without amphimixis.

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¹) In this, as in the previous part of this paper, I draw freely from data on *Ficus* given by CORNER (in litt. to VAN DER VECHT and WIEBES, and personal communication).

²) Serious criticism on the botanical data in CUNNINGHAM's paper was published by VAN DER PIJL (1934, pp. 179—181). CUNNINGHAM's remarks on the identity of the wasp species too, as well as its identification by WOOD-MASON with a species of "*Eupristis*", are to be regarded with extreme caution.

BUSCALIONI & GRANDI (1938, p. 243) recorded that in *F. carica* Linn.: "la cellula ova non fecondato va a male".

JOHRI & KONAR (1938) contributed a short preliminary note on the embryology of *F. religiosa* Linn.

There are many more papers on this problem, an account of which may be found in the bibliography in JOSEPH (1958), mainly on normal and abnormal development in the edible fig, but new experiments on wild figs are badly wanted. Admittedly apogamy and parthenocarpy occur, but I doubt whether these phenomena are of general occurrence under natural conditions.

However this may be — whether the insects give the stimulus by stinging the stigmata, or bring the stimulus in the form of pollen, or both — there are many records of figs cultivated in foreign countries that did not fructify until their particular species of wasps were introduced (*F. carica* Linn. and *Blastophaga psenes* (L.) in California: HOWARD (1901); *F. macrophylla* Desf. and *Pleistodontes froggatti* Mayr in the Hawaiian Islands: PEMBERTON (1921), SWEZEY (1923), TIMBERLAKE (1924); *F. rubiginosa* Desf. and *P. imperialis* Saunders in the Hawaiian Islands: SWEZEY (l.c.), TIMBERLAKE (l.c.); etc.¹)).

There are some records of one species of *Ficus* harbouring different species of Agaonidae, and of one species of fig wasp inhabiting different species of *Ficus*.

Although it is rather premature to discuss all these cases before the various genera have been revised, I give an annotated list of these records. Some were already mentioned by other authors, e.g., NIKOLSKAJA (1956, p. 573), and they tend to be discussed over and over again in literature. Oddly enough, however, these reputed cases do not appear to be very important. It is easily understandable that one species of *Ficus* can harbour two (sub-)species of Agaonidae in different parts of its area, or that the host of one species of fig wasp may show some geographic variation.

Some forms, both botanical and entomological, that are treated as separate species, are perhaps only subspecifically distinct. As already stated on p. 85, I treat the wasps as full species until more material from more localities gives evidence to the contrary. As to the species of *Ficus*, some of the forms, although inseparable in flower characters, are so distinct in the field that, for the time being, CORNER maintains them as separate species.

By presenting the following list I hope to attain that the attention in future be concentrated on the important records, and that all records that have no actual interest to our problem be expelled from the discussion.

1. The record of *Blastophaga brasiliensis* Mayr from several species of figs, is based on the following passage from MÜLLER (1886a, p. 57): "Hier [in Itajahy, Brazil]wurde ein und dieselbe *Blastophaga* (*Bl. brasiliensis*) in sieben verschiedenen Feigen (*Ficus* II, III, IV, V²), VI, VII, IX) gefunden; sind auch drei derselben (II, IV, VI) so ähnlich, dass sie vielleicht zur selben Art gerechnet werden

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¹) The statement by JUDD (1921) on the introduction of fig wasps to the Hawaiian Islands may be of some historical interest.

²) According to MAYR (1906, p. 185), MÜLLER's *Ficus* V is *F. dolaria. Ficus dolaria* Martinus, nomen nudum, = *F. gomelleira* K. & B.

können, so bleiben doch mindestens fünf scharf geschiedene und zum Teil weit verschiedene, am gleichem Orte wachsende Feigenarten auf eine einzige *Blastophaga* als wichtigsten[1]) Bestaübungsvermittler angewiesen". This statement wants confirmation.

2. GRANDI (1927a, p. 326) already discussed the case of *Blastophaga browni* (Ashmead), recorded from *Ficus ulmifolia* Lamk. and *F. heterophylla* Linn., both from the Philippine Isles. The latter species of *Ficus,* however, does not occur in the Philippines, and all Philippine specimens identified with *F. heterophylla* actually belong to *F. ulmifolia.*

3. JOSEPH (1953c, p. 267) described *Blastophaga constabularis* Joseph from *Ficus infectoria* Roxb. (India, = *F. virens* Ait.), but from the Sumatran *F. infectoria, B. coronata* Grandi (1928b, p. 75) was already known. Judging from the descriptions, the two are synonyms.

4. The record of *Blastophaga grossorum* Gravenhorst (= *B. psenes* (L.)) from *Ficus serrata* Forsk. (=*F. exasperata* Vahl) by MAYR (1885, pp. 153, 179, "Wüste am rothen Meere") may well have resulted from the misidentification of the *Ficus.* It might have been *F. palmata* Forsk., which is close to *F. carica* Linn., and which harbours *B. vaidi* Joseph (1954, p. 401; India), which is close to *B. psenes.* MAYR (l.c.) also recorded *B. grossorum* from *F. pseudocarica* Miq. (Abyssinia) and *F. persica* Boiss. (Iran), which both are synonyms of *F. carica* Linn.

5. *Blastophaga longicornis* Grandi (1926, p. 354) was described from *Ficus rostrata* Lamk. (Sumatra, E. JACOBSON, no. 2130), *B. dubia* Grandi (1926, p. 356) from *F. rostrata urophylla* Wall. (Java, Hort. Bog., n.VII, G. 46). The identification of E. J. 2130 with *F. rostrata* Lamk. (= *F. sinuata* Thunb.) is correct; Hort. Bog. n.VII, G. 46 probably is *F. urophylla* Wall., the correct name of which is *F. heteropleura* Bl.

6. GRANDI (1916b, p. 225) described the females of *Eupristina saundersi* Grandi from *Ficus religiosa* Linn. (India), from which MAYR (1885, p. 176) described *Blastophaga quadraticeps* Mayr (Malaya). GRANDI (1923a, p. 296), JOSEPH (1953c, p. 277), and JOHRI & KONAR (1955, p. 384) recorded *B. quadraticeps* from *Ficus religiosa* in India and Ceylon, and I find the same symbiosis in a sample from Israel (probably introduced).

There is some more confusion as to the host of *Eupristina saundersi*: the males were recorded from *F. retusa* Linn. var. *nitida* King[2])! GRANDI's host record of *E. saundersi* is probably incorrect, as is, most probably, his presumption (1952c, p. 96) that the host of *Pleistodontes semiruficeps* Girault (1929, p. 318: "on Banyan figs, Lord Howe Island") might be the same as *F. religiosa.* It might more likely have been *F. macrophylla* Desf., or one of its relatives.

7. I find *Ceratosolen constrictus* (Mayr)[3]) in *Ficus fistulosa* Reinw. (Java), and in *F. dimorpha* King (Sumatra). The latter, however, is so close to the former,

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[1]) MÜLLER (see also 1887b, p. 163) considered the possibility that some Idarninae transmit pollen with the pubescent ovipositor.

[2]) *F. retusa,* as used by botanists, is *F. microcarpa* Linn.f., and it is not genuine *F. retusa* Linn., which has been known as *F. truncata* Miq.

[3]) For the records of the species of *Ceratosolen,* I refer to the data given in the systematic part of this paper.

that it is probably a variety only, but it is insufficiently known botanically.

I have no check on the record of *C. hewitti* Waterston from *F. chartacea* Wall. (Malaya). In the Malayan *F. fistulosa*, *C. hewitti* is found, and from *F. chartacea* I possess an undescribed species of *Blastophaga*. Here is a case of a geographic variation in the wasps (*C. constrictus* and *C. hewitti*), that is not, or less, evident in the *Ficus*.

8. *Ceratosolen emarginatus* Mayr is found in both *Ficus auriculata* Lour. and *F. oligodon* Miq. The two forms of *Ficus* are very close. Their ranges seem to be the same for the greater part, but *F. oligodon* extends further south in Malaya, and hybrids are known from Indo-China, where the forms intergrade. Here is a case of a variation in the *Ficus,* which is not evident in the wasp.

The record of *C.? crassitarsus*: Grandi from Malayan *F. roxburghii* Wall. (= *F. auriculata* Lour.) is probably incorrect.

9. Mayr described *Ceratosolen appendiculatus* (Mayr) from *Ficus umbellata* Hort. Bog., nec Vahl, and *C. striatus* Mayr from *F. variegata* Bl., both collected in Java. Solms (in Mayr, 1885, p. 193) considered *F. umbellata* Hort. Bog. to be the same as *F. hirta* Vahl, from which, however, *Blastophaga javana* Mayr is known (from var. *setosa* King; Java).

One specimen in the Leiden Herbarium (sheet no. 908, 188—1895), labelled "*Ficus umbellata* Vahl, Kondang, Cult. in Hort. Bog.", was identified by Corner with *F. variegata* Bl., which supports the suggested synonymy of *C. striatus* and *C. appendiculatus.*

The other figs, recorded to harbour *C. appendiculatus*, are very close to *F. variegata*: *F. garciae* Elmer and *F. sycomoroides* Miq. were recently recognized as varieties, and *F. viridicarpa* Corner should perhaps be regarded as a variety too. The latter is an example of a form that is so distinct in the field, although very close in structural characters to *F. variegata*, that Corner prefers the two to be maintained as separate species.

10. *Ficus ribes* Reinw. (Java) is known to be the host of *Ceratosolen crassitarsus* (Mayr). The Philippine variety of *F. ribes*, var. *cuneata* (Miq.) Corner, harbours *C. gracilis* Wiebes. Here again a geographic variation in casu in both the *Ficus* and the wasp.

11. *Ceratosolen notus* (Baker) is recorded from *Ficus nota* (Blanco) Merrill and from *F. congesta* Roxb., both occurring in the Philippines. *F. congesta* seems to be more sylvan in habit than *F. nota,* but the two are so close that they can only with difficulty be distinguished in the field and in most cases not at all in herbarium specimens. The *Ficus nota* complex is in need of more examination botanically.

12. *Ficus hispida* Linn.f. harbours *C. s. solmsi* (Mayr) in Malaya and the Eastern Archipelago, and on the Asiatic mainland it is inhabited by *C. s. marchali* Mayr.

Mayr recorded *C. solmsi* also from *F. canescens* Kurz (?, unknown to Corner, possibly a manuscript name), and *Covellia didyma* Miq., both from Java The latter is a synonym of *F. lepicarpa* Bl., which was (see also no. 14) obviously misidentified by Solms.

13. I cannot find any constant differences between the wasps from *Ficus beccarii* King var. *latifolia* Corner and those from *F. subterranea* Corner, and I refer

both to *Ceratosolen humatus* Wiebes. The figs, although very close, are distinctly different in leaf-shape, and the distinction is approximately of the same magnitude as that between *F. beccarii latifolia* and *F. uncinata* Becc. var. *strigosa* Corner, which harbours a distinct form of *Ceratosolen, C. albulus* Wiebes.

This problem needs further study.

14. *Ceratosolen bisulcatus* (Mayr) was described from *Ficus lepicarpa* Bl. (Java). In the receptacles of this *Ficus,* however, I find *C. vechti* Wiebes (Java, Sumatra). *C. bisulcatus* inhabits the figs of *F. septica* Burm.f. in Java, Bali, and New Guinea, whereas in the Philippine *F. septica, C. jucundus* Grandi is found. SOLMS, who identified MAYR'S *Ficus*, evidently did not understand *F. lepicarpa* properly, as is, moreover, seen by his identification of the host of *C. solmsi* (see no. 12) with *Covellia didyma* (= *F. lepicarpa*).

15. *Ceratosolen fusciceps* (Mayr), known to be the symbiont of *Ficus racemosa* Linn. (from India to Queensland), was also recorded from *F. lucescens* Miq. (=*F. racemosa* var. *elongata* (King) Barrett) and *F. covellii* Roxb. (not known to CORNER).

From Australian *F. glomerata* (= *F. racemosa*), GIRAULT described *Blastophaga nigriscapus* Girault (1925, p. [2]) and *B. niveipes* Girault. Thanks to the kindness of Dr. E. F. RIEK, Canberra, I had the opportunity to study some female specimens of *B. niveipes,* which might actually belong to *C. fusciceps.* I did not see *B. nigriscapus.* Material from Queensland, ex *Ficus racemosa* (coll. WILLIAMS, HSPA), is identical with *C. fusciceps*; indeed, this species seems to be little variable over the whole of its very large range.

Ceratosolen mysorensis Joseph (India) is, in my opinion, identical with *C. fusciceps* (Mayr). The species was recorded from *F. mysorensis* Hayne (= *F. drupacea* Thunb. var. *pubescens* (Roth) Corner), but, a year later, *Eupristina belgaumensis* Joseph (1954, p. 409) was described from the same *Ficus.* As *F. drupacea* belongs to the group of strangler figs allied to *F. benghalensis* Linn., which all seem to harbour species of *Eupristina,* I presume the record of *E. belgaumensis* to be correct. *F. drupacea* may have been growing on a tree of *F. racemosa,* thus resulting in the confusion[1]) of the *Ficus* species.

16. SAUNDERS (1883, p. 6) described *Eupristina masoni* Saunders from *Ficus indica* Linn. (India). In 1928 (a, p. 81), GRANDI recorded *E. ?masoni* from *F. benghalensis* Linn., which, however, he considered to be the same as *F. indica.* From *F. benghalensis* was recorded (JOSEPH, 1953c, p. 282) *E. grassii* Grandi, of which the author stated (GRANDI, 1928c, p. 225): "è specie affine e, probabilmente, identica a *Masoni* Saunders".

In this, as in the following two problems, one must be aware of the fact that the host relations of the genus *Eupristina* can only be solved by a close cooperation between the botanist and the entomologist. The host *Ficus* are very close, and were not infrequently confused. The same is true for the species of *Eupristina.*

17. *Ficus benjamina* Linn. (Sumatra) is known to harbour *Eupristina jacobsoni*

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[1]) Either by the collector, in taking wasps from the one species, and botanical material from the other; or by the wasp, which might be unable to distinguish between fig receptacles of the different species, once the tree is found (?, cf. the experiments by WILLIAMS, discussed in this paper, p. 93).

Grandi (1926, p. 358), which is very close to *E. koningsbergeri* Grandi from *F. benjamina* var. *comosa* King (GRANDI, 1917, p. 52; Java). This variety is distinguished by having a much larger, rounded fig than typical *F. benjamina*. JOSEPH (1954, p. 415) recorded *E. koningsbergeri* from *F. benjamina* in India.

18. A similar problem exists in the wasp species recorded from *Ficus retusa* Linn. (= *F. microcarpa* Linn.f., see note on p. 96): *Eupristina verticillata* Waterston is known (GRANDI, 1926, p. 358) from the typical form (Sumatra, and presumably, sub *Grandiella* (WILLIAMS, 1928, p. 13), also from the Philippines), whereas ISHII (1934, p. 85) described *E. okinavensis* Ishii from the Japanese var. *nitida* Thunb. (see also this list, no. 6).

19. In 1961 (a, p. 231) I described *Agaon paradoxum modestum* Wiebes from *Ficus brachypoda* Hutch. (Uganda). The nominate subspecies is known (GRANDI, 1952a, p. 31) from *F. ovata* Vahl (West Africa). The figs, however, are so close that CORNER would not insist on the specific diversity of *F. ovata* and *F. brachypoda*.

20. For the sake of completeness I mention the cases of *Pleistodontes* spp., which were recorded from Australian figs (see GRANDI's catalogue, 1955b, p. 129). The confusion between *Ficus columnaris* Müll.[1]), *F. macrophylla* Desf., *F. australis* Willd.[2]), *F. rubiginosa* Desf.[3]), and *F. eugenioides* Müll.[4]) (PEMBERTON, 1944, p. 17), recorded by various authors as hosts of *Pleistodontes froggatti* Mayr, *P. imperialis* Saunders, and *P. nigricaput* Girault, may be due to a misunderstanding of the taxonomic status of the *Ficus*, and also to some misinterpretation of the wasp species.

PHYLOGENETIC SPECIFICITY

Additional, indirect evidence in favour of a specific relation between fig wasps and figs is supplied by the observation that related species of figs harbour related species of fig wasps. Mutatis mutandis, this principle was expressed in "FAHRENHOLZ's Rule" of parasitologists, in which is stated (I quote from SZIDAT, 1956, p. 243), that "bei stetigen Parasiten aus der Systematik der Parasiten meist unmittelbar auch auf die Verwandtschaft der Wirte schliessen [lässt]".

Tables II and III give a survey of the data on the host records of the Agaonid genera[5]), and of most species of *Ceratosolen*, respectively.

All host records of the Agaonidae known to me are incorporated in Table II. Specific records of the African fig wasps were mentioned by WIEBES (1961b, table I); specific records of the American Agaonidae will be listed in a later paper.

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[1]) = *Ficus macrophylla* Desf.

[2]) = *Ficus rubiginosa* Desf.

[3]) *Ceratosolen silvestrianus* Grandi (1916a, p. 160) was recorded from *F. ferruginea* Desf. (Africa!), which is the same as the Australian *F. rubiginosa* Desf. (with *Pleistodontes imperialis* Saunders).

[4]) = *Ficus obliqua* Forst.f. The sample, from which *Blastophaga greenwoodi* Grandi (1931, p. 8) was recorded, may have been *F. prolixa* Forst.f.

[5]) Host records are known of species of the following genera or subgenera: *Blastophaga* Gravenhorst, *Elisabethiella* Grandi, *Waterstoniella* Grandi, *Julianella* Grandi, *Valentinella* Grandi, *Kradibiella* Girault, *Ceratosolen* Mayr, *Eupristina* Saunders, *Tetrapus* Mayr, *Allotriozoon* Grandi, *Agaon* Dalman, and *Pleistodontes* Saunders.

As to the Indo-Australian wasps I have taken into account many species in our collection that are as yet only generically identified.

Many records had to be incorporated on which I have no check. In the evaluation of the data from the tables another reservation must be borne in mind. The groups of *Ficus* and the genera or species of the Agaonidae are presented in a linear sequence, and one cannot ever hope to depict but poorly the intricate multidimensional relationships in a linear system.

A similar, more conclusive list of the host records should be given when more genera are monographically revised, and when the classifications of *Ficus* and the Agaonidae have been reconsidered in a joint revaluation by the botanist and the entomologist.

The following notes may accompany this first, tentative draft of the host records of the Agaonidae.

The subgenera *Urostigma* and *Pharmacosycea*; tentative remarks on the African, American, and Australian genera of the Agaonidae

1. The relations within the subgenus *Urostigma*, as well as those in the Agaonidae, are very intricate, and they cannot be evaluated properly in this cursory review. I want to state here, that I am not satisfied with the usual generic division of the Agaonidae. In my opinion, *Elisabethiella* should not be regarded as a subgenus of *Blastophaga* s.l.; *Eupristina*, on the other hand, probably should; it appears to be the Asiatic analogon of American *Julianella*.

2. The record of *Ceratosolen silvestrianus* Grandi from the section *Malvanthera* (*Ficus rubiginosa* Desf.; Africa, see WIEBES, 1961a, p. 239) is doubtful. The record of a species of *Ceratosolen* from the section *Galoglychia* is based on the description of *C. myersi* Grandi (1955a, p. 92) from *F. rhodesiaca* Warb. (Africa). All other African species of *Ceratosolen* live in figs of the subgenus *Sycomorus*.

3. Some species of the section *Urostigma* and some of the subsection *Varinga*, subgenus *Ficus*, are known to occur in Africa, but the pollinating wasps are not known. The Indo-Malayan species harbour *Blastophaga* s.str.

4. Two species of *Elisabethiella* were recorded from figs of the section *Galoglychia*. One species (*Blastophaga* (*Elisabethiella*) *wanei* Risbec, 1951, p. 386) was recorded from *Ficus gnaphalocarpa* Steud. (subgenus *Sycomorus*), but I have reasons to assume this record to be incorrect.

5. The section *Oreosycea* harbours *Blastophaga*, but from one species (*Ficus pritchardii* Seem., of uncertain position) a species of *Ceratosolen* is known (p. 8), and from *F. vasculosa* Wall. ex Miq. (Singapore, ? cultivated) I have an insect that seems to belong to *Pleistodontes*.

6. The record of *Tetrapus* is based on the observation by MÜLLER (1887a, p. X) that *Tetrapus* appears to be limited to *Pharmacosycea*, but no specific records are available.

The subgenera *Ficus* and *Sycomorus*, and the Agaonid genera *Blastophaga*, *Kradibiella*, and *Ceratosolen*

7. As far as known, all series of the section *Ficus* harbour *Blastophaga* s.str.,

TABLE II. *Ficus* AND THE GENERA OF THE AGAONIDAE

Ficus Linn.	Agaonidae
Urostigma (Gasp.) Miq.	
Urostigma	Blastophaga
Leucogyne Corner	Eupristina
Conosycea (Miq.) Corner	Blastophaga, Eupristina, Waterstoniella
Stilpnophyllum Endl.	Blastophaga
Malvanthera Corner	Pleistodontes, Ceratosolen
Galoglychia (Gasp.) Endl.	Elisabethiella, Allotriozoon, Agaon, Ceratosolen
Americana Miq.	Julianella, Valentinella
Pharmacosycea Miq.	
Pharmacosycea	Tetrapus
Oreosycea (Miq.) Corner	Blastophaga, Ceratosolen, Pleistodontes
Ficus	
Ficus	
Pseudopalmeae Corner	Ceratosolen
other series	Blastophaga
Sycidium Miq.	
Sycidium	
Prostratae Corner	Ceratosolen
Pungentes Corner	Ceratosolen
Phaeopilosae Corner	Blastophaga
Copiosae Corner	Blastophaga
Scabrae Miq.	Blastophaga, Kradibiella
Varinga (Miq.) Corner	Blastophaga
Palaeomorphe (King) Corner	Blastophaga
Rhizocladus Endl.	Blastophaga
Kalosyce (Miq.) Corner	Blastophaga
Sinosycidium Corner	
Adenosperma Corner	
Neomorphe King	Ceratosolen
Sycocarpus Miq.	Ceratosolen
Sycomorus Miq.	Ceratosolen

with the exception of the *Pseudopalmeae*: *Ceratosolen bakeri* Grandi lives in the figs of *Ficus pseudopalma* Blanco. This wasp has aberrant characters for the genus *Ceratosolen*, but it appears to be related to *C. abnormis* and to the *C. armipes* group. The *Ficus* was classified in the section *Ficus* because of its bistaminate male flowers, but it does show some relationships with *F. dammaropsis* Diels, the host of *C. abnormis* Wiebes.

8. The species of *Blastophaga* from the various series of the sections *Ficus, Sycidium, Rhizocladus*, and *Kalosyce* belong to several species groups. The general impression is, that there is a good correspondence between the classifications of the figs and the fig wasps, but a more positive statement cannot be given before the species of *Blastophaga* have been revised.

9. A species of *Kradibiella* was recorded from the Australian *Ficus stephanocarpa* Warb. (= *F. coronata* Spin.) by WAKEFIELD (1960), and its description will shortly be given by RIEK. I should add here, that I am not convinced of the need for a distinct genus *Kradibiella*: it would seem to represent merely a species group in the genus *Blastophaga*. The alternative to the inclusion of *Kradibiella* in *Blastophaga* is to recognize probably as many as five or six other genera.

10. The greater part of the Indo-Malayan and Papuan species of *Ceratosolen* live in figs of the sections *Neomorphe* and *Sycocarpus*, but some are known from two series of *Sycidium*. It is interesting to note that these series have usually been placed in *Sycocarpus*, and only recently have been assigned to *Sycidium*. Botanically, these groups "point to an ancestor which would combine *Sycidium* with *Sycocarpus* and *Sycomorus* [here including *Neomorphe*]" (CORNER, 1958, p. 31).

In my opinion, the wasp from the series *Prostratae* (*Ceratosolen gravelyi* Grandi, ex *Ficus semicordata* Ham. ex Smith) connects those from the section *Neomorphe* with those from the subgenus *Sycomorus* (see Table III), and the wasps from the series *Pungentes* (*C. pygmaeus* Grandi, and *C. nanus* Wiebes, from *F. minahassae* Miq. and *F. pungens* Reinw., respectively) appear to be related to the wasps from the section *Sycocarpus*. The botanical parallel is not clear.

11. In figs of the series *Phaeopilosae* and *Copiosae*, I find the grades between *Blastophaga* and *Ceratosolen* alluded to in a previous part of the present paper (p. 4). These are the groups that should be studied before the genera *Ceratosolen* and *Blastophaga* can be more exactly defined.

TABLE III. *Ficus (Neomorphe, Sycocarpus,* AND *Sycomorus)* AND THE INDO-MALAYAN AND PAPUAN SPECIES OF *Ceratosolen*

Ficus Linn.	Ceratosolen Mayr
	C. appendiculatus group
subgenus Sycomorus Miq.1)	
F. racemosa Linn.	C. fusciceps (Mayr)
do., var. elongata (King) Barrett	C. fusciceps (Mayr)
(subgenus Ficus)	
sectio Neomorphe King	
series Auriculatae Corner	
F. auriculata Lour.	C. emarginatus Mayr
F. oligodon Miq.	C. emarginatus Mayr
series Variegatae Corner	
subseries Variegatae	
F. variegata Bl.	C. appendiculatus (Mayr)
do., var. garciae (Elmer) Corner	C. appendiculatus (Mayr)
do., var. sycomoroides (Miq.) Corner	C. appendiculatus (Mayr)
F. viridicarpa Corner	C. appendiculatus (Mayr)
subseries Laciniatae Corner	
F. semivestita Corner	C. grandii Wiebes
sectio Sycocarpus Miq.	
	C. armipes group
subsectio Auriculisperma Corner	
series Cynaroides Corner	
F. cynaroides Corner	C. sordidus Wiebes
series Theophrastoides Corner	
series Vitienses Corner	
F. salomonensis Rech.	C. boschmai Wiebes
subsectio Papuasyce Corner	
F. microdictya Diels	C. spec.
F. itoana Diels	C. armipes Wiebes

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1) For convenience' sake, I begin this table with the subgenus *Sycomorus*, although it is usually placed at the end of the botanical system (cf. Table II).

Ficus Linn.	Ceratosolen Mayr
subsectio Dammaropsis (Warb.) Corner[1]	C. abnormis group
F. dammaropsis Diels	C. abnormis Wiebes
subsectio Lepidotus Corner	
subsectio Macrostyla Corner	
subsectio Sycocarpus	
	C. crassitarsus group, p.p.
series Longetuberculatae Sata	
F. ribes Reinw. ex Bl.	C. crassitarsus (Mayr)
do., var. cuneata (Miq.) Corner	C. gracilis Wiebes
F. botryocarpa Miq.	C. corneri Wiebes
do., var. subalbidoramea (Elmer) Corner	C. corneri Wiebes
series Tuberculifasciculatae Sata	
subseries Praestantes Corner	
F. praestans Corner	C. praestans Wiebes
subseries Calopilinae Corner	
F. calopilina Diels	C. calopilinae Wiebes
F. bernaysii King	C. hooglandi Wiebes
F. iodotricha Diels	C. iodotrichae Wiebes
F. obpyramidata King	C. nugatorius Grandi
subseries Congestae Corner	
F. congesta Roxb.	C. notus (Baker)
F. nota (Blanco) Merrill	C. notus (Baker)
F. subcongesta Corner	C. orientalis Wiebes
do., var. symmetrica Corner	C. ?orientalis Wiebes
subseries Hispidae Corner	
	C. solmsi group, p.p.
F. hispida Linn.f.	C. solmsi (Mayr)
	(C. crassitarsus group, continued)
F. moderata Corner	C. moderatus Wiebes
F. hispidioides S. Moore var. succosa Corner	C. dentifer Wiebes
subseries Axillares Corner	
F. lepicarpa Bl.	C. vechti Wiebes
	C. pilipes group, p.p.
subseries Fulvidulae Corner	
F. cereicarpa Corner	C. pilipes Wiebes
F. francisci Winkler	C. josephi Wiebes
	(C. solmsi group, continued)
F. treubii King	C. brongersmai Wiebes
subseries Geocarpicae Corner	(C. pilipes group, continued)
F. uncinata Becc. var. strigosa Corner	C. albulus Wiebes
F. beccarii King var. latifolia Corner	C. humatus Wiebes
F. subterranea Corner	C. humatus Wiebes
F. stolonifera King	C. spec. (group?)
subseries Tuberculifasciculatae	
	C. pygmaeus group, p.p.
F. fistulosa Reinw.	C. constrictus (Mayr)
do.	C. hewitti Waterston
do., var. tengerensis O.K.	C. constrictus (Mayr)
F. dimorpha King	C. constrictus (Mayr)
	C. bisulcatus group
F. septica Burm.f.	C. bisulcatus (Mayr)
do.	C. jucundus Grandi

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[1] By CORNER (1960, p. 38) placed between subsections Auriculisperma and Pomifera (now, pp. = Papuasyce, and p.p. = Lepidotus; see CORNER, 1962, pp. 395— 396).

12. The wasps from the sections *Neomorphe* and *Sycocarpus* and the subgenus *Sycomorus* are listed in Table III.

The species of the *Ceratosolen appendiculatus* group live in the receptacles of the section *Neomorphe* and in those of the subgenus *Sycomorus*, and one species is known from the series *Prostratae* (see no. 10). The occurrence of a group of so closely related species, as the *C. appendiculatus* group apparently is, in the figs of both dioecious *Neomorphe* and monoecious *Sycomorus*, would suggest that the floral characters in which *Neomorphe* is very close to *Sycomorus* are more important than the distribution of the flowers in the receptacles. A parallel is found in *F. microdictya* Diels, which is the only monoecious species in dioecious *Sycocarpus.*

13. The wasps from the section *Sycocarpus* can be classified in two large divisions, which coincide with the first three subsections of *Sycocarpus* (no records are known from the subsections *Lepidotus* and *Macrostyla*), and the subsection *Sycocarpus,* respectively.

Some characters of the species of the *C. armipes* and *C. abnormis* groups, which form the first large division, suggest of a relationship with *C. bakeri* (see no. 7). I am inclined to regard the common character of the *C. armipes* group and the *C. pilipes* group, the tibial comb of the female fore leg, as the result of a parallel evolution, and not as an indication of a close relationship.

14. The second large division of *Ceratosolen* contains the *C. crassitarsus, C. solmsi*, *C. pilipes*, and *C. bisulcatus* groups.

In this assemblage, the *C. pilipes* group is aberrant in the female and (less) in the male sex, and the *C. solmsi* and *C. bisulcatus* groups are distinct in the male sex only.

In general, the classifications of *Sycocarpus* and the groups of *Ceratosolen* run parallel, be it that the two species of the *C. solmsi* group break the sequence. *C. solmsi*, however, seems to be closest to the species of the *C. crassitarsus* group, amongst which it is listed, and *C. brongersmai* shows some connections with the *C. pilipes* group. I will not insist on the value of the *C. solmsi* group, which had to be established on the entomological evidence, but may prove to be redundant when more data are available.

The same reservation must be made for the *C. bisulcatus* group, which is based on the bilobate epistomal margin of the males. The subseries *Tuberculifasciculatae* contains, next to *Ficus septica*, the hosts of *C. constrictus* and *C. hewitti*, which I classify with the *C. pygmaeus* group. The connections with two series of the subsection *Sycidium* (see no. 10) and with *F. pritchardii* (see no. 5) are not clear botanically. The problem of the relationships between *C. constrictus* and *C. hewitti* on the one hand, and *C. bisulcatus* and *C. jucundus* on the other hand, is the more confusing as in the Philippines *F. fistulosa* seems to grade into, or hybridize with, *F. septica.*

The figs of the subseries *Fulvidulae* and *Geocarpicae* harbour *C. brongersmai*, already mentioned above, and the species of the *C. pilipes* group. The *C. pilipes* group consists of two pairs of species, which correspond with the subseries of the hosts. A fifth species, from *F. stolonifera*, could not be described on the scanty and badly preserved material, but it does not show what I assume to be the most important character of the *C. pilipes* group, viz., the blunt tooth in the dorsal comb of the female fore tibia.

The sequence in which I listed the species of the *C. crassitarsus* group, and in which I tried to depict some of the relationships, does not correspond with the list of hosts as classified by CORNER. Although the correlation might be better in a multidimensional system, some species of wasps defy the classification suggested by the botanist. *C. corneri*, for instance, is so abnormal in the male sex that it is difficult to accept its classification with *C. crassitarsus* and *C. gracilis*, which, moreover, do not support the close relationship between their hosts.

The wasps of *Ficus calopilina, F. nota*, and *subcongesta* are so close that I am doubtful of their specific diversity, although the figs are classified in two distinct subseries.

Ceratosolen nugatorius and *C. dentifer*, finally, both show the peculiar tibial spur in the male hind leg, but it may be that these spurs are not homologous. I could accept the classification as suggested in the botanical system.

Tentative remarks on the Agaonidae

15. Omitting all doubtful cases, a general survey would show the species of the genus *Blastophaga* as pollinators in three subgenera of *Ficus*, viz., *Urostigma, Pharmacosycea*, and *Ficus*. In all three, different types have evolved: several subgenera of *Blastophaga* in Asia (*Blastophaga, Eupristina, Waterstoniella*), *Pleistodontes* in Australia, *Julianella, Valentinella*, and *Tetrapus* in America, and *Elisabethiella, Agaon* and *Allotriozoon* in Africa¹). The parallel evolution of fig wasps with long faces and denticulate mandibles in the female sex, in Australia (*Pleistodontes*), Africa (*Agaon*), and America (*Tetrapus*), is mentioned here as a curious fact, well worth of closer research and comparison.

Ceratosolen appears to consist of three original stocks, roughly coinciding with *Neomorphe* and *Sycomorus*, the first part of the section *Sycocarpus*, and the subsection *Sycocarpus*, respectively. The genus *Ceratosolen* appears to be a derivate of *Blastophaga*, and seems to be still connected with it in the wasps from the subsection *Sycidium*.

CONCLUDING REMARKS

I shortly summarize the line of thought which led to the research on figs and fig wasps as presented in the preceding chapters.

To find in a taxonomical revision of a group of fig wasps a high specificity in the close relation between fig wasps and their hosts is to ask the question whether or not this absolute specificity is of general occurrence in the family. It appears that most host records confirm to the principle; others do not, but these are either not documented, and therefore they have no evidential value, or there is reason to doubt the taxonomical evidence.

The next problem is the nature of the specificity. In the chapter relating to this matter it was suggested that there exists a phylogenetic specificity, in other words, *Ficus* and the Agaonidae are supposed to have evolved together. The evidences in

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¹) *Blastophaga* s.str. is not yet known from Africa, except for the introduced *Blastophaga psenes* (L.).

favour of a phylogenetic specificity are convincing, as seen in the classification of the larger groups. The parallelism in the classification of the smaller divisions, and in that of the species, is less satisfactory. This, however, does not affect the hypothesis of the phylogenetic specificity, as both the botanical and the entomological classifications should be reconsidered later. For the time being, CORNER and myself try to base our classifications of figs and fig wasps, as much as possible, exclusively on botanical and entomological evidence, respectively. In the long end we search for a classification that satisfies both the entomologist and the botanist. Should such a system be found we may turn the argument and open the discussion on the principles of our classification and on the evolution of the symbiosis. This is, of course, what we have in mind and what was stated before by VAN DER VECHT (1956, p. 103) and CORNER (1960, p. 370). Our taxonomic revisions are intended to be means to that end.

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New specific names are indicated by an asterisk *; synonyms in *italics*

AGAONIDAE

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UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

INHOUD:

Tijdschrift voor Entomologie, deel 106, afl. 2. Gepubliceerd 15-V-1963

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A REVISION OF THE PALAEARCTIC SPECIES OF THE NIGRIPES GROUP OF THE GENUS AGROMYZA FALLÉN (DIPTERA, AGROMYZIDAE)

BY

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CONTENTS

INTRODUCTION

The species of the *nigripes* group of the genus *Agromyza* Fallén are exclusively feeders on Gramineae, including the cultivated forms. They often come to the notice of the applied entomologist, and there are numerous references to them in the literature. This paper, although written primarily from a taxonomical point of view, is intended also to assist the work of the applied entomologist. Past work in this field has sometimes been confused through the author failing to realise that he was dealing with more than one species with different life-histories; the host-relationships too have not hitherto been very clear. It is hoped that this paper will provide a sound taxonomic basis for future work.

The need for a complete revision of the group has been apparent for some time. The external characters of the adult do not provide many good specific differences, and it was clear that an attempt to use the characters of the male genitalia for classification needed to be made. These had not been employed by HENDEL (1931). Also the larval key hitherto in use, originating from DE MEIJERE (1943), has proved to be almost unworkable. I have decided to make a fresh start with a new key.

The terminology used for the external morphology of the adult in this paper is an English version of that of HENDEL (1931), as has been commonly used for the Agromyzidae. The genitalia and larval terminology largely follow FRICK (1952), though I have preferred the term "spine" to FRICK's "cuticular process". Figs. 1 and 2 explain the genitalia terminology. The plant names are as given in CLAPHAM, TUTIN and WARBURG (1952).

CHARACTERISATION OF THE GROUP

The term "*nigripes* group" is used in this paper in a narrow sense to include those grass-feeding species of *Agromyza* in which the costa reaches to m_{1+2}. It is closely related to the *ambigua* group, in which the costa only reaches r_{4+5}. This distinction may ultimately prove untenable on a world basis, but it is a convenient one for dealing with he Palaearctic species. The distinctive characters of these two groups may be summarised as follows.

Group of *nigripes* Meigen

External morphology

Lunule very narrow, occupying less than $^1/_4$ of the distance from the antennal base to the front ocellus: ocellar triangle coming to a point well before the front ocellus. Dorsocentrals basically six (four postsuturals and two presuturals), decreasing markedly in length forwards: in most species only three or four of the postsuturals are longer than the acrostichals. Mesonotum more or less shining. Inner post-alar bristle present. Legs coarsely haired: middle tibiae with a pair of outstanding posterodorsal bristles. Costa reaching m_{1+2}.

Male genitalia

Cerci elongate, club-shaped, with long hairs at their tips. Ninth sternite reaching $^1/_2$—$^2/_3$ of the length of the aedeagal apodeme. Postgonites small, rounded or club-shaped, closely adpressed to the pregonites: pregonites completely fused with the ninth sternite. Phallophore small, more or less triangular. Basiphallus consisting of a pair of broad plates, but subject to various modifications. Distiphallus of characteristic S-shape.

Larva

No patch of spines below the mandibles. Prothoracic girdle consisting of 8—12 rows of extremely minute spines. Spinal bands well developed at least on the metathorax and first three abdominal segments, consisting of short pointed spines with broad bases: these point dorsally or posteriorly.

Two species (*oryzae* and *distorta*) show special adaptation to an aquatic environment: the front spiracles (Fig. 47c) are enormously enlarged and bear at least 75 bulbs: there are patches of bristle-like spines on the locomotory humps (Kriechwülsten) of at least the metathorax and first three abdominal segments.

Group of *ambigua* Fallén

This group differs from the *nigripes* group in the following particulars.

External morphology

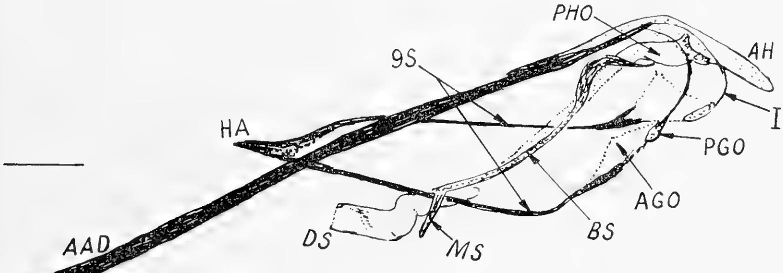
The dorsocentrals are stronger and although they decrease markedly in length forwards, in most species the two pairs of presutural dorsocentrals are still longer than the acrostichals. Costa reaching only r_{4+5}.

Male genitalia

The basiphallus and mesophallus are generally reduced to narrow strips of chitin which form a cradle for the large distiphallus. This is similar in form to that of the *nigripes* group, but longer than in most species of that group.

Larva

There is a characteristic patch of spines below the mandibles.



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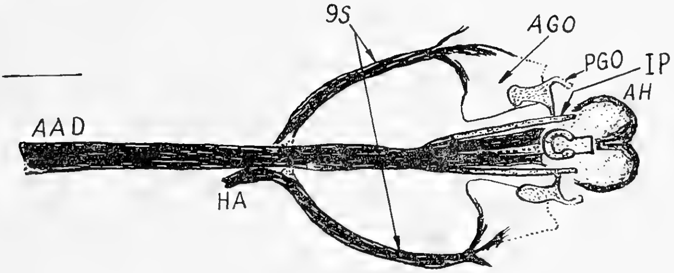

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Fig. 1. Male genitalia of *albipennis* Mg. in lateral view, showing the terminology employed.
Fig. 2. Aedeagal apodeme, 9th. sternite etc., of *nigripes* Mg. in dorsal view, showing the terminology employed.

AAD — Aedeagal apodeme;
AGO — Pregonite;
AH — Aedeagal hood;
BS — Basiphallus;
DS — Distiphallus;
HA — Hypandrial apodeme;
IP — Inner dorsal process of postgonite
MS — Mesaphallus;
PGO — Postgonite;
PHO — Phallophore;
9S — 9th sternite

The species which I can definitely include in the *ambigua* group are *ambigua* Fallén, *mobilis* Meigen, *nigrociliata* Hendel, *veris* Hering, *niveipennis* Zetterstedt, *ocellaris* Hendel, *nigrifemur* Hendel and *yanonis* Matsumura. Other species which probably belong here (but whose larvae and genitalia I have not examined) are *megalopsis* Hering and *frontosa* Becker.

Taken together the *nigripes* and *ambigua* group as defined above form a very natural unit, which contains a large number of species in many parts of the world. The form of the male genitalia is quite distinct from that of other species of *Agromyza,* and this character alone is sufficient to recognise a species as belonging here. SASAKAWA (1958) has found further characteristic features in the female genitalia. All the known larvae are feeders on Gramineae.

The only other grass-feeding species of *Agromyza* are the members of the small group of *cinerascens* Macquart, with three known species. These are *cinerascens* Macquart, *intermittens* Becker and *luteitarsis* Rondani. This group is not related to the *nigripes* and *ambigua* groups, and indeed in several features stands well apart from the rest of *Agromyza.* The genitalia of *cinerascens* are figured by HERING (1951b). The phallus is very elongate, quite different from that of most *Agromyza* species, though perhaps there is some approach to this condition in *Agromyza rubi* Brischke and *A. celtidis* Nowakowski. The cerci are very large and bear a patch of spines at their tips. The group is further distinct on various external characters, as given in HENDEL's (1931) key. The larvae, however, are still little known, and their description might throw some new light on the phylogeny of the Agromyzinae.

The *nigripes* group outside the Palaearctic region

The distribution of the *nigripes* group is probably worldwide. In North America two species are known (FRICK, 1959). *Agr. parvicornis* Loew is a pest of maize (*Zea mays* L.). The larval mouthparts are figured by PHILLIPS (1914) as having two large teeth; the hind spiracles of the puparium are only narrowly separated. This suggests a species closely related to the Palaearctic *phragmitidis* Hendel, *spenceri* sp.nov. and *hendeli* sp.nov. FRICK also records *nigripes*; this record however requires confirmation. I suspect from his description and figure that this species is *albipennis.*

Many of the species described for Africa by SPENCER (1959 and 1960) belong here, including *penniseti* Spencer, *susannae* Spencer, *pallidifrons* Spencer, *catherinae* Spencer, *oliviae* Spencer and *graminivora* Spencer. The life-history of two of these species, *penniseti* and *graminivora* is known. Some of these are close to Palaearctic species, but they all appear distinct. DE MEIJERE (1940) also described the larvae of two species from *Pennisetum* in Java.

COMMENTS ON EARLIER TREATMENTS OF THE GROUP

The following detailed criticism of DE MEIJERE's and HENDEL's work is necessary in order to clarify the points in which the present treatment disagrees with theirs, and to explain why I have felt it necessary to modify their conclusions.

DE MEIJERE in "Die Larven der Agromyzinen" (1925) described larvae of "*nigripes*" and *phragmitidis.* The first was described from *Phragmites* and refers to *hendeli* sp.nov. Both these descriptions are accurate.

In his first supplement (1928) he adds a description of the larva of *lucida* (as *airae* Karl), which is also accurate. The second supplement (1934) includes a short description of the larva of *albipennis.* This is erroneous in one important point: DE MEIJERE interprets the mandibles as consisting of two pairs of alternating teeth: in fact here are four pairs of non-alternating teeth.

In his seventh supplement (1943) he discusses the larvae of the group at some length and gives a key. This key is vitiated in two respects. First, the misinterpretation of the mouthparts of the *albipennis* larva noted above, secondly a confusion of the larvae of *hendeli* (as *lucida*) and *nigripes.* This must have occurred through confusion of the data as these larvae are easily distinguished from each other; in fact the key contradicts the earlier description of the *hendeli* larva (as *nigripes* in 1925) which was accurate. Also the textfigures accompanying this article are not properly labelled, and there is considerable doubt as to which species many of them represent. The result is that there has been a great deal of confusion over the larval characters of this group, as DE MEIJERE's key has been the only one hitherto available.

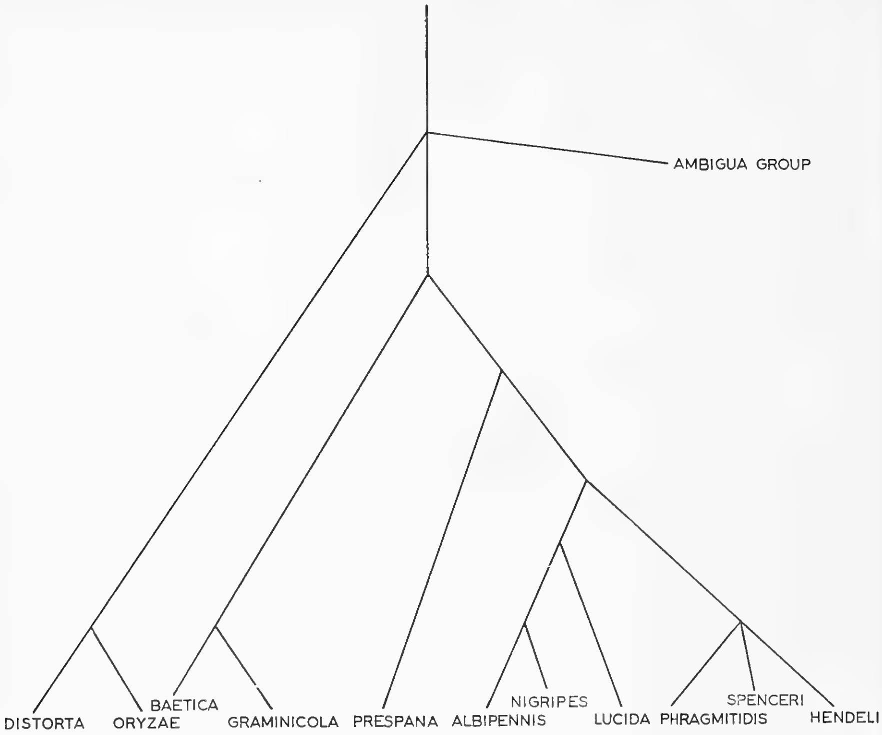
HERING in his "Bestimmungstabellen der Blattminen von Europa" (1957) unfortunately incorporated DE MEIJERE's key into his work and perpetuated these errors, as no subsequent studies had been made of the larval morphology of this group.

The study of this group owes a great deal to HENDEL. However there are two points on which his treatment in "Die Fliegen der paläarktischen Region" (1931) requires criticism. First, although the specimens which he used to describe *albipennis* and *nigripes* were correctly determined, his use of the relative width in profile of the cheeks and jowls as diagnostic characters to separate these species cannot be upheld. The key given is accordingly misleading on this point.

The second point of criticism is more serious. In 1920 he described *Agr. lucida* from a swept specimen: later he identified flies bred by HERING from *Phragmites* with this species. When writing his later description, HENDEL (1931) described one of these specimens, not the type (not unreasonably, as the type is pinned directly on a long fragile pin and is dangerous to handle). Unfortunately HENDEL had included two species under the name *lucida,* and his 1931 description does not refer to the same species as the type. Consequently the name has been employed incorrectly for the *Phragmites*-feeding species ever since. In this paper the name *lucida* is returned to the original species, and the *Phragmites*-feeding species redescribed as *hendeli* sp.nov. I have made HENDEL's specimens the types of this.

PHYLOGENY

In this assessment of the relationship between the various members of the *nigripes* group I have tried to take account of the larval and genitalia characters, as well as the external morphology of the adult. The best generic characters are in fact to be found in the larval stages, which are far easier to classify than the adults.



Graph I. Phylogeny tree of the *Agromyza nigripes* group

There are two obvious pairs of species. *A. oryzae* and *A. distorta* both have dimorphic puparia, and the larvae are strikingly modified in adaptation to an aquatic environment. The enormously enlarged front spiracles (Fig. 47c) of these species are unparalleled elsewhere in the Agromyzidae. The strong dorsocentrals too are characteristic of both these species. The genitalia and external morphology of the adult however show that these species are best classified as aberrant members of the *nigripes* group.

Another obvious pair of species is formed by *A. graminicola* and *A. baetica.* Both have identical large antennae (Figs. 23 and 24), and their mesophalli (Figs. 12c and 13c) are modified to form club-shaped appendages. The striking genitalia modifications of *baetica* are clearly of recent origin. The separation of these species must be due to recent geographical isolation.

Three species, *phragmitidis, hendeli* and *spenceri,* all produce identical mines on *Phragmites.* They have a very characteristic habit of laying a row of eggs on the leaf, which at once distinguishes their mines from those of other species. The larval mandibles of all three are identical (Figs. 41a, 42a and 43a), and they all possess narrow ejaculatory bulbs (Figs. 8a, 9a and 10a), and fairly large distiphalli. Therefore in spite of the external differences, I have no doubt that these three species are closely related.

The evidence for placing *albipennis, nigripes* and *lucida* together is also strong. *A. nigripes* and *A. lucida* are close in respect of their genitalia, and, although the *albipennis* genitalia are very characteristic, in external facies and larva it stands very close to *nigripes.* All these species have a broad frons (in contrast to the *Phragmites*-feeders mentioned above).

A. prespana is not classified so easily. The genitalia of this species (Fig. 11) are fairly typical of the group, but the larval characters do not allow it to be closely associated with any of the above groups. The mandibles (Fig. 44a) have two teeth, but are small, and the hind spiracles (Fig. 44d) are widely spaced and situated on obvious projections.

We are thus left with four species-groups and *A. prespana* as species sola. However the differences which distinguish the *oryzae/distorta* and *graminicola/baetica* groups are obviously much more radical than those separating the rest. Probably their separation must antedate that of the other groups.

It is also interesting to note which characters prove to be of no phylogenetic value. The colour of the squamal fringe is a good specific character, but of no generic importance. The antennae too are enlarged in several not closely related species (viz., *hendeli* and *albipennis/nigripes*): clearly a tendency to variation in the shape of the antennae is part of the ancestral genetic make-up of this group. In classifying the larvae too we must take account of the shape of the mandibles, not merely the number of teeth. Six species have larvae with two teeth, but there are differences in the shape of the mandibles. The three *Phragmites* species, *phragmitidis, hendeli* and *spenceri*, have large broad mandibles: those of *graminicola* and *baetica* are narrower, and those of *prespana* smaller still. Probably two was the original number of teeth for the group, and its retention therefore not necessarily indicative of close affinity. The large number of teeth shown by two species-groups would then represent an innovation. The fact that DE MEIJERE's Javan species (1940) and the American *A. parvicornis* Loew (PHILLIPS, 1914) also possess two teeth lends support to this view.

HOST RELATIONSHIP

A balanced assessment of the degree of host specialisation in this group is hampered by two difficulties. First the botanists' ideas on the classification of the Gramineae are not yet very stable. Secondly our knowledge of the host-range of Agromyzids is largely biased in favour of the more easily recognised grasses, such as *Phragmites, Glyceria, Phalaris* and *Deschampsia.* Accurate records from other hosts are relatively meagre, but this is clearly more the fault of the entomologists than the flies.

However, regarding these four hosts, one can speak with reasonable certainty. The first striking fact is that *Phragmites* is the host of five monophagous species. This is clearly good circumstantial evidence for botanical systems which make the Arundineae a separate tribe. Of the other three hosts, *Glyceria* and *Deschampsia* share two species, neither of which occurs on *Phalaris,* while *albipennis,* which is abundant on *Phalaris* and occurs on many other grasses (particularly the Hordeae), never occurs on *Glyceria,* though it was once bred from *Deschampsia.* Probably we should be unwise to base any argument on the host-selection of *albipennis* which is clearly very catholic in its tastes: but the fact that *lucida* is common on these two plants and rarely occurs on any others does seem of significance. We thus have a priori grounds for welcoming a possible connection between the Glycerieae and Aveneae, but they are admittedly not based on very strong evidence in the present state of our knowledge of this group.

The following list uses the classification given in CLAPHAM, TUTIN and WARBURG (1952).

* recorded from this host once only.

Oryzeae	_Oryza sativa_ L.	_oryzae_ (Munakata)
	Zizania latifolia Turcz.	_oryzae_ (Munakata)
Arundineae	_Phragmites communis_ Trin.	_baetica_ sp.nov.
		graminicola Hendel
		hendeli sp.nov.
		phragmitidis Hendel
		spenceri sp.nov.
Glycerieae	_Glyceria maxima_ (Hartm.) Holmb.	_distorta_ Griffiths
		lucida Hendel
		nigripes Meigen
	Glyceria fluitans (L.) R.Br.	_nigripes_ Meigen
Festuceae	_Festuca_ sp.	*_albipennis_ Meigen
	Poa spp.	_albipennis_ Meigen
	Echinaria capitata Desf.	*_lucida_ Hendel
Brachypodieae	_Brachypodium sylvaticum_ (Huds.) Beauv.	_nigripes_ ssp. _brachypodii_ ssp. nov.
Hordeae	_Triticum aestivum_ L.	_prespana_ Spencer
		*_albipennis_ Meigen
	Secale cereale L.	*_albipennis_ Meigen
	Hordeum spp.	_albipennis_ Meigen
Aveneae	_Arrhenatherum elatius_ (L.) J. & C. Presl.	*_albipennis_ Meigen
	Holcus spp.	_nigripes_ Meigen
	Deschampsia caespitosa (L.) Beauv.	_lucida_ Hendel
		*_albipennis_ Meigen
		*_nigripes_ Meigen
Agrosteae	_Agrostis stolonifera_ L.	*_albipennis_ Meigen
	Agrostis canina L.	*_nigripes_ Meigen
	Phleum pratense L.	*_albipennis_ Meigen
Phalarideae	_Phalaris arundinacea_ L.	_albipennis_ Meigen
	Phalaris erucaeformis L.	_albipennis_ Meigen
Paniceae	_Setaria viridis_ Beauv.	*_albipennis_ Meigen

I note that in many classifications the Seslerieae (including *Echinaria*) are erected as a separate tribe and placed next to the Aveneae. This certainly makes the record of *lucida* from that plant look more reasonable: *lucida* obviously has a narrow range of hosts.

There are many references in the literature on Applied Entomology to "*Agromyza nigripes*" occurring as a pest of cereal crops. Unfortunately very few of the specimens concerned have been examined by specialists, and I have thought it best to disregard these records for the purpose of this paper. The available evidence suggests that these records will mainly refer to *A. albipennis,* which is clearly the commonest species on the Hordeae. This species has been confirmed on barley in Japan and Germany, and on wheat in Great Britain. The other species which has occurred on wheat is the recently discovered *A. prespana,* which may possibly be found in Britain. References to "*Agr. nigripes*" having only one generation a year might well apply to this species. The record of true *A. nigripes* has not been confirmed from cereal grasses.

Discussion of the host selection of the individual species in cases where oligophagy occurs will be found under the species concerned.

KEYS FOR IDENTIFICATION

ADULTS[1])

1. 5 of 6 pairs of dorsocentrals clearly developed as bristles, exceeding the height of the acrostichals in profile (1 or 2 pairs being presutural). Eyes with short white pubescence. On aquatic grasses 2

— At most only the four postsutural dorsocentrals clearly visible as bristles in profile. Eyes bare or weakly pubescent 3

2. Frons broad, $1^1/_2$—2 times the eye-width; 2—3 strong lower orbital bristles (Fig. 23). Ocellar bristles reaching as far as the base of the 2nd upper orbitals. Acrostichals 8-rowed. ♂: ejaculatory bulb (Fig. 14a) small, transparent in distal $^1/_3$, the central channel reaching $^2/_3$ of its length; thorn-like process of the left side of the mesophallus (Fig. 14c) very strongly developed. Europe. On *Glyceria maxima* . . . . *distorta* Griffiths

— Frons narrower: normally 3—5 short lower orbital bristles (Fig. 26). Ocellar bristles very short, not reaching as far as the base of the 2nd upper orbitals. Acrostichals 6-rowed. ♂: ejaculatory bulb (Fig. 15a) larger, moderately sclerotised except along its distal edge; central channel reaching nearly the distal edge; mesophallus without thorn-like process. Siberia and Japan. On *Oryza* and *Zizania* . . . . *oryzae* (Munakata)

3. Squamal fringe white 4

— Squamal fringe normally ochreous; wing-membrane brownish tinged. Normally only 4 orbital bristles (Fig. 17). Frons broad, 1.2—1.8 times the eye-width. 3rd antennal segment somewhat broadened apically: *nigripes* Meigen[2]) . 8

— Squamal fringe black 9

4. 3rd antennal segment small and rounded (Fig. 21); 5 orbital bristles, usually

---

[1]) Excluding *lunulata* Sasakawa.

[2]) A very common, variable species. If squamal fringe darker (as often in Scandinavian specimens) it may be confused with *lucida* or *hendeli*; the former is distinguished by the shape of the antennae: the latter by the narrower frons and more numerous orbital bristles.

fairly weak. Narrow frons (0.8—1.2 times the eye-width). ♂: ejaculatory bulb (Fig. 10a) dark and narrow. On *Phragmites*. . . *phragmitidis* Hendel

— 3rd antennal segment larger. ♂: ejaculatory bulb broader and paler . . 5

5. 3rd antennal segment very much enlarged (Figs. 23 and 24). At least the first pair of lower orbital bristles directed more or less backwards. ♂: ejaculatory bulb not so broad: mesophallus (Figs. 12c and 13c) developed into a pair of club-shaped appendages 6

— 3rd antennal segment not enlarged so much (Fig. 16). Lower orbitals all directed more or less inwards. ♂: ejaculatory bulb (Figs. 3a and 4a) broad; mesophallus not as above: *albipennis* Meigen 7

6. 4—5 orbital bristles (Fig. 23). Frons narrow, 1—1.3 times the eye-width. Eyes bare. ♂: 9th sternite symmetrical: aedeagal apodeme normal. Northern, central and eastern Europe. On *Phragmites*. . . . . *graminicola* Hendel

— 5—6 orbital bristles (Fig. 24). Frons broader, 1.5 times the eye-width. Eyes with short pubescence. Cheeks and orbits clearly visible in profile. ♂; 9th sternite asymmetrical (Fig. 13d), the left side about twice as long as the right; aedeagal apodeme considerably broadened posteriorly. Southern Spain. On *Phragmites* . . . . *baetica* sp.nov.

7. ♂: ejaculatory bulb (Fig. 3a) broad, scallop-shaped. Common species. On various grasses, especially *Phalaris* . . . . . . *albipennis* Meigen s.s.

— ♂: ejaculatory bulb (Fig. 4a) very short, much wider than high, with a contrasting black central channel which bifurcates at its tip. Finland. *albipennis fennica* subsp. nov.

8. Wing length 2.0—2.8 mm. ♂: ejaculatory bulb (Fig. 5a) with its distal edge at least partially black. Common species. On *Glyceria, Holcus* and other grasses . . . . *nigripes* Meigen s.s.

— Wing-length 1.8—2.2 mm. ♂: ejaculatory bulb (Fig. 6a) mostly transparent, but with an obvious black patch at its base on one side. Corsica. On *Brachypodium* . . . . *nigripes brachypodii* subsp. nov.

9. 3rd antennal segment sexually dimorphic (Figs. 22 and 22a), in the female longer than high with a short fringe of upturned hairs, in the male larger, with a very long fringe. Antennae pointing downwards, the frons projecting above them. Facial keel clearly projecting in profile. On *Triticum* . . . . *prespana* Spencer

— 3rd antennal segment without such a fringe. Facial keel not prominent. Antennae not markedly pointing downwards 10

10. 3rd antennal segment enlarged (Fig. 19). 5—6 strong orbital bristles, directed more or less backwards. Frons narrow, 0.8—1.2 times the eye-width. ♂: ejuculatory bulb (Fig. 8a) narrow and black. On *Phragmites* . . . . *hendeli* sp.nov. (= *lucida* Hendel 1931 p.p. nec 1920)

— 3rd antennal segment small and rounded, 4—5 orbital bristles 11

11. 4th costal segment short (Fig. 31): ratio of 2nd to 4th costal segments 4—4.2. Face-line very flattened (Fig. 20). ♂: characteristic enlarged distiphallus (Fig. 9b). Alpine species. On *Phragmites* . . . . *spenceri* sp.nov.

— 4th costal segment longer (Fig. 29): ratio of 2nd to 4th costal segments 2.7—4.0. Face-line not so obviously flattened (Fig. 18). ♂: distiphallus (Fig. 7b) of moderate size, rather elongate. Widespread. Mainly on *Deschampsia* and *Glyceria* . . . . *lucida* Hendel (= *airae* Karl)

LARVAE

1. Mandibles (Fig. 47a) with 5 (rarely 4) alternating teeth. Front spiracles (Fig. 47c) large and circular with at least 75 bulbs. At least the metathorax and first three abdominal segments with thick patches of bristle-like spines ventrally on the locomotory humps (Kriechwülsten). On aquatic grasses . 2

— Mandibles with 2—4 teeth, not or only slightly alternating. Front spiracles small, with less than 25 bulbs. No special spines ventrally 3

2. Front spiracles with 75—160 bulbs. Patches of bristle-like spines on the locomotory humps present on mesothorax, metathorax and all abdominal segments. Japan and Siberia. On *Oryza* and *Zizania* . . *oryzae* (Munakata)

— Front spiracles (Fig. 47c) with 200—250 bulbs. Patches of bristle-like spines on the locomotory humps present only on metathorax and first three abdominal segments. Europe. On *Glyceria maxima* . . . . . . *distorta* Griffiths

3. Mandibles with 2 teeth 4

— Mandibles (Fig. 40a) with 3 teeth. Mesothoracic girdle absent. 6th to 8th abdominal segments with clear bands of spines laterally. Mainly on *Glyceria* and *Deschampsia* . . . . *lucida* Hendel (= *airae* Karl)

— Mandibles with 4 teeth (Figs. 38a and 39a). Mesothoracic girdle represented by at least a patch of spines ventrally 8

4. Hind spiracles separated by more than twice their own width. Eggs laid singly near the edge of the leaf 5

— Hind spiracles separated by less than twice their own width. Eggs laid usually in a row of 3 or 4, the resulting larvae producing a communal mine. On *Phragmites* 7

5. Hind spiracles only on small projections. On *Phragmites* 6

— Hind spiracles (Fig. 44d) on large projections. Mandibles (Fig. 44a) relatively small. On *Triticum* . . . . *prespana* Spencer

6. Adjacent bulbs of the hind spiracles (Fig. 46d) forming an angle of 80°. Pupation outside the mine. Southern Spain . . . . *baetica* sp.nov.

— Adjacent bulbs of the hind-spiracles (Fig. 45d) forming an angle of 90°—100°. Pupation in the mine. Northern, central and eastern Europe . . . . *graminicola* Hendel

7. Processes of the paraclypeal phragma (Fig. 42b) consisting of transparent chitin . . . . *phragmitidis* Hendel

— Processes of the paraclypeal phragma (Figs. 41b and 43b) consisting of mainly brown and black chitin . . . . *hendeli* sp.nov. (= *lucida* Hendel 1931 p.p. nec 1920) and *spenceri* sp. nov. (Alpine species).

(No larvel preparation of *spenceri* was available for close comparison).

8. Hind spiracles (fig. 39d) contiguous: their adjacent bulbs forming an angle of 80°. On various grasses, especially *Phalaris* . . . *albipennis* Meigen
— Hind spiracles (Fig. 38d) separated by 1½—2 times their own width: their adjacent bulbs forming an angle of 100°. On *Glyceria, Holcus* and other grasses . . . . *nigripes* Meigen

A. nigripes brachypodii subsp. nov. was bred from *Brachypodium* in Corsica. Larval morphology not known.

DESCRIPTIONS

Agromyza albipennis Meigen 1830

Agromyza albipennis Meigen, 1930, Syst. Beschr. bekann. eur. zweifl. Insekt,, vol. 6, p. 171.

Agromyza albo-hyalinata Zetterstedt, 1848, Dipt. Scand., vol. 7, p. 2742. **Syn. nov.**

Agromyza nigripes Hendel (nec Meigen) pro parte, 1920, Arch. Naturgesch., vol. 84, p. 112.

Textfigures 1, 3a, 3b, 3c, 16, 27, 39a, 39b, 39c, 39d, 48.

The Zetterstedt species *albo-hyalinata* is synonymised as a result of my examination of the ♂ genitalia of the type.

Frons of the broader type, 1.2—2 times the width of an eye at the level of the front ocellus; not or only slightly narrowing forwards. Antennae a little separated at their bases. In profile (Fig. 16) the cheeks and orbits usually clearly visible as a narrow ring around the eye, often slightly projecting at the level of the antennae.

Ratio of the eye height to the height of the jowls usually 3.5—5 (though occasionally the jowls may be narrower, the ratio being as much as 11). 4—5 orbital bristles (one specimen has 6 on one side only). Upper and lower orbitals clearly distinguished, the later directed inwards or inwards and backwards. When a third lower orbital bristle is present this is usually small. Third antennal segment somewhat broadened apically with a rounded tip. Colour of head variable: usually at least the first antennal segment pale; sometimes the frons and the first two antennal segments yellowish brown.

6—8 rows of acrostichals. Legs variable in colour. Usually at least the front femora yellow at their tips. Often the tips of all femora, and the front tarsi yellowish. Sometimes however the legs are completely black.

Ratio of 2nd and 3rd costal segments (Fig. 27) 2.5—4.0; 2nd and 4th 3.5—5. Wing tip usually between the ends of r_{4+5} and m_{1+2}. All wing veins, except sometimes the costa, yellowish, especially towards the base of the wing. Membrane transparent or slightly whitish tinged. Squama white with a white fringe, only its border being sometimes yellowish. Wing length 2.0—3.0 mm.

♂ genitalia. Distance from the end of the aedeagal apodeme to the end of the aedeagal hood about 1 mm. The aedeagal apodeme is conspicuously thickened at its anterior end and slightly bent downwards over its length. The strengthened part posterior to the attachment of the inner processes of the postgonites occupies about $^1/_5$ of the whole apodeme. The 9th sternite is long, strongly bowed downwards especially towards the tip. Hypandrial apodeme not clearly differentiated, being more or less continuous with the 9th sternite. The tip of the hypandrial apodeme reaches $^2/_3$ of the length of the aedeagal apodeme. Pregonites as shown for *nigripes* (Fig. 2) though relatively smaller. Postgonites small, more or less club-shaped, similar to those of *nigripes* (Fig. 2). Aedeagal hood weakly chitinised; its width about twice that of the posterior end of the aedeagal apodeme. Phallophore as figured (Fig. 1).

Basiphallus (Fig. 3c) very long and moderately slender, consisting of two rods, both clearly defined, the right rod somewhat stouter than the left. Mesophallus consisting of two small triangular plates which are narrowly separated at their tips where they meet beneath the distiphallus. The distiphallus (Fig. 3b) is more weakly bent than in any other species, its rear part not bent downwards. Distiphallus clearly shorter than the basiphallus.

The ejaculatory bulb (Fig. 3a) is large and scallop-shaped, clearly broader than long. Sometimes the medial channel is visible. Its sclerotisation is moderately strong. Stem short and broad.

Larva. Antennae very small; maxillary palpus large and thick: slender but strong longitudinal sclerite. Narrow mandibular abductor apodeme present. Mandibles (Fig. 39a) rather narrow, with 4 teeth, the lower two smaller; usually an obvious protuberance posteriorly behind the point of attachment of the labial sclerite. 2—3 pairs of inconspicous filaments above the mandibles.

Labial sclerite (Fig. 39b) and paraclypeal phragma slender, but strongly sclerotised. Small antero-dorsal process at base of paraclypeal phragma.

Head without spines. Prothoracic girdle consisting of about 8 rows of minute spines. Mesothoracic girdle present only ventrally, with about 4 irregular rows of spines. Metathorax to 4th abdominal segment with broad bands of large spines pointing postero-dorsally; metathorax with 6—7 rows of spines, 1st to 3rd abdominal segments 8—10 rows, 4th abdominal segment 6 rows; all bands weaker dorsally. 5th abdominal segment with a well developed band at least laterally, with 3—5 rows of spines. Following segments bare laterally, with a few spines ventrally in 2 rows. Also numerous small sharp spines in the anal region.

Front spiracles (Fig. 39c) with 12—16 bulbs, consisting of two almost equal horns on a long somewhat twisting atrium. Hind spiracles (Fig. 39d) contiguous: their bulbs oval-shaped, of moderate size; adjacent bulbs forming an angle of 80°.

Length (full-grown) 3.75—4.5 mm.

Biology. Mine (Fig. 48) on upperside of leaf. Eggs laid singly near the edge of the leaf, usually some distance from the leaf tip. The larva at first makes a narrow linear mine towards the leaf tip, then turns and produces a broad irregular channel, eating towards the base of the leaf. Frass irregularly spaced, in large particles. In fresh mines the zig-zag pattern of the feeding lines is often visible.

Pupation follows either inside or outside the mine: if outside, the puparia adhere to the leaf near the mine. At the Ash Vale locality (Surrey) about 50% of the larvae were observed to pupate in the mine. The colour of the puparia varies from black to red.

There are two or probably often three generations. Adults are found first in

June and continue to early September. Mines from June to October, but especially common in early September.

Material examined. In the author's collection. ♂, 2 ♀ Woodwalton Fen, Hunts., 17—22.VIII.60, ex *Phalaris arundinacea*: emerged 29.VIII, 3.IX, 30.III.61. ♀ Woodwalton Fen, Hunts., 22.VIII.60 ex *Arrhenatherum elatius*: emerged 29.VIII. 3 ♂, 9 ♀, swept from Woodwalton Fen, Hunts., 16—25.VIII.60 (4 preparations made with Woodwalton material). 3 ♂, 3 ♀, Ash Vale, Surrey, 5.IX.53, ex *Phalaris arundinacea*: emerged Sept. 53 and May-July 54. ♂, 6 ♀, Ash Vale, Surrey, 15.VIII.54 ex *Phalaris arundinacea*: emerged August/Sept. 54 and June 55, ♀ swept at Ash Vale, Surrey, 5.IX.53. 10 ♂, 16 ♀, Ash Vale, Surrey, 5.IX.60, ex *Phalaris arundinacea*: emerged March/April 61 (4 preparations made from Ash Vale material). ♂ (with preparation), ♀ Rickmansworth, Herts., ex *Phalaris arundinacea* 17.IX.53: emerged 13.V.54. ♀ Finchley, Middx., 31.VIII.53, ex *Phalaris arundinacea*: emerged 17.XI.

Larval preparations from Ash Vale, Surrey, 5.IX.60 (5 preparations) and Woodwalton Fen, Hunts., 16.VIII.61 and 29.VIII.61 (3 preparations) (all from *Phalaris arundinacea*).

In K. A. SPENCER's collection. ♂ (with preparation), Oxford, 2.X.52: emerged 5.V.53 ex *Phalaris arundinacea.*

In the HENDEL collection (Vienna). ♀ ex *Hordeum muralis,* Wien. ♀ Prater (Wien). ♂ (with preparation) labelled "T" in red (No data: presumably Vienna. Probably the specimen used by Hendel for his description in Hendel (1931)). ♀ Hortobágy leg. Kertész. ♀, Madara, 928, leg. Santády, VI.30, ♂, Silesia, leg. Kertész. ♀ Südtirol, VIII. ♂ Ebenew, 1.VIII.81, leg. Becker. 3 ♂, 2 ♀, no data (presumably Vienna area). ♂ (with preparation), Montserrat, Spain, col. Strobl. ♂ (with preparation), Böhmerwald, Rachel, 24.VIII.15, leg. Zerny.

In the GROSCHKE collection (Stuttgart). ♀, 3.VII.49, ex *Setaria viridis,* Mecklenburg, Schwaan, Buhr, 63.

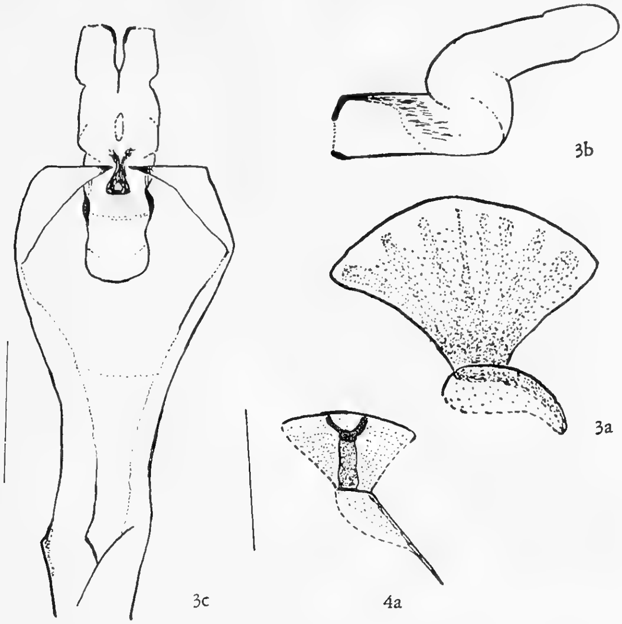
In the HERING collection (Berlin), 2 ♀, ex *Secale cereale*, Mecklenburg, Gr. Lüsewitz 168 & 169, 16.VII.51, leg. Buhr. ♀ ex *Hordeum vulgare*, 16.VII.49, Mecklenburg, Rostock, Buhr, 499. ♂ ♀, ex *Phalaris arundinacea* Grünhof b. Stettin, leg. v. Oethingen. ♀ Mecklenburg, Rostock, Buhr, 16.VII.49 (swept). ♀, ex *Agrostis alba,*, 16.VII.49, Mecklenburg, Rostock, Buhr, 435. ♀, ex *Deschampsia caespitosa*, 16.VII.49, Mecklenburg, Rostock, Buhr, 462. ♀, ex *Phleum pratense*, 9.VII.49, Mecklenburg, Rostock, Buhr, 483. ♂ (with preparation), ex *Poa trivialis*, 8.VII.49, Mecklenburg, Rostock, Buhr, 487. ♂, ex *Poa* sp., 13.VII.49, Mecklenburg, Schwaan, Buhr, 275. ♀, ex *Festuca* sp., 12.VII.49, Mecklenburg, Rostock, Buhr, 402. ♂ (with preparation), ex *Phragmites communis,* Verson b. Caen, 21.VII.42, Buhr, 79. ♂, swept at Berlin, Finkankg. 6.V.29. Also a larval preparation from Lüsewitz, 30.III.32, No. 5884, ex *Phalaris arundinacea.*

In the RYDÉN collection (Hälsinborg, Sweden). ♀ Äng. 23.VII.33. ♀ Vg. Torpa 22.VI.46. ♂ (with preparation), Gotland, Etelheim, 19.VII.50. ♂ Gotland, 15.VII.50. ♂ (with preparation) Gotland, Bogeviken Slite, 15.VIII.50. 4 ♂, 2 ♀, Närke Mulhytten tf. Lillån, 4—5.VII.52. 2 ♂, 4 ♀, Skåne, Skälderviken, 5.VIII.55. ♀ Skåne, Sköralid, 18.V.48. ♀ Skåne, Bölinge, 16.VI.55. ♀, Kullaborg, 20.VIII.40. ♀, Ängelh., 15.VI.50. ♀, Väster Götland, Ulricehamn, 14.VII.47. ♀ Ängermanland, Docksta, 18.VI.54.

In the ZETTERSTEDT collection (Lund). ♂ (with preparation), type of the synonymous *albo-hyalinata* Zett. from Esperöd. The differences noted by Zetterstedt in his description are due to the specimen having been killed soon after emergence before its colours had set.

There are also accurate records for Holland (DE MEIJERE 1934) and Scotland (SPENCER 1956). SASAKAWA (in litt.) knows this species from Japan.

Distribution. Great Britain (incl. Scotland), France, Northern Spain, Holland, Sweden, Germany, Austria, North Italy, Hungary, Czechoslovakia, Poland, Japan. Two ♀ from Kamtschatka were referred here by HENDEL (1931). I cannot be certain if these are *albipennis.* The matter must rest until a ♂ is obtained.



Figs. 3—4. Male genitalia of *Agromyza*: 3, *albipennis* Meigen sensu stricto; 4, *albipennis fennica* subsp. nov.: a — ejaculatory bulb; b — lateral view of phallus or distiphallus; c — ventral view of phallus

The species is generally common. After the ubiquitous *nigripes* it is the next commonest species to turn up in swept material.

Host plants. Gramineae, tribes Festuceae, Hordeae, Aveneae, Agrosteae, Phalarideae and Paniceae.

The species is always abundant on *Phalaris arundinacea* L. Many of the records from other genera have only been made on one occasion, and many of them may therefore only be occasional foodplants (particularly the record from *Deschampsia* from which *lucida* has been bred many times but *albipennis* and *nigripes* once only). I therefore now give a separate list of the known normal food-plants of this species from those from which it has been bred on one occasion only.

Normal food-plants: Festuceae, *Poa* (bred from *P. trivialis* L. and *Poa* sp.). Hordeae, *Hordeum* (bred from *H. vulgare* L. and *H. murinum* L.). Phalarideae, *Phalaris arundinacea* L. (very common here).

Recorded as food-plants once only: Festuceae, *Festuca* sp. Hordeae, *Secale cereale* L. Aveneae, *Arrhenatherum elatlius* (L.) J. & C. Presl. *Deschampsia caespitosa* (L.) Beauv. Agrosteae, *Agrostis stolonifera* L. (= *alba*) *Phleum pratense* L. Paniceae, *Setaria viridis* Beauv.

There are several references in the British literature (by SPENCER and myself) to this species being bred from *Phragmites*. These are all due to confusion of the food-plant, which was *Phalaris,* not *Phragmites.* There is one male in HERING's collection (listed above) labelled *Phragmites* collected by Dr. Buhr. He cannot however trace the mine from which it was bred, so that I regard this record as doubtful. In any case *Phragmites* cannot be a normal food-plant: observation in this country has shown that where *Phragmites* and *Phalaris* grow together, *albipennis* occurs in profusion on *Phalaris,* but is never found on *Phragmites.*

Records of this species on *Glyceria* are inaccurate and refer to *nigripes.*

Agromyza albipennis Meigen **fennica** subspec. nov.

Textfigure 4a.

Frons broad, 1.8 times the width of an eye at the level of the front ocellus. Cheeks and jowls clearly visible in profile. Eye small, ratio of eye-height to the height of the jowls 3.0. 3 strong lower orbital bristles.

Wing-veins brown; membrane whitish tinged with fairly obvious pubescence. Squamal fringe dull white. Wing-length 1.8 mm.

Not distinguishable on external characters from small examples of the typical form.

♂ genitalia. Aedeagal apodeme, 9th sternite, postgonites, pregonites and aedeagal hood as for the typical form. Basiphallus consisting of two long rods with an obvious ventral appendage composed of transparent chitin (in typical *albipennis* this is vestigial). Distiphallus as in the typical form: distiphallus and basiphallus of equal length.

The ejaculatory bulb (Fig. 4a) much smaller than in the typical form; much broader than long with a strongly sclerotised central channel which bifurcates at its tip. The stem is very large (contrast the typical form).

Larval stage and biology unknown.

Material examined. In the Hendel collection. Type ♂ (with preparation), Messuby, coll. Frey.

I associate with this specimen 2 ♀ labelled Kuusamo and Kuopio, coll. Frey.

Distribution. Finland.

The genitalia of this subspecies are strikingly distinct from the typical form of *albipennis.* However the external morphology is not incompatible with that of small specimens of *albipennis,* and the distiphallus is of the characteristic *albipennis* type. I have accordingly given the form only subspecific rank.

Agromyza nigripes Meigen 1830 pro parte

Agromyza nigripes Meigen, 1830, pro parte, Syst. Beschr. bekann. eur. zweifl. Insekt., vol. 6, p. 170. (nec Zetterstedt, Schiner, Rondani, Stary pro parte et passim).

Agromyza nigra Zetterstedt, 1840, Ins. Lap., p. 788.

Agromyza carbonaria Zetterstedt, 1848, pro parte. Dipt. Scand., vol. 7, p. 2739, et 1860, loc. cit., vol. 14, p. 6451 (var. b duplo fere minor): etiam Schiner, Bezzi et passim.

Agromyza agrosticola Hering, 1927, Z. angew. Ent., vol. 13, p. 191.

Textfigures 2, 5a, 5b, 5c, 17, 28, 38a, 38b, 38c, 38d, 38e, 49

A fuller account of the synonymy is given by Hendel (1931). There is one small deletion to make. The specimen of *Agr. holosericea* Strobl. nec Bouché is *lucida* Hendel.

Frons of the broader type, 1.2—1.8 times the width of an eye at the level of the front ocellus, parallel-sided. Antennae clearly separated at their bases. In profile (Fig. 17) the cheeks and orbits are usually visible at least narrowly. Ratio of the eye-height to the height of the jowls 3.5—7, though occasionally the jowls are narrower, the ratio being as much as 11. 4 strong orbital bristles (rarely a small 5th), the lower pair usually directed inwards and backwards. 3rd antennal segment slightly broadened apically, rounded at its tip. Colour of head usually completely black; occasionally the frons and first two antennal segments dark brown.

Acrostichals in 6—8 rows. Legs completely black, or the tips of the front femora only yellow.

Ratio of 2nd and 3rd costal segments (Fig. 28) 2.7—3.4; 2nd and 4th 3.3—5. Wing-tip between the ends of r_{4+5} and m_{1+2}, rarely nearer the former. Wing veins brown, membrane obviously brownish tinged. Squamal fringe usually ochreous or brown, but varying from almost black to greyish white (in particular most Scandinavian specimens have a dark-brown to blackish fringe). Wing-length 2.0—2.8 mm.

♂ genitalia. Distance from the end of the aedeagal apodeme to the end of the aedeagal hood 0.8 mm. Aedeagal apodeme thick, heavily sclerotised, the strengthened part posterior to the attachment of the inner processes of the postgonites occupying $^1/_5$ of the whole apodeme. 9th sternite short and rounded, bearing a narrow hypandrial apodeme which occupies $^1/_5$ of the length of the whole sternite, its tip reaches a little over ½ of the length of the aedeagal apodeme. Pregonites large, postgonites small (Fig. 2). Aedeagal hood moderate-sized, strongly sclerotised around its edges. Phallophore as shown for *albipennis* (Fig. 1).

Basiphallus (Fig. 5c) consisting of two strongly sclerotised rods, the right rod broader than the left. There are small ventral appendages composed of transparent

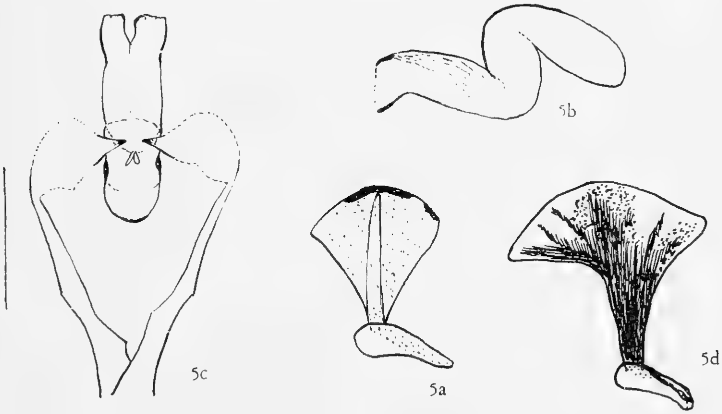
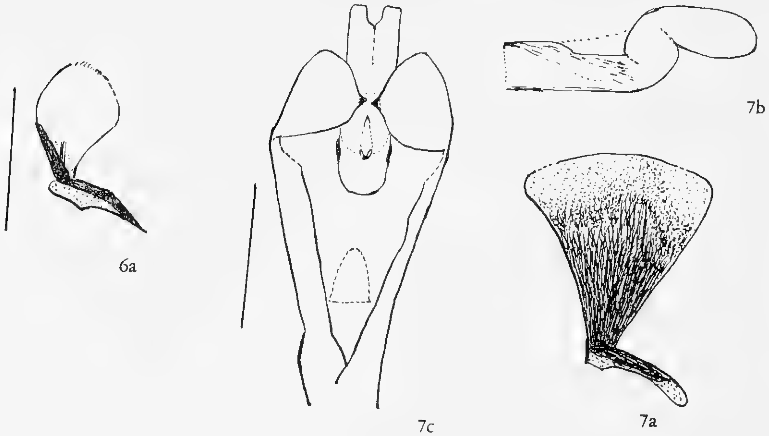


Fig. 5. Male genitalia of *Agromyza nigripes* Meigen s.s.: a — ejaculatory bulb; b — lateral view of distiphallus; c — ventral view of phallus; d — an aberrant ejaculatory bulb shown by one Viennese specimen



Figs. 6—7. Male genitalia of *Agromyza*: 6, *nigripes brachypodii* subsp. nov.; 7, *lucida* Hendel: a — ejaculatory bulb; b — lateral view of distiphallus; c — ventral view of phallus view of phallus

sclerotin. Mesophallus consisting of two plates, coming to a point where they almost meet beneath the distiphallus. Distiphallus (Fig. 5b) with its rear part strongly bent downwards; usually also slightly bent at its tip (compare *hendeli*). Size of distiphallus variable: usually at least slightly longer than the basiphallus, sometimes very much so.

Ejaculatory bulb (Fig. 5a) small and weakly sclerotised; central channel usually clearly visible. Its distal edge characteristically black marked, at least centrally, in most examples. Stem short.

This species shows considerable variation in the colour of the squamal fringe. Generally it is darker in the males, especially from Scandinavia. In large females it may be almost white. Also the phallus is rather variable; many specimens from Central Europe have a very large distiphallus and broader rods to the basiphallus. However intermediates are common, and variation is often very marked even in specimens from the same locality.

One Viennese specimen has a very unusual ejaculatory bulb, but is otherwise normal. This is shown in Fig. 5d. I regard this specimen merely as an aberration of *nigripes*.

Larva. Antennae small; maxillary palpus large and thick; slender longitudinal sclerite only weakly sclerotised. No mandibular abductor apodeme. Mandibles (Fig. 38a) rather narrow, with 4 teeth, the lower two smaller; a protuberance posteriorly beneath the point of attachment of the labial sclerite. 3 pairs of filaments above the mandibles.

Labial sclerite (Fig. 38b) slender and straight. Paraclypeal phragma slender but strongly sclerotised; its dorsal and median processes fused apically; small anterodorsal process at its base.

Head without spines. Prothoracic girdle consisting of about 8 rows of extremely minute spines. Mesothoracic girdle very reduced, consisting only of a patch of small irregular spines ventrally. Methathorax and first five abdominal segments with continuous bands of irregular dorsally and posterodorsally directed spines (Fig. 38c) in 7—9 rows; all spines smaller than in *albipennis*. 6th abdominal segment with a weaker, irregular band of spines in about 5 rows laterally and ventrally; bare dorsally. 7th and 8th segments with about 4 rows of slender pointed spines, mainly ventrally. Also anal region with numerous small pointed spines.

Front spiracles (Fig. 38c) small, with two horns, the anterior being clearly longer than the posterior; 16—20 small bulbs in two rows; atrium long, with several kinks. Hind spiracles (Fig. 38d) separated by 1½—2 times their width; their bulbs oval-shaped, rather widely separated from each other; adjacent bulbs forming an angle of 100°.

Length (full-grown) 3.75—4.5 mm.

Biology. Mine (Fig. 49) on upperside of leaf. Eggs laid singly, usually on the edge of the leaf or near the tip. The narrow early channel of the larva usually swallowed up by its later broader mine. Frass particles fairly conspicuous, irregularly scattered. The mine is deep; on *Glyceria* parts of the lower parenchyma are consumed, but the larva generally does not cross the midrib, forming its mine on one side of the leaf.

Pupation follows outside the mine, the puparia adhering to the leaf near the mine. Puparia usually black, sometimes reddish.

Two generations. Flies in May/June and again in August/early September. First generation of larvae in June, second in late August to September.

Material examined. In the author's collection. ♂ (with preparation) Ash Vale, Surrey, 5.IX.53, ex *Glyceria maxima*: emerged 15.VI.54. 6 ♂ (with 2 preparations), 7 ♀, Ash Vale, Surrey, 5.IX.60, ex *Glyceria maxima*: emerged Sept. 60 and March/April 61. ♀, Beaconsfield, Bucks. 6.IX.53, ex *Holcus lanatus*: emerged 29.IV.54. ♂ 2, ♀, swept at Woodwalton Fen, Hunts., Aug./Sept. 60. 2 ♀, swept from Chippenham Fen, Cambs., 5.VI.55. ♀ swept at Bookham, Surrey, 23.V.54.

Larval preparations from Ash Vale, Surrey, 5.IX.60, ex *Glyceria maxima* (two preparations) and Woodwalton Fen, Hunts., 25.VIII.60, same host.

In K. A. SPENCER's collection. ♀ Chippenham Fen, Cambs., 4.VII.58, ex *Deschampsia caespitosa*: emerged 11.VII.58.

In the HENDEL collection. 2 ♂ (with preparations), ♀, Messuby, Frey. ♂ (with preparation), 2 ♀, Pojo, Frey. 2 ♂ (with preparations), 2 ♀ Karislojo, Frey. ♀, Kuopio, Frey. ♀, Summatti, Frey. 2 ♂ (with 1 preparation), Hammern, Öst. sup., leg. Mik, 6.VIII.83. ♀, Hammern, Öst. sup., 10.IX.72, leg. Mik. ♀, Linz, Öst. inf., 4.VII.67, leg. Mik. ♂ (with preparation), Hainfeld, Öst. inf., 21.VII.97, leg. Mik. 2 ♂ (with preparations), Freistadt, Öst sup., 26.VI.68, leg. Mik. ♂ (with preparation), Baarn, Holland, 14.VI, leg. de Meijere. ♂ Felsöhági, leg. Méhely. ♀, Körösmezö, leg. Kertész, July 1917. ♂ (with preparation), Tisawitz (?), Aug. 1919. ♂ (with preparation), Caltenlichtgeben, Öst. inf. August. 4 ♂ (with preparations), ♀ Ossiach, Kärnten, July/August, leg. Hendel. 2 ♂ (with preparations), Hoheneich, Öst. inf., leg. Zerny. ♂ (with preparation), Almsee, Öst. sup., leg. Czerny. ♂ (with preparation), 2 ♀, Prerbaum, Öst. inf., 1.VI.17. ♂ (with preparation), 2 ♀ Langenzersdorf, Öst. inf. July. 2 ♂ (with preparation), Prater, Wien, May col. Hendel. 6 ♂ (with 4 preparations), 6 ♀ without data, presumably Vienna region, leg. Hendel (including a specimen labelled "T" in red, presumably the specimen used for the description in Hendel (1931)).

In the GROSCHKE collection. 2 ♀, Baienfurt, Württemburg, 19.VI.55, leg. Groschke. ♂ ♀, Stempeda, Harz, 19 & 23.VI.27, Nos. 3161 & 3142, Hering.

In the Hering collection, ♀, Güntersberg an Oder, 5.IX.24, ex *Glyceria maxima*, Hering 2600. ♂ (with preparation), Maribo, Denmark, 4.V.32, ex Glyceria maxima, leg. Sönderup. ♀, Prerow (Darss.), July 1926, ex *Agrostis canina*: emerged 24.VIII, Hering, 2978 (type of the synonymous *agrosticola* Hg.). 4 ♂, ♀, Stempeda, Harz, 19—27.VI.27, Hering, nos. 3141, 3142, 3148, 3161. 2 ♂ (with 1 preparation), Krippen, Sächs. Schweiz, 27.VI.37, leg. Hering.

In the Rydén collection. 4 ♂ (with 1 preparation), 4 ♀, Vg. Ulricehamn, June/July 46—48. ♂ (with preparation), ♀, Bohuslän, Ljungskile, 9 and 11.VIII.51. ♀, Saxnäs, 29.VI.47 leg. Ringdahl. ♀, Sodermanland, Groningen, 14.VI.54. ♀, Ängermanland, Docksta, 18.VI.54. ♀, Råå 5.V.46. 3 ♂, Skåne, Väderön, 7.VII.34, 24.VIII.49 & 30.V.52. ♂, Uppland, Österskär, 12.VIII.48, ♂, Arild, 11.II.25. ♀, Vallbo, 29.VI.35. ♀, Skåne Bästad, 30.V.52. ♂, Mölle, 19.VII.56, leg. Ringdahl. ♂, Skåne, Tyringe, 30.VIII.47. ♂ ♀, Skåne, Kullaborg 20.VIII.49. ♀, Bolmen, 15.VI.54. ♂ ♀, Narke Mulhytton tf. Lillån, 5.VIII.52. 3 ♂ (with one preparation), ♀, Närke, Hjälmarsberg, 6.VIII.52. ♀, Gotland, Västerheide, 27.VI.50. ♂, Ängermanland, Hampnäs, 18.VI.54. ♂, (with preparation), ♀, Norbotten, Vågåmo, 14. VII.53. 4 ♂ (with one preparation), Torne Lappmark, Björkliden, 12 & 17.VII.54, 2 ♂, Torne Lappmark, Abisko-omr., 22—23.VII.54.

There are also accurate records for Scotland (Spencer 1956) and France (Séguy 1934).

Distribution. Great Britain (incl. Scotland), France, Switzerland, Holland, Sweden (including Lappland), Denmark, Germany, Austria, Czechoslovakia, Hungary, Finland.

Several of the distribution records given by Hendel (1931) were based on misidentifications and must be deleted. In particular the Syrian specimen is *A. hiemalis* Becker.

American records of this species (see Frick 1959) need confirmation. Frick describes his *nigripes* as having a white squamal fringe, which is not the case in European *nigripes.*

The species is one of the commonest Agromyzids to appear in the sweep-net in Northern Europe.

Host plants. Gramineae: tribes Glycerieae, Aveneae and Agrosteae. The species is always in abundance on *Glyceria maxima* (Hartm.) Holmb. At the Ash Vale locality I also observed it on *Glyceria fluitans* (L.) R.Br. De Meijere (1925) also took this species on *Holcus mollis* L.

Hering (1957) keys this species under several other genera: *Phalaris* (3668), *Setaria* (4811), *Agropyron* (151), *Alopecurus* (273) and *Hordeum* (2607). Of these the *Phalaris* record is almost certainly incorrect: according to my observation in this country *nigripes* occurs freely on *Glyceria* but never on *Phalaris* when the plants grow together. Some of the other records are probably correct but they cannot be accepted without confirmation as they are not based upon bred material, and considerable confusion has hitherto reigned over the larval characters of this group. The following list of known food-plants will no doubt be enlarged in the future, considering the ease with which *nigripes* is swept.

Normal food-plants: Glycerieae; *Glyceria maxima* (Hartm.) Holmb.; *G. fluitans* (L.) R.Br. Aveneae: *Holcus* (recorded from *H. lanatus* L. and *H. mollis* L.) Recorded as food-plants once only: Aveneae: *Deschampsia caespitosa* (L.) Beauv.; Agrosteae: *Agrostis canina* L. Old records of this species on *Phragmites* refer to *hendeli* (described below).

One form of *nigripes* appears to merit subspecific rank.

Agromyza nigripes Meigen **brachypodii** subspec. nov.

Agromyza albipennis Buhr (nec Meigen), 1941. Stettin. ent. Ztg., vol. 102, p. 90. **Syn. nov.**

Textfigure 6a

Identical on external characters with small specimens of the typical form. Squamal fringe ochreous. Small size characteristic; wing-length ♂ 1.8 mm, ♀ 2.2 mm.

♂ genitalia. Aedeagal apodeme, 9th sternite, postgonites, pregonites and aedeagal hood as for the typical form. Basiphallus consisting of two broad but fairly ill-defined rods, with small ventral appendages (as in the typical form). Mesophallus poorly sclerotised except at its outer edges. Distiphallus fairly small, about as long as the basiphallus.

The ejaculatory bulb (Fig. 6a) is small, evenly rounded, transparent except for a contrasting black patch on one side near its base. Stem strongly sclerotised and fairly long.

Larva. Unknown.

Biology. BUHR (1941) states that puparia were found in a large communal blotch-mine on 7.IX.30. Pupation is thus in the mine (in contrast with the typical form). The mine specimens are unfortunately not extant.

Material examined. In the HERING collection. Type ♂ (with preparation) Sagone, Corsica ex *Brachypodium sylvaticum*, leg. Buhr: emerged 17.IX.30. Allotype ♀ same data, emerged 15.IX.30. Paratype ♂ (with preparation) same data, emerged 16.IX.30.

I erect this subspecies on account of the distinct ejaculatory bulb (not paralleled in 38 preparations of the typical form from numerous localities) and the unusual food-plant. *Brachypodium* is an easily recognised grass, and can be said with reasonable certainty not to be attacked by *Agromyza* spp. in this country. The combination of these two facts with the unusual locality makes it probable that we are dealing with a case of geographical variation. It will be interesting if further material can be obtained from the Mediterranean region.

Distribution. Corsica.

Host plant. *Brachypodium sylvaticum* (Huds.) Beauv.

Agromyza lucida Hendel 1920

Agromyza lucida Hendel, 1920, Arch. Naturgesch., vol. 84, part A, fasc. 7, p. 121. (as subspecies of *Agromyza reptans* Fallén (1823)) (nec Hendel, 1922. Wien. ent. Ztg., vol. 39, p. 66, et 1931. Flieg. pal. Reg., vol. 59, p. 129: nec passim apud Hering, de Meijere et alibi).

Agromyza holosericea Strobl (nec Bouché) 1893 Wien. ent. Ztg., vol. 12, p. 135, et alibi. **Syn. nov.**

Agromyza airae Karl, 1926, Stettin. ent. Ztg., vol. 87, p. 138: etiam Hering, de Meijere et passim.

Agromyza nigripes Stary (nec Meigen), 1930, pro parte. Acta Soc. Sci. nat. Morav., vol. 6, p. 143. **Syn. nov.**

Textfigures 7a, 7b, 7c, 18, 29, 40a, 40b, 40c, 40d, 50.

Agr. holosericea Strobl. (nec Bouché) is synonymised as a result of my examination of the specimen in Hendel's collection, thus determined in Strobl's handwriting. Stary's "*nigripes*" on *Glyceria* is clearly *lucida* as shown by his figure of the larval mouthparts.

The type of *A. lucida* Hendel is mounted on a long fragile pin rendering examination hazardous. It is a freshly emerged specimen whose colours are not properly developed (as noted by Hendel, 1931). Its specific identity is however quite clear. The name *lucida* cannot be retained for the *Phragmites*-feeding species, which is redescribed below as *hendeli.* The type was obviously not used for Hendel's description in 1931 (naturally enough in view of the fragile mount), and the description given applies to the species described below as *hendeli,* not the original *lucida.* Consequently most subsequent authors have applied the name *lucida* to the wrong species.

Frons usually broad, though sometimes approaching the narrow type, 1.0—1.5 times the width of an eye at the level of the front ocellus: parallel-sided or narrowing forwards. Antennae usually clearly separated at their bases. In profile (Fig. 18) the orbits narrowly visible, the cheeks usually not so. Eyes large, slightly pubescent. Jowls narrow: ratio of the eye-height to the height of the jowls 5—13. Facial keel only slightly protruding in profile. 4 or 5 strong orbital bristles: lower orbitals directed either backwards or inwards. 3rd antennal segment small and rounded: antennal pubescence rather coarse. Frons dark-brown, sometimes yellow-brown centrally. First two antennal segments usually brown or yellow-brown.

Acrostichals in 8—9 rows. Legs of variable colour: usually at least the front legs with yellow tips to the femora, brown tibiae and yellowish tarsi. Sometimes also the other tarsi brown and pale tips to all the femora.

Ratio of 2nd and 3rd costal segments (Fig. 29) 1.6—3; 2nd and 4th 2.7—4. Wing-tip usually nearer the end of r_{4+5} than m_{1+2}. Wing-veins brown: membrane clear or slightly brownish tinged. Squama white, grey or ochreous, usually ochreous on its margin, with a thick black or dark brown fringe. Wing-length 2.2—3.0 mm.

One of the largest species in the group.

♂ genitalia. Distance from the tip of the aedeagal apodeme to the end of the aedeagal hood 1 mm. Aedeagal apodeme more or less straight, the strengthened part posterior to the attachment of the inner process of the postgonites occupying rather more than $^1/_5$ of the whole apodeme. 9th sternite fairly slender, somewhat less rounded than in *nigripes* (compare Fig. 2), strongly bent downwards towards its tip: short hypandrial apodeme, its tip reaching almost $^2/_3$ of the length of the aedeagal apodeme. Pregonites smaller than in *nigripes* (compare Fig. 2): postgonites a little larger, more quadrate. The aedeagal hood projects further forward than that of *albipennis* (compare Fig. 1), and is fairly weakly sclerotised. Phallophore as figured for *albipennis* (Fig. 1) but relatively longer.

Basiphallus (Fig. 7c) consisting of two short, fairly broad rods, the right being a little broader than the left. A pale wedge-shaped sclerite lies in the membrane beneath the basiphallus. Mesophallus consisting of two large elliptic plates, which almost meet beneath the distiphallus. Distiphallus (Fig. 7b) fairly long, being about as long as the basiphallus or clearly longer than it. Tensile membrane across the top of the distiphallus slightly sclerotised.

Ejaculatory bulb (Fig. 7a) large and strongly sclerotised, often almost completely black: about as broad as long. Stem short and curved, also strongly sclerotised.

Larva. Antennae small: maxillary palpus large and thick: slender but strong longitudinal sclerite. Narrow mandibular abductor apodeme present. Mandibles (Fig. 40a) long, with three teeth, the lower one being smaller than the upper two: usually a slight protuberance posteriorly below the point of attachment of the labial sclerite. 2—3 pairs of filaments above the mandibles.

Labial sclerite (Fig. 40b) long, its lower edge curved: paraclypeal phragma more strongly sclerotised basally than apically; the ventral process is heavily sclerotised for half its length: antero-dorsal process weak.

Head without spines. Prothoracic girdle consisting of about 10 rows of minute spines: stronger ventrally. Mesothoracic girdle absent. Metathoracic girdle with about 10 rows of small spines laterally; about 2 rows dorsally and ventrally. Abdomen with more numerous spines than in other species: these are small but sharply pointed: rather irregular but mostly pointing dorsally or postero-dorsally. All bands at their broadest laterally, weaker ventrally: dorsal edge almost bare. 1st segment with 16—20 rows of spines: 2nd to 5th segments with 14—16 rows: 6th with 10—12 rows: 7th with 7—8 rows (laterally only): 8th with 5—6 weak rows (laterally only). Also numerous spines in the anal region.

Front spiracles (Fig. 40c) small, on a short twisting atrium, with 12—14 small bulbs: the anterior horn slightly larger than the posterior. Hind spiracles (Fig. 40d) separated by 1½—2 times their own width; their bulbs elongate-oval, rather widely separated from each other: adjacent bulbs forming an angle of 90°. Atrium similar to that of the front spiracles.

Length (full-grown) 4.5—5.5 mm.

Biology. Mine (Fig. 50) on upperside of leaf. Eggs laid singly on the edge of the leaf, usually near the leaf-tip. The larva at first eats towards the leaf-tip, but soon turns and produces a broad shallow blotch, on *Deschampsia* occupying the whole leaf-breadth. Frass particles fine and inconspicuous. The mine is shallow and the lower parenchyma is left untouched (contrast, *nigripes*). The larva crosses the midrib freely. On *Glyceria* several eggs are often laid on one leaf and the resulting mines coalesce to consume the whole leaf.

Pupation follows outside the mine, the puparia adhering to the leaf near the mine. Puparia black or dark red.

Two generations. Flies occur in June and again in August. First generation larvae found in June/July; second generation larvae in September/October (later than *nigripes*).

Material examined. In the HENDEL collection. Type ♀, Öst. sup., Altsee 26.VIII, leg. Czerny (swept). ♀ Stolp i. P., 10.II.26, ex *Deschampsia caespitosa* leg. Karl. ♀ Kartashevka, Petrograd 2.VII.26, leg. Stackelberg. ♂ (with preparation) ♀, Alte Sammlung, Klostenenburg. ♀ "*Agr. carbonaria* Zett. B *holosericea* Bouché" det. Strobl. ♀, no data (presumably Vienna region).

In the author's collection. 3 ♂ (with 1 preparation), 4 ♀ Ash Vale, Surrey, 5.IX.60, ex *Glyceria maxima*: emerged Oct. 60 and March/April 61. 4 larval preparations, Ash Vale, Surrey, 5.IX.60 ex *Glyceria maxima.*

In the GROSCHKE collection. ♂ (with preparation) Soritz, Beutzen, 28.VII.27, ex *Deschampsia caespitosa* leg. Schülze. ♀ Mecklenburg, Rostock, 16.VII.49, ex *Deschampsia caespitosa,* no. 462, Buhr.

In the HERING collection. ♂ paratype of the synonymous *airae* Karl (with preparation) ex *Deschampsia caespitosa.* ♀ Chippenham Fen, Cambs., emerged 22.VII.58, ex *Deschampsia caespitosa,* Hering, 6317. 2 ♀ Soritz, Beutzen 17.VII.27, ex *Deschampsia caespitosa,* leg. Schütze. ♀ Mecklenburg, Rostock, ex *Deschampsia caespitosa,* no. 479, Buhr. ♂ (with preparation), Mecklenburg, Rostock, 25.VII.31, ex *Echinaria capitata,* leg. Buhr. ♀ Crossen-an-Oder, 7.V.30, ex *Glyceria maxima* Hering, 3598. ♀ swept at Stempeda, Harz, 25.VI.27, Hering, 3179.

In the NOWAKOWSKI collection (Warsaw). ♂ 16.I.16, ex *Deschampsia caespitosa,* leg. Karl.

In the RYÉN collection (Hälsinborg, Sweden). 2 ♀ Västergötland, Ulricehamn, 27.VI.47. ♂ Docksta, Ängermanland.

In addition to these records DE MEIJERE (1943) knew this species from Holland, and STARY figures the larva from Czechoslovakia.

Distribution. England, Holland, Sweden, Germany, Austria, Czechoslovakia, Poland, Russia. Not uncommon where its host-plants grow: turns up sparingly in swept material.

Host plants. Gramineae: Tribes Glycerieae, Festuceae and Aveneae. Normal food-plants: Glycerieae; *Glyceria maxima* (Hartm.) Holmb. Aveneae: *Dschampsia caespitosa* (L.) Reauv. Recorded as food-plant once only: Festuceae: *Echinaria capitata.*

HERING (1957) also keys this species under *Agropyron* (150), *Bromus* (955) and *Holcus* (2588). I regard these records as requiring confirmation, as they are not based upon bred material.

Agromyza hendeli sp. nov.

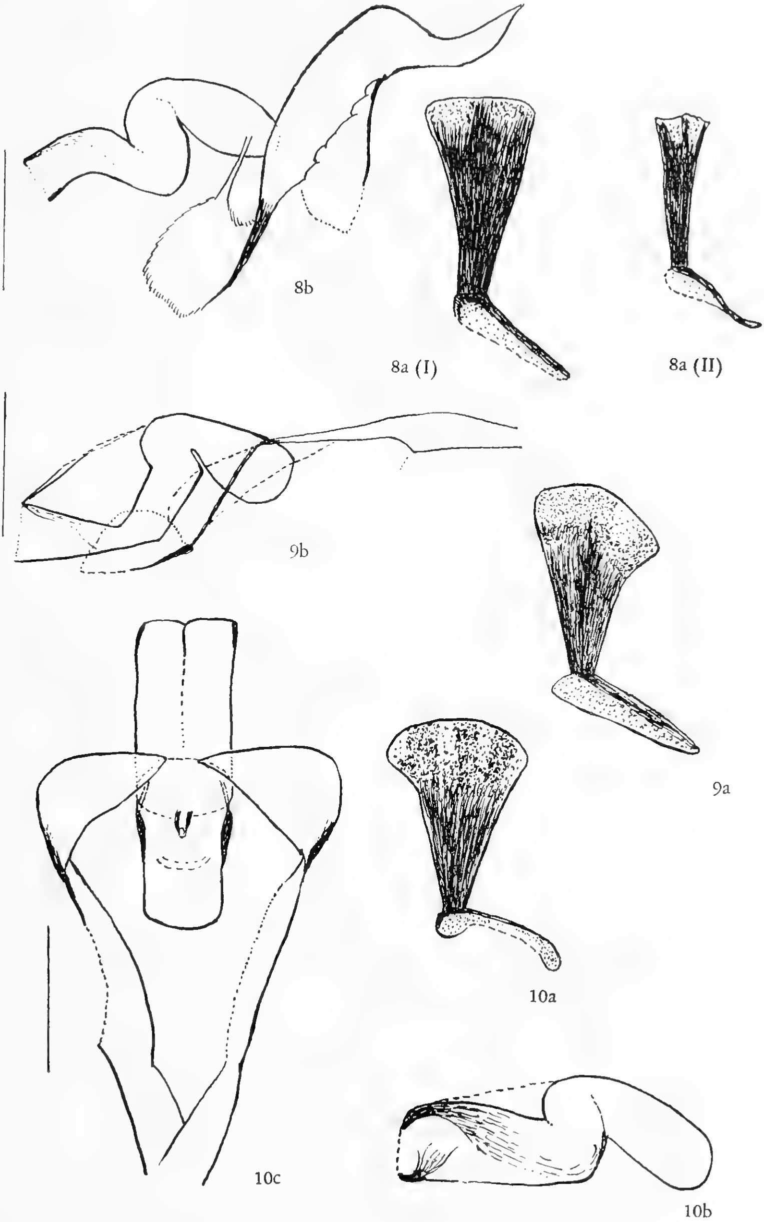
Agromyza nigripes Kaltenbach (nec Meigen), 1856, Verh. naturh. Ver. preuss. Rheinl. & Westph., vol. 13, p. 242, et 1874, Die Pflanzenfeinde aus der Klasse der Insekten, p. 764: etiam de Meijere pro parte, Hering pro parte et passim.

Agromyza lucida Hendel 1922 (nec Hendel 1920), Wien. ent. Ztg., vol. 39, p. 66, et 1931, Flieg. pal. Reg., vol. 59, p. 129: etiam passim apud Hering, de Meijere et alibi.

Textfigures 8a(i), 8a(ii), 8b, 19, 30, 41a, 41b, 41c, 41d

Examination of the type of *lucida* shows that the name can no longer be used for this species. A new name is required although the species has been known for over a hundred years.

Frons narrow, 0.8—1.2 times the width of an eye at the level of the front ocellus; narrowing somewhat forwards. Antennae practically touching at their bases. In profile (Fig. 19) the cheeks usually not visible except very narrowly beneath the eye. Orbits barely visible. Eyes large, faintly pubescent; their height 4—8 times the height of the jowls. 5—6 strong orbital bristles, all directed more or less posteriorly: no clear distinction between upper and lower orbitals. Third



Figs. 8—10. Male genitalia of *Agromyza*: 8, *hendeli* sp. nov.; 9, *spenceri* sp. nov.; 10, *phragmitidis* Hendel: a — ejaculatory bulb; b — lateral view of phallus or distiphallus; c — ventral view of phallus

antennal segment large, broadened apically, somewhat deeper than in *nigripes*. The row of hairs on the second segment strongly developed. Peristomal hairs often longer and more numerous than usual; bristles at the end of the palp strongly developed. Usually the 1st and 2nd antennal segments and the frons are brown, though sometimes the head is completely black.

Acrostichals in 6—9 rows. Legs with usually at least the front femora yellow at their tips; sometimes the tips of all femora yellow and the front tarsi brown.

Ratio of 2nd and 3rd costal segments (Fig. 30) 2.5—3; 2nd and 4th 3.5—4.8. Wing-tip between the ends of r_{4+5} and m_{1+2} or nearer the latter. Veins usually pale (compare *albipennis*): membrane clear. Squama white, with a contrasting black or dark brown fringe. Wing-length 2.0—2.6 mm.

♂ genitalia. Distance from the tip of the aedeagal apodeme to the end of the aedeagal hood about 1 mm. Aedeagal apodeme almost straight; strongly strengthened posterior to the attachment of the inner processes of the postgonites, this part occupying $^1/_5$ of the whole apodeme. 9th sternite small, rather rounded, with a well-defined hypandrial apodeme occupying $^1/_5$ of the total length of the 9th sternite: its tip reaches only to $^1/_2$ of the length of the aedeagal apodeme. Pregonites smaller than those figured for *nigripes* (Fig. 2): postgonites more squarely shaped. Aedeagal hood very large, but weakly sclerotised, in profile clearly raised above the level of the aedeagal apodeme. Phallophore less indented posteriorly when viewed in profile than that figured for *albipennis* (Fig. 1).

Basiphallus consisting of two broad rods, dentate on their lower edge with additional appendages ventrally (Fig. 8b). These are larger than in other species (e.g., *nigripes*) and at least partially composed of dark sclerotin: particularly the posterior edge is clearly defined. Mesophallus consisting of a pair of ill-defined lobes, strongly sclerotised on their outer edges (in profile this gives the impression of a second pair of appendages from the basiphallus). Distiphallus with its rear part strongly bent downwards; also the tip obviously bent down (more markedly so than in *nigripes*). Distiphallus about equal in length to the basiphallus.

Ejaculatory bulb (Figs. 8a(i), 8a(ii) strongly sclerotised, appearing black or dark brown; very narrow, at least twice as long as broad. Stem long, more or less straight.

Larva. Antennae small; maxillary palpus fairly large: slender longitudinal sclerite. Narrow mandibular abductor apodeme present. Mandibles (Fig. 41a) large and powerful with two teeth. Smal mandibular adductor apodeme present. 2—3 pairs of inconspicuous filaments above the mandibles.

Labial sclerite (Fig. 41b) somewhat curved, especially on its lower edge: paraclypeal phragma with its processes composed of brown and black sclerotin (contrast *phragmitidis*): antero-dorsal process very small.

Head with a few small scattered spines below the mandibles, otherwise bare. Prothoracic girdle consisting of about 8—10 rows of minute spines; mesothoracic girdle absent, or at most a few spines in two rows dorsally. Metathorax and first five abdominal segments with strong bands of large spines; in each band the posterior 3 or 4 rows consist of larger spines pointing more or less posteriorly; the other spines point generally dorsally or postero-dorsally; bands weakening dorsally and ventrally, the dorsal edge of the abdomen being quite bare, the ventral nearly so. Metathorax with about 8 rows of spines; 1st to 4th abdominal segments with 10—14 rows; 5th with about 8 rows; 6th to 8th segments with some scattered rather blunt spines laterally in 3—4 rows, but these bands very inconspicuous by comparison with those of the preceding segments. Also the anal region with some spines.

Front spiracles (Fig. 41c) small, with two almost equal horns bearing 10—12 small bulbs: atrium relatively short, evenly curved but not twisted. Hind spiracles (Fig. 41d) separated by their own width or a little more: their bulbs elongate-oval, almost touching each other centrally; adjacent bulbs forming an angle of 60°.

Length (full-grown) 3.75—4.5 mm.

Biology. Mine (compare Fig. 51) on upperside of leaf. Eggs laid usually in a row of 3 or 4. The resulting larvae produce a communal mine, at first eating towards the leaf-tip in a gradually broadening communal channel. In the third instar the larvae often split up producing a large irregular blotch, often too there are several egg-groups on the same leaf, and the resulting mines coalesce. Frass in large scattered particles; zig-zag feeding lines often visible in fresh mines.

Pupation follows normally outside the mine, the puparia adhering to the leaf near the mine. Puparia black or brown.

Two generations. The larvae have been found in June and August: the second generation is earlier than that of *phragmitidis*. Flies have been swept from June to August.

Material examined. In the HENDEL collection. Type ♂ with preparation), Grünwald, emerged 21.III.20, ex *Phragmites communis,* leg. Hering, 1331. Allotype ♀, Bredow b. Nauen, emerged 9.IV.23 ex *Phragmites communis,* leg. Hering, 2154. Paratypes ♀, Wien, 19.VII.78, leg. Mik. ♂, no. data leg. Bgst.

In the author's collection. Paratypes. 2 ♂ (with preparations), swept at Woodwalton Fen, Hunts., 21 & 25.VIII.60. 2 ♀, Woodwalton Fen, Hunts., 16.VIII.60, ex *Phragmites communis*: emerged 12.IX.60. 5 larval preparations from Woodwalton Fen, Hunts., 10.VIII.60, 22.VIII.60 and 21.VI.61.

In K. A. SPENCER's collection. Paratype ♂ (with preparation), Lake Garda, Italy, 25.X.56, ex *Phragmites communis*: emerged 10.III.57.

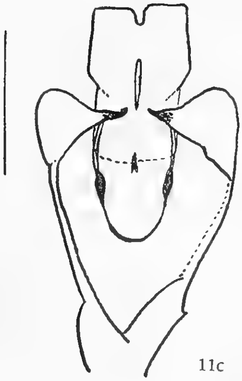
In the GROSCHKE collection. Paratypes: ♂, Bredow b. Nasar, 12.IV.23, ex *Pragmites communis*, Hering, No. 2154. ♂ ♀, Baienfurt, Wttbg. (Fuchsenloch), 17.VI.55, leg. Groschke. ♂, Mecklenburg, Mönkweden, 1.IV.50, ex *Phragmites communis*, Buhr 600/49.

In the HERING collection. Paratypes: ♂ (with preparation), Soritz, Beutzen, 15.VIII.27, ex *Phragmites communis*, leg. Schütze. ♀, Soritz, Beutzen Spring, '28, ex *Phragmites communis*, leg. Schütze. 2 ♀, Berlin, Botanische Garten, 16.VII, ex *Phargmites communis*, no. 58, Hering 1951. ♀ (with preparation), Grünewald, April 1930, ex *Phragmites communis*, 1331, Hering. Also a larval preparation ex *Phragmites communis,* Berlin, Bot. Gart., 18.VI. 57.

In the NOWAKOWSKI collection. Paratype ♂, Puzcza Kampinoska, Mfokiny, 29.VI.57; puparium 1.VII, imago 11.VII, ex *Phragmites communis*, Caricetum, leg. Nowakowski, Inst. Zool. P.A.N., Warszawa, No. 20/57.

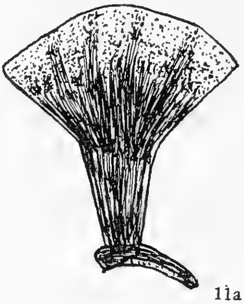
In the RYDÉN collection. Paratypes: 3 ♂ (with 1 preparation), 2 ♀, Skåne, Landskrone, 7.VI.50 and 15.VIII.52.

(22 paratypes in all.)



11c

11b



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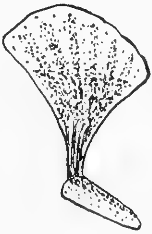

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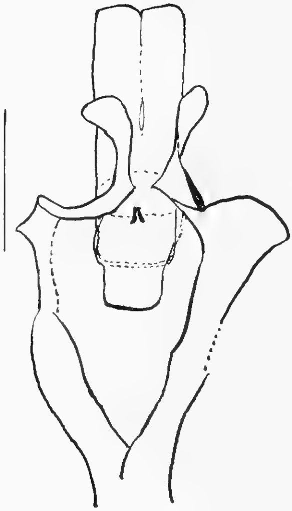

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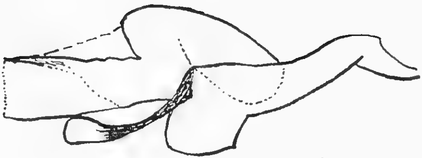
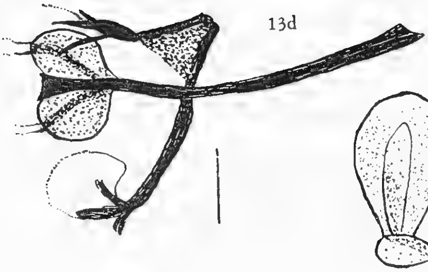


12b



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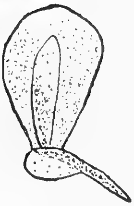
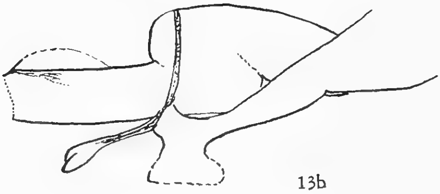
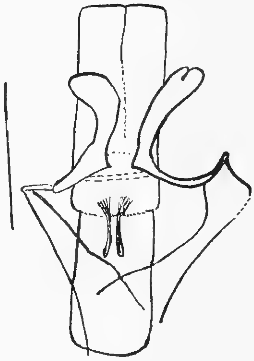


13a



13b



13c

In addition to the above records DE MEIJERE knew this species from Holland and SPENCER (1956) records it (as *lucida*) from Scotland. There are many other references to the mines of this species having been observed (as *nigripes* and *lucida*): however only records resulting from bred material can be trusted as the mines of *hendeli, spenceri* (described below) and *phragmitidis* are not distinguishable, and the larval characters have been hitherto confused.

Distribution. Great Britain (incl. Scotland), Holland, Sweden, Germany, Austria, North Italy, Poland. Common in northern Europe where its host occurs.

Host plant: *Phragmites communis* Trin.

Agromyza spenceri sp. nov.

Textfigures 9a, 9b, 20, 31, 43a, 43b, 43d

Frons narrow, 1—1.2 times the width of an eye at the level of the front ocellus, strongly narrowing forwards. Antennae practically touching at their bases. In profile (Fig. 20) the cheeks not visible, the orbits barely so. Eyes large, faintly pubescent, their height 6—8 times the height of the jowls. Face-line very flattened in profile. 4 strong orbital bristles, all directed more or less backwards. Third antennal segment small and rounded (compare *phragmitidis*). Frons and first two antennal segments brown: head otherwise black.

Acrostichals in 8 rows. Legs with the front femora broadly yellow at their tips, the others narrowly so. Front tarsi yellow. Legs otherwise dark brown.

Ratio of 2nd and 3rd costal segments (Fig. 31) 2.5—3: 2nd and 4th 4—4.2 (contrast *lucida*). Wing-tip between the ends of r_{4+5} and m_{1+2}. Wing veins brown: membrane brownish tinged. Squama white with an ochreous margin and strong jet-black fringe. Wing-length 2.2—2.6 mm.

♂ genitalia. Distance from the end of the aedeagal apodeme to the end of the aedeagal hood 0.8 mm. Aedeagal apodeme stout, almost straight: the strengthened part posterior to the attachment of the inner processes of the postgonites occupying $^1/_5$ of the whole. 9th sternite stout, broad and rounded, bearing a well-defined hypandrial apodeme: this occupies about $^1/_4$ of the total length of the 9th sternite: its tip reaches $^3/_5$ of the length of the aedeagal apodeme. Pregonites large, as figured for *nigripes* (Fig. 2), but forming a rounded lobe on their inner anterior corners. Postgonites as figured for *nigripes* (Fig. 2). Aedeagal hood strongly sclerotised at its edges. Phallophore as shown for *albipennis* (Fig. 1).

The sclerotisation of the basiphallus and mesophallus is weak and ill-defined. Basiphallus short and slender, though its right rod slightly broader than its left. Mesophallus very faintly sclerotised except on its outer edge, forming a large ill-defined lobe beneath the distiphallus. The distiphallus (Fig. 9b) is very large and of characteristic shape, being elongated in its central part: the membrane stretching across the top of the distiphallus is partially sclerotised along its edge. Distiphallus about $1^1/_2$ times as long as the basiphallus.

Figs. 11—13. Male genitalia of *Agromyza*: 11. *prespana* Spencer; 12, *graminicola* Hendel; 13, *baetica* sp. nov. a — ejaculatory bulb; b — lateral view of phallus or distiphallus; c — ventral view of phallus; d — aedeagal apodeme and 9th sternite in ventral view

Ejaculatory bulb (Fig. 9a) narrow, moderately sclerotised in its basal $^2/_3$, more weakly so in its distal $^1/_3$: faint medial streak visible. Stem straight.

Larva. There are no extant larval specimens. However the following characters have been described from the puparia. Mandibles (Fig. 43a) with 2 strong teeth (as in *hendeli* and *phragmitidis*). Labial sclerite (Fig. 43b) very long: processes of the paraclypeal phragma consisting of brown sclerotin. Hind spiracles (Fig. 43d) separated by a little over their own width: adjacent bulbs forming an angle of 70°.

As far as these characters go the larvae cannot yet be distinguished from those of *hendeli.*

Biology. The mines are identical with those of *hendeli* and *phragmitidis* (compare Fig. 51): the description under those species applies here also.

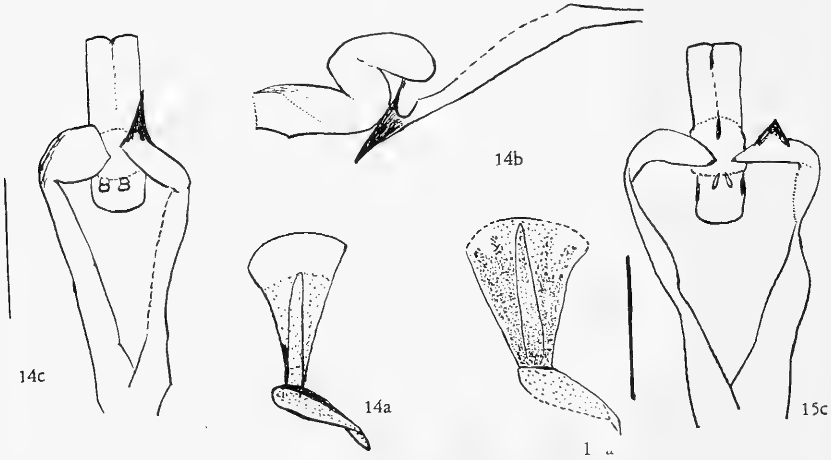
The puparia are reddish brown and are attached to the leaf near the mine. Probably only one generation, as larvae taken in late July did not produce flies until the following year.

Material examined.

In K. A. SPENCER's collection. Type ♂ (with preparation) collected on 26.VII. 54, at a small lake between Briançon and Argentières, Basses Alpes, France, at an elevation of about 3,100 ft. (946 metres): ex *Phragmites communis*; emerged 26.VI.55. Paratypes: 2 ♂ and 3 ♀, same data, emerged 23—29.IV.55.

Distribution. French Alps.

Host plant. *Phragmites communis* Trin.



Figs. 14—15. Male genitalia of *Agromyza.* 14, *distorta* Griffiths; 15, *oryzae* (Munakata). a — ejaculatory bulb; b — lateral view of phallus; c — ventral view of phallus

Agromyza phragmitidis Hendel 1922

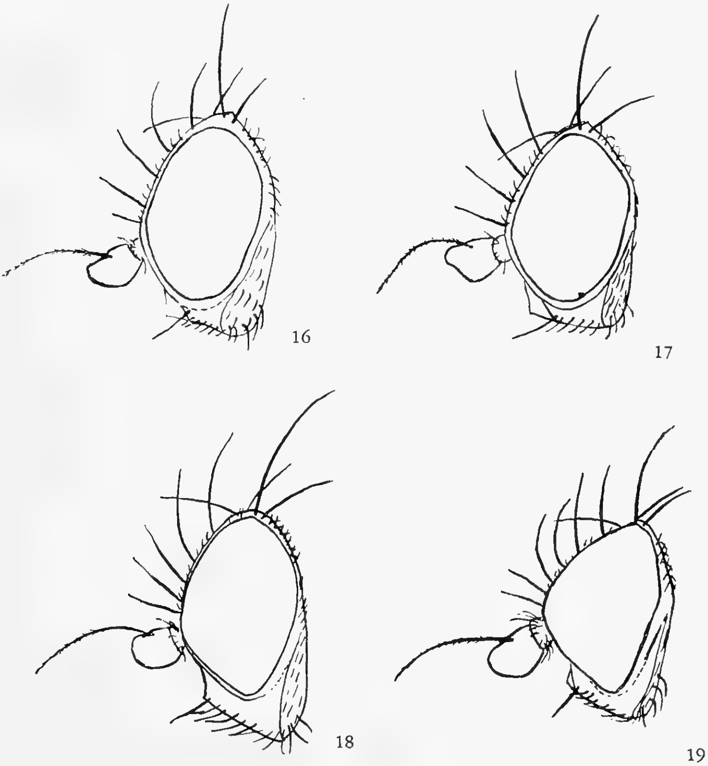
Agromyza phragmitidis Hendel, 1922, Wien. ent. Ztg., vol. 39, p. 65.

Textfigures 10a, 10b, 10c, 21, 32, 42a, 42b, 42c, 42d, 51

Frons narrow, 0.8—1.2 times the width of an eye at the level of the front ocellus: narrowing forwards: the antennae practically touching at their bases. In profile (Fig. 21) the cheeks not visible, and the orbits not or barely so. Eyes very large, slightly pubescent. Jowls normally extremely narrow: ratio of eye-height to the height of the jowls 5—11 (in one specimen the jowls are almost eliminated). 5 weak orbital bristles, normally clearly divided into 2 upper orbitals and 3 lower, the latter nearer to each other than the former: often the orbitals are rather small and adpressed to the frons. 3rd antennal segment small and rounded. Frons, orbits and first two antennal segments clearly brown, sometimes yellow-brown. Arista yellow basally.

Acrostichals 8-rowed. Legs with the tips of all the femora clearly yellow, the front femora more broadly so. All tarsi at least brown, often clearly yellow.

Ratio of 2nd and 3rd costal segments (Fig. 32) 2.5—3.2; 2nd and 4th 3.5—4.5. Wing-tip just after the end of r_{4+5}. Costa often weak between r_{4+5} and m_{1+2}.



Figs. 16—19. Heads in profile of *Agromyza*: 16, *albipennis* Meigen; 17, *nigripes* Meigen; 18, *lucida* Hendel; 19, *hendeli* sp. nov.

Wing-veins pale: membrane clear or whitish. Squama white with a white fringe. Wing-length 2.2—2.8 mm.

A large species. The basic colour of the whole body is sometimes dark brown, not black.

♂ genitalia. Distance from the end of the aedeagal apodeme to the end of the aedeagal hood a little over 1 mm. Aedeagal apodeme more or less straight: the strengthened part posterior to the attachment of the inner processes of the postgonites occupying nearly $^1/_4$ of the whole apodeme. 9th sternite long and narrow, more or less straight-sided in dorsal view; in lateral view obviously bent downwards towards its tip. Hypandrial apodeme large, but not clearly differentiated, being continuous with the rest of the 9th sternite: it occupies about $^1/_3$ of the total length of the sternite: its tip reaches $^2/_3$ of the length of the aedeagal apodeme. Pregonites much smaller than those figured for *nigripes* (Fig. 2): postgonites as figured. Aedeagal hood large, weakly sclerotised, clearly raised above the level of the aedeagal apodeme in profile (compare *hendeli*). Phallophore forming a short double ridge in dorsal view, lacking the indentation shown posteriorly in *albipennis* (Fig. 1).

Basiphallus (Fig. 10c) consisting of two long clearly defined rods of moderate width. Mesophallus consisting of two triangular plates which draw together beneath the distiphallus. Distiphallus (Fig. 10b) large and thick: its rear part bent downwards: a little longer than the basiphallus.

Ejaculatory bulb (Fig. 10a) narrow (but not so narrow as in *hendeli*), strongly sclerotised, appearing black or brown. Its stem long, somewhat curved.

Larva. Antennae small: maxillary palpus large, long: longitudinal sclerite strongly developed. Mandibular abductor apodeme weak, barely visible. Mandibles (Fig. 42a) large and powerful with two teeth. Sometimes a small mandibular adductor apodeme present. 3 pairs of long filaments above the mandibles: these clearly reaching beyond the mandibular teeth.

Labial sclerite (Fig. 42b) long, slightly curved: paraclypeal phragma strongly sclerotised only at its base: all three processes consisting of transparent sclerotin: the ventral process is open at its tip: end of the dorsal process clearly separated from the medial process: antero-dorsal process vestigial.

Head bare apart from 2 or 3 small spines beneath the mandibles. Prothoracic girdle consisting of about 12 rows of minute spines. Mesothoracic girdle absent, or only a small patch of spines present ventrally. Metathorax and first four abdominal segments with strong bands of large spines: in each band the posterior 3—4 rows consist of larger spines pointing more or less posteriorly: the other spines pointing dorsally or posterodorsally. Bands weakening dorsally and ventrally: the dorsal edge of the abdomen almost completely bare: only the bands of the first two abdominal segments continue over the ventral edge. Metathorax with 8—10 rows of spines: 1st and 2nd abdominal segments with 10—12: 3rd segment with 8—10 rows: 4th with 6—8 rows: 5th segment with a very weak band of spines present only laterally in about 4 rows: 6th and 7th segment without bands: 8th segment band represented by a few spines ventrally: also a few spines in the anal region.

Front spiracles (Fig. 42c) fairly small, two-horned, the anterior horn being slightly longer than the posterior: they bear 10—12 bulbs: atrium somewhat twisted. Hind spiracles (Fig. 42d) separated by about their own width: their bulbs elongate-oval, almost touching each other centrally: adjacent bulbs forming an angle of 60°—70°.

Length (full-grown) 4.5—6 mm.

Biology. The mines (Fig. 51) are identical with those of *hendeli*; the description given under that species applies here also. Pupation follows normally outside the mine: the puparia adhere to the leaf near the mine. Puparia very variable in colour, ranging from black to almost yellow.

Two generations. The larvae are particularly common in late September and October. Adults have been swept in May/June and again in September. The autumn generation is later than that of *hendeli*.

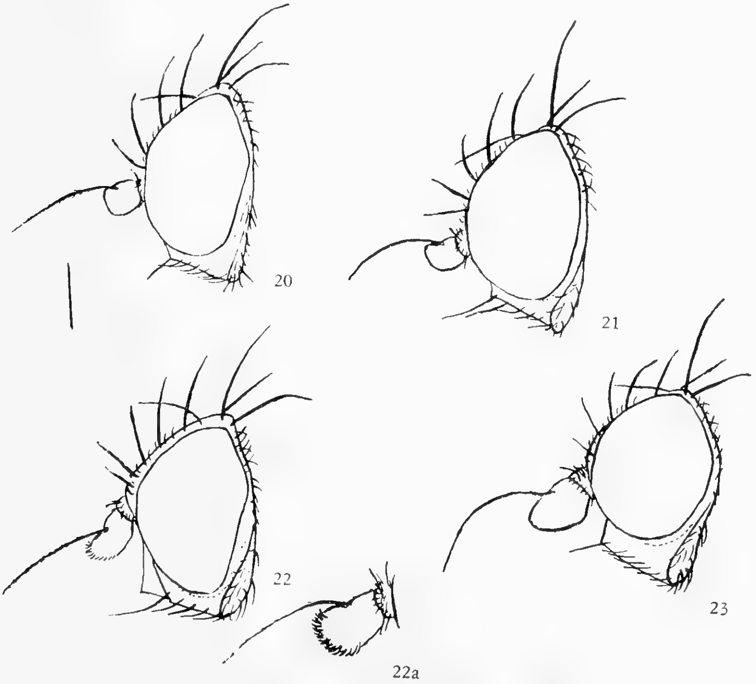
Material examined. In the HENDEL collection. Types ♂ ♀ (both on the same mount), Güntersberg-an-Oder, 6.III.29, ex *Phragmites communis*, leg. Hering.

2 ♂, 2 ♀, same data, emerged Feb-Apr. 29, Hering, no. 729. ♀, Verebély, Kertész, May 33. ♀, Austria, Alte Sammlung, labelled "*carbonaria* det. Schiner".

In the author's collection. ♂ (with preparation), Woodwalton Fen, Hunts., 23.VIII.60, ex *Phragmites communis*: emerged 27.X.60. ♂ ♀, same data, emerged April 1961.

Larval preparations ex Woodwalton Fen, Hunts., ex *Phragmites communis*.

In K. A. SPENCER's collection. 2 ♂ (with preparations), Wonwells, Devon, 15.IX.54, ex *Phragmites communis*: emerged 26.V.55 and 1.VI.55.



Figs. 20—23. Heads in profile of *Agromyza*: 20, *spenceri* sp. nov.; 21, *phragmitidis* Hendel; 22, ♀ *prespana* Hendel; 22a, male antenna of same; 23, *graminicola* Hendel

In the Groschke collection. ♂ ♀, Güntersberg-an-Oder, 28.II.29, ex *Phragmites communis*, leg. Hering. ♂, Neü-Freier (?), 29.IX.53, ex *Phragmites communis.*

In the Hering collection. 3 ♂ (with 1 preparation), ♀, Güntersberg-an-Oder, ex *Phragmites communis*: emerged Feb. '29: Hering, 3348. ♂ (with preparation), ♀, Crossen-an-Oder, Sept., ex *Phragmites communis.* ♂ (with preparation), Soritz, Beutzen, ex *Phragmites communis*, Spring, 1928, no. 62, leg. Schütze. ♀, same data, emerged 29.IX.27, leg. Schütze.

Puparial preparations from Bradons b. Nassau, end Sept., 1922: and St. Peter-Bord, 10.VIII.54, ex *Phragmites communis*, leg. Ludwig.

In the Nowakowski collection. ♂ (with preparation), Puzcza Kampinoska, Mfokiny, ex *Phragmites communis*; Saliceto-Populetum, larva 15.IX.55, puparium 27.IX, imago 11.VI.56, leg. Nowakowski: Inst. Zool. P.A.N., Warszawa, 60/57.

In the Rydén collection. ♀, Råå, Skåne, 2.VIII.35.

Besides the above records de Meijere (1925) knew this species in Holland (as *nigripes*), and Sasakawa (1956) records it for Japan. There are some other published records based on the mines being observed, but these require confirmation, as the mines are not distinguishable from those of *spenceri* and *hendeli.*

Distribution. England, Holland, Sweden, Germany, Austria, Hungary, Poland, Japan. Common in northern Europe where its host grows.

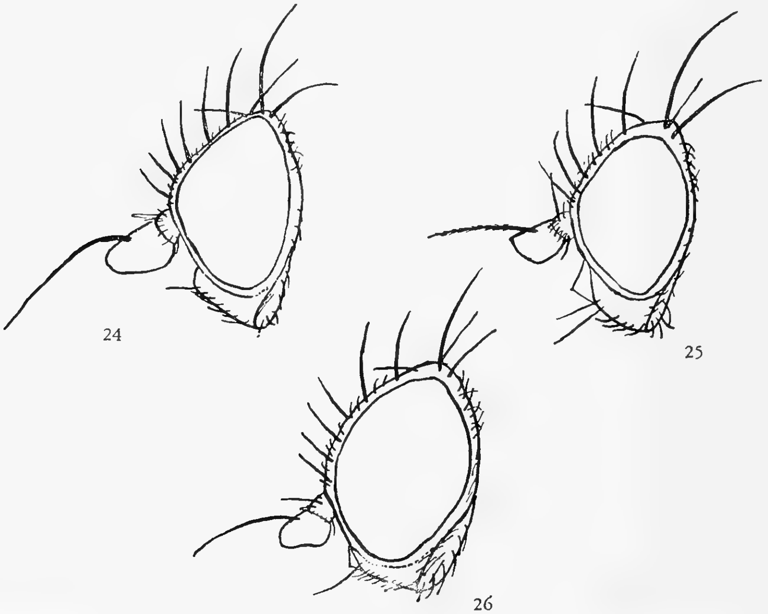
Host plant. *Phragmites communis* Trin.

Agromyza prespana Spencer 1957

Agromyza prespana Spencer, 1957, Ent. mon. Mag., vol. 93, p. 35.
Agromyza sp. b Hering, 1953, Tijdschr. PlZiekt., vol. 59, p. 109—191.

Textfigures 11a, 11b, 11c, 22, 22a, 33, 44a, 44d

Frons 1.4—1.5 times the width of an eye at the level of the front ocellus,



Figs. 24—26. Heads in profile of *Agromyza*: 24, *baetica* sp. nov.; 25, *distorta* Griffiths; 26, *oryzae* (Munakata)

slightly narrowing forwards; the antennae are separated at their bases. In profile (Fig. 22) the eye is large, its height about 7 times the height of the jowls at their centre. The orbits project above the antennae. Cheeks extremely narrow, almost eliminated below the antennae. 2nd antennal segment with its upper edge lengthened, so that the 3rd segment is directed downwards. 3rd antennal segment sexually dimorphic: in the male (Fig. 22a) larger with a very long fringe of upturned hairs: in the female (Fig. 22) a little longer than high with the fringe of hairs shorter. Facial keel clearly projecting in profile. 2 + 3 orbital bristles, fairly weak, the lower 3 directed inwards. Ocellar bristle also weak. Frons dark brown, first two antennal segments, sometimes also the third, yellow-brown, orbits and ocellar triangle shining black, lunule grey.

Acrostichals in 6—8 rows. Mesonotum very shining black. Legs with the tips of the femora yellow (especially the front pair) and all tarsi yellow-brown; sometimes also tibiae yellow-brown. The pubescense of the legs is short and fine.

Ratio of 2nd and 3rd costal segments (Fig. 33) 2.8—3.2; 2nd and 4th 3.6—4.2. Wing-tip nearer the end of r_{4+5} than m_{1+2}. Veins yellow-brown: membrane clear. Squama clear or white with a contrasting black fringe. Wing-length 1.9—2.1 mm.

♂ genitalia. Distance from the end of the aedeagal apodeme to the end of the strengthened portion posterior to the attachment of the inner processes of the postgonites occupying slightly less than $^1/_5$ of the whole apodeme. Pregonites small, but strongly sclerotised, with obvious sensory pores on their inner edges. Postgonites small, club-shaped. Aedeagal hood very small and narrow, but strongly sclerotised. Phallophore much as in *albipennis* (Fig. 1), but with its postero-dorsal edge straight and strongly sclerotised.

Phallus fairly typical of the group. Basiphallus (Fig. 11c) consisting of two short rods, the right being broader than the left. Mesophallus consisting of two more or less triangular plates, pointed where they almost meet beneath the distiphallus (Fig. 11b). Distiphallus large, clearly longer than the basiphallus, its rear part strongly bent downwards.

Large characteristic ejaculatory bulb (Fig. 11a), broadened out like a fan distally. Stem by comparison very small.

Larva. The following characters have been described from the puparia. Mandibles (Fig. 44a) very small and narrow, with two teeth. Small protuberance posteriorly beneath the point of attachment of the labial sclerite.

Hind spiracles (Fig. 44d) situated on large projections: separated by over three times their own width: their adjacent bulbs forming an angle of about 90°.

The larval specimen figured by HERING (1953) as "*Agromyza* sp. *b*" is almost certainly identical with this species. This specimen shows a moderate-sized maxillary palpus, small antenna and a long narrow longitudinal sclerite (as normally in this group): also a clearly defined mandibular abductor apodeme. Labial sclerite strong and straight: processes of the paraclypeal phragma strongly sclerotised, but not widely splayed (contrast *graminicola*). Prothoracic girdle with about 6 rows of minute spines: mesothorax bare. Metathorax and first six abdominal segments with strong bands of spines, mostly directed posterodorsally: all bands broadest laterally, but strong dorsally too, continuing over the dorsal edge with several rows of spines: weaker ventrally. All spines somewhat blunt. Metathorax with about 10 rows laterally; first three abdominal segments with 14—18 rows; 4th and 5th with 10—14 rows; 6th with 12 rows of fine spines laterally, much weaker dorsally and ventrally: 7th and 8th segments and the anal region nearly bare. Front spiracles with 11—14 bulbs; bulbs of the hind spiracles characteristically twisted in side view (see HERING's figure).

Biology. There is one extant mine-specimen of *Agr.* spec. *b.* This is a gradually broadening mine beginning at the leaf tip, length about 4 cm, maximum width 4 mm. The frass particles are clearly defined.

Pupation probably outside the mine. The puparia are large and reddish.

One generation. Flies have been swept only in May/June. GROSCHKE's bred material did not emerge until the following May.

Material examined. In the British Museum (Natural History). Type ♂, Lake Prespa, Macedonia, swept from vegetation near the lake, mid-June 1955, leg. Coe, B.M., 1955—460.

2 ♂ (with one preparation), 3 ♀, paratypes, same data. ♀, paratype, Lake Ochrid, Macedonia, early June 55.

♀ Polje, Dalmatia, Novigrad (in valley amid olive trees etc.), 27—31.V.58, leg. Coe, B.M., 1958—417.

In K. A. SPENCER's collection. ♂ (with preparation), ♀, paratypes; same data as type.

In the HENDEL collection. ♀ Prater, Wien, 19.V, leg. Hendel.

In the GROSCHKE collection. ♀, Öffingen, Wttbg., 24.V.55, ex *Triticum*, leg. Groschke. ♀, Nekarrems, Wttbg. 18.V.55, ex *Triticum*, leg. Groschke. ♀ Berlin, Frohnen, 24.VI.28, leg. Hering.

In the RYDÉN collection. ♀, Skåne, Kullaberg, 20.VI.48.

In the HERING collection (Berlin). Larval preparation of "*Agromyza* sp.b", Görlitz, Kunnersdorf, 20.VI.52, ex *Triticum aestivum*, Hering, no. 5860.

Besides these records the puparia which DE MEIJERE (1937) described from Czechoslovakia may belong here (see also HERING, 1957, no. 5305), but the description is inadequate.

Distribution. Southern Sweden, Germany, Austria, Jugoslavia (Dalmatia and Macedonia). It seems probable that this species was originally a southern form, which has spread northwards by becoming associated with wheat. In the Jugoslavian localities it is most unlikely that wheat was the food-plant.

Host plant. *Triticum aestivum* L.

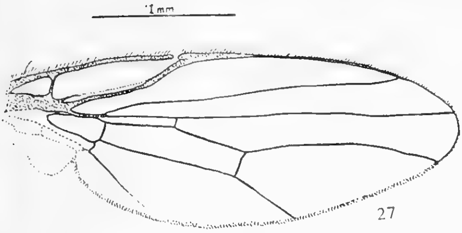
Agromyza graminicola Hendel 1931

Agromyza graminicola Hendel, 1931, Flieg. pal. Reg., vol. 59, p. 122.

Textfigures 12a, 12b, 12c, 23, 34, 45a, 45b, 45d, 52

Frons narrow, 1—1.3 times the width of an eye at the level of the front

Figs. 27—37. Wing maps of *Agromyza*: 27, *albipennis* Meigen; 28, *nigripes* Meigen; 29, *lucida* Hendel; 30, *hendeli* sp. nov.; 31, *spenceri* sp. nov.; 32, *phragmitidis* Hendel; 33, *prespana* Spencer; 34, *graminicola* Hendel; 35, *baetica* sp. nov.; 36, *oryzae* (Munakata); 37, *distorta* Griffiths



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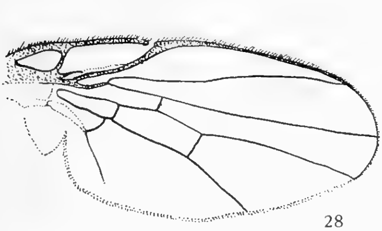

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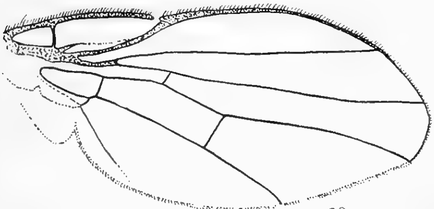

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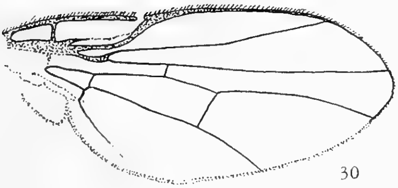

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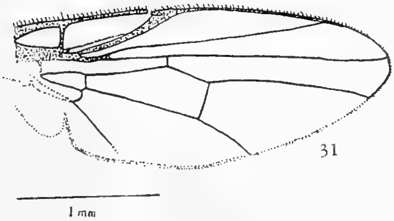

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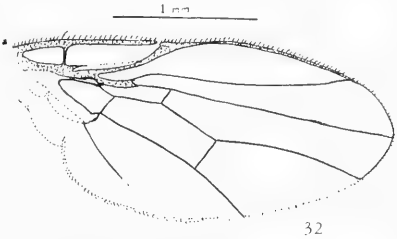

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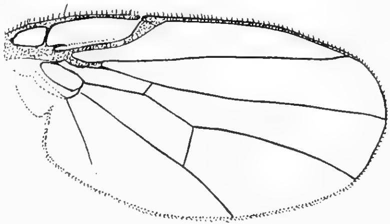

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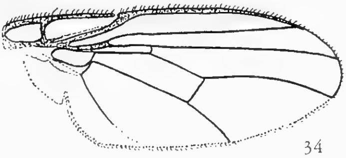

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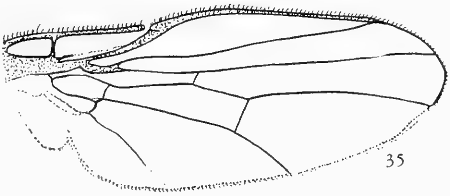

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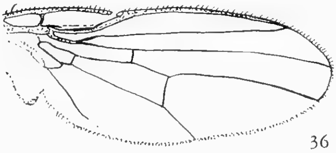

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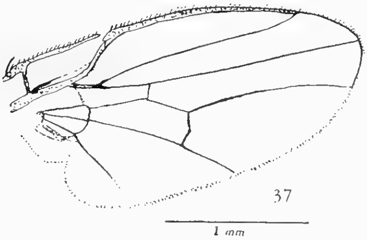


37

ocellus: usually narrowing forwards. Antennae narrowly separated at their bases. In profile (Fig. 23) the cheeks are narrowly visible, but not clearly defined, below the eye. Orbits narrowly visible. Ratio of the eye-height to the height of the jowls 4—9. Eyes bare. 4—5 orbital bristles, not clearly differentiated into upper and lower orbitals: the third orbital directed more or less backwards: all orbitals often fairly small and weak. 3rd antennal segment very large, its lower margin evenly curved. Pubescence of antennae and arista fine. Frons and first two antennal segments dark brown.

Acrostichals 8-rowed. Legs dark brown to black, the front femora broadly yellow at their tips: tarsi sometimes brown.

Ratio of 2nd and 3rd costal segments (Fig. 34) 2.7—3.6: 2nd and 4th usually 5—5.8 (rarely as little as 4): 4th segment usually very short. Wing-tip between the ends of r_{4+5} and m_{1+2}. Veins pale: membrane clear. Squama white with a white fringe. Wing-length ♂ 2.0—2.2 mm, ♀ 2.4—2.6 mm.

♂ genitalia. Distance from the end of the aedeagal apodeme to the end of the aedeagal hood 0.8 mm. Aedeagal apodeme thickened at its anterior end, more or less straight. The strengthened part posterior to the attachment of the inner processes of the postgonites is relatively short, occupying $^1/_6$ of the whole apodeme. 9th sternite stout and rounded, bearing a long hypandrial apodeme, which occupies about $^2/_5$ of the total length of the sternite: 9th sternite symmetrical (contrast *baetica*): tip of the hypandrial apodeme reaching nearly $^2/_3$ of the length of the aedeagal apodeme. Pregonites large, as figured for *nigripes* (Fig. 2), but with an anteriorly directed lobe on their inner anterior corners. Postgonites as figured for *nigripes* (Fig. 2): inner processes somewhat thickened where they curve down beneath the aedeagal hood. Aedeagal hood much deeper in profile than that figured for *albipennis* (Fig. 1): it is strongly sclerotised on its posterior surface. Phallophore relatively larger than that figured for *albipennis* (Fig. 1).

Basiphallus (Fig. 12c) short and broad, asymmetrical, the left rod being obviously broader than the right. At the junction of the mesophallus and distiphallus on the left side a large downwards directed lobe. Mesophallus modified to form two club-shaped appendages, which lie beneath the distiphallus: the left appendage is slightly larger. Distiphallus (Fig. 12b) very large, a little longer than the basiphallus: its rear part bent downwards.

Ejaculatory bulb (Fig. 12a) fairly broad with a ribbed appearance: a characeristic "waist" at its base (contrast *baetica*): its sclerotisation moderate. Stem short, more or less straight.

Larva. There are no extant larval specimens. However the following characters have been described from the puparia. Mandibles (Fig. 45a) with 2 strong teeth: not so broad as those of *hendeli, spenceri* and *phragmitidis*. Labial sclerite (Fig. 45b) strongly thickened posteriorly: paraclypeal phragma strongly sclerotised, its processes large and widely splayed. Hind spiracles (Fig. 45d) separated by about 3 times their own width, with elongate-oval bulbs: adjacent bulbs forming an angle of 90°—100°.

Biology. Mine (Fig. 52) on upperside of leaf. Eggs laid singly near the edge of the leaf. The resulting larva produces a gradually broadening channel at first towards the leaf-tip, then turns towards the base of the leaf. Frass fairly conspicuous, in two irregular rows. Width of the mine channel not exceeding 4 mm.

Pupation follows in the mine (Hering, 1951a); puparia reddish-brown.

Hering (1951a) gives some interesting comments on the biology of this species. According to his observations it never attacks *Phragmites* standing in water, but only dwarf plants growing on quite dry ground.

At least two generations. Larvae taken in October produced flies in October and the following year. Rydén swept the flies in May and August.

Material examined. In the Hendel collection. Type ♂ ♀ (both on the same mount), Crossen-an-Oder, emerged 10.X.34, ex *Phragmites communis*, Hering, no. 4295. 3 ♀, labelled Alte Sammlung, Wien. ♂, Hungaria, Lac. Fert., leg. Podkorny (with genitalia extruded).

(The original type mentioned by Hendel (1931) was bred in the Vienna region, and must be presumed lost. There is no room for doubt as to the identity of this species.)

In the author's collection. ♂ (with preparation), Crossen-an-Oder, emerged 9.III.35, ex, *Phragmites communis*, Hering, no. 4295.

In the Groschke collection. ♀ ♂, same data as type.

In the Hering collection. ♂ (with preparation), 2 ♀, same data as type, emerged Oct. 34 and March 35, Hering, no. 4295.

Also a puparial preparation ex Crossen-an-Oder, 8.X.34, ex *Phragmites communis*. Hering, no. 4295.

In the Nowakowski collection. ♂ (with preparation), Szeroky Bòr, Poland, ex *Phragmites communis*: puparium 17.VIII.58, imago 23.VIII, leg. Szepanski.

In the Rydén collection. ♀, Råå, 26.V.25. ♂ (with preparation), Skåne, Skälderviken, 15.VIII.55, leg. Ringdahl. 2 ♂ Skåne, Landskrone, 15 & 18.VIII.52.

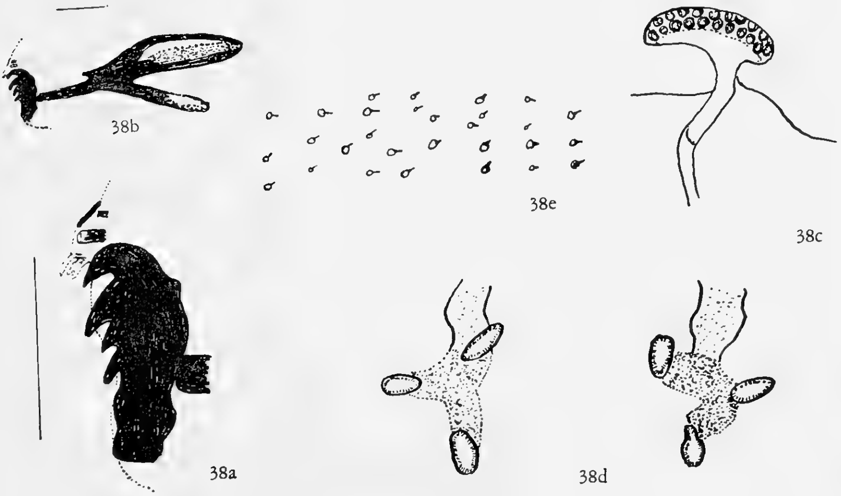


Fig. 38. Larval parts of *Agromyza nigripes* Meigen: a — mandibles; b — larval mouthparts; c — front spiracles; d — hind spiracles; e — section of the spinal band of the first abdominal segment laterally

HERING (1951) also observed this species in the Stockholm area, so that its range extends quite far north.

Distribution. Sweden, East Germany, Poland, Austria, Hungary.

Apparently this species does not reach Western Europe.

Host plant. *Phragmites communis* Trin.

HERING (1957) also keys this species under *Arundo*. I do not know the origin of this record, but must regard it as requiring confirmation, especially in view of the discovery of a related species in the Mediterranean area (described as *baetica* below).

Agromyza baetica spec. nov.

Textfigures 13a, 13b, 13c, 13 d, 24, 35, 46d, 53.

Frons fairly broad, 1.5 times the width of an eye at the level of the front ocellus: parallel-sided. Antennae separated by the width of their first segment at their bases. Cheeks and orbits clearly visible in profile (Fig. 24), especially the orbits above the antennae. Ratio of the eye-height to the height of the jowls 4—7. Eyes with obvious pubescence. 5—6 weak orbital bristles, all directed more or less backwards. Antennae with very large 3rd segment as in *graminicola.*

Legs black, apart from the tips of the front femora.

Ratio of the 2nd and 3rd costal segments (Fig. 35) 3—3.2, 2nd and 4th 3.2 to 4.5 (contrast *graminicola*): 4th segment relatively long. Veins pale: membrane pale. Squama white with a white fringe. Wing-length ♂ 2.1 mm, ♀ 2.6—2.8 mm.

Otherwise as for *graminicola.*

Male genitalia. Distance from the end of the aedeagal apodeme to the tip of the aedeagal hood 0.75 mm. Aedeagal apodeme short and thick, strongly bent along its length: its posterior end (after the attachment of the inner processes of the postgonites) broadened into a large head 4 times the width of the rest of the apodeme: this head occupies $^1/_6$ of the whole apodeme. 9th sternite (Fig. 13d) completely asymmetrical, its left side about twice as long as its right: it bears a large broad hypandrial apodeme about equal in length to the right (small) side of the 9th sternite: the tip of the hypandrial apodeme reaches nearly $^1/_2$ of the length of the aedeagal apodeme. Pregonites large: the left one rather angulate: the right folding over and joining with the phallophore. Postgonites conspicuous, not adpressed against the pregonites as in other species: inner process on left side short and strong: on the right side the phallophore, inner processes of the postgonite and the pregonite are obscured and partially fused. Aedeagal hood broad, deep in profile (as in *graminicola*).

Phallus (Fig. 13c) dominated by the enormous distiphallus which reaches back beyond the base of the basiphallus. Basiphallus V-shaped, short and strong, the left side broader than the right. Large anvil-shaped lobe on the left side at the junction of the basiphallus and mesophallus: this hangs downwards and is larger than in *graminicola.* Mesophallus developed into two large club-shaped appendages, the left one larger, bilobed at its tip. A conspicuous sclerotised band joins the two sides of the mesophallus across the top of the distiphallus. Distiphallus (Fig. 13b) as in *graminicola* but larger, over $1^1/_2$ times the length of the basiphallus.

Ejaculatory bulb (Fig. 13a) fairly broad, rounded, with a clearly defined central channel.

On external characters close to *graminicola.* The genitalia are however considerably modified.

Larva. There are no larval specimens. However the following characters have been described from the puparium with the type. Mandibles (Fig. 45a) and paraclypeal phragma (Fig. 45b) as described for *graminicola.* Hind spiracles (Fig. 46d) separated by 3—3½ times their own width, with elongate-oval bulbs: adjacent bulbs forming an angle of 80° (contrast *graminicola*). (More material is needed to confirm the constancy of this last character.)

Biology. Mine (Fig. 53) on upperside of leaf. Eggs laid singly near the leaf-margin, often several at different places on the same leaf. The resulting larvae eat first towards the leaf-tip, then turn and head for the base of the leaf. The mine gradually increases in width, but does not exceed 4 mm wide, remaining semi-linear. Frass in large conspicuous particles.

Pupation follows outside the mine, the puparia adhering to the leaf near the mine (contrast *graminicola*). Puparia reddish brown.

At least two generations. Larvae found in April produced flies between July and September. This suggests that in the wild the puparia aestivate (as with many Mediterranean species) and that there will be 2—3 generations during autumn, winter and spring.

Material examined. In K. A. SPENCER's collection. Type ♂ (with preparation), Algeciras, Spain, 25.IV.55, ex *Phragmites communis*: emerged 6.VII.55. Allotype ♀, same data, emerged 24.IX.55. Paratypes 5 ♀, same data, emerged July-Sept. 55.

In the author's collection. Paratype ♀, same data, emerged 22.IX.55.

HERING (1951a) also observed this species at a neighbouring locality (as *graminicola*).

Distribution. Southern Spain.

Host plant. *Phragmites communis* Trin.

Agromyza oryzae (Munakata, 1910)

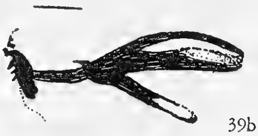
Oscinis oryzae Munakata, 1910, Konchu Sekai, vol. 14, p. 7—11.
Oscinis oryzella Matsumura, 1915. Man. Inj. Ins. Japan, vol. 2, p. 53.
Agromyza oryzae Hendel, 1931, Flieg. pal. Reg., vol. 59, p. 142; etiam Kuwayama et Kato.
Agromyza oryzella Yuasa & Koyama, 1938, Bot. & Zool., vol. 6, p. 820.

Textfigures 15a, 15c, 26, 36

A fuller synonymy is given by KATO (1956) from which the above is abridged. The following treatment owes much to that paper, which analysed the external characters of 165 Japanese specimens.

Frons narrow, as broad as, or a little exceeding the eye-width at the level of the front ocellus, parallel-sided. Antennae clearly separated at their bases. In profile (Fig. 26) the cheeks and orbits clearly visible, forming a continuous ring around


39a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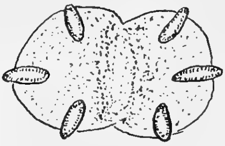
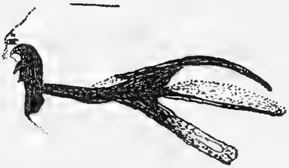

39d


39c


40a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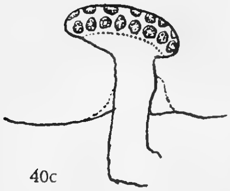
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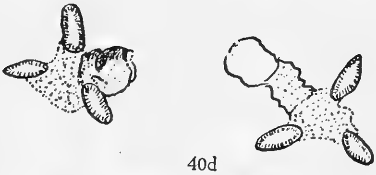
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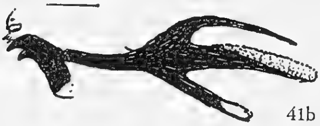
41a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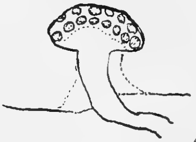
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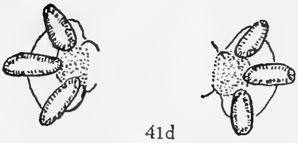
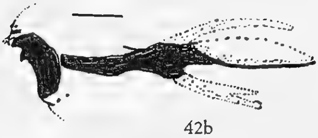

41d


42a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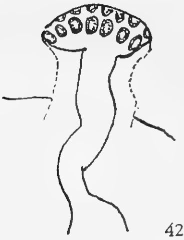
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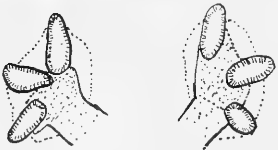
42d

the eye. Eyes with scattered white hairs. Eye-height about 5 times the height of the jowls. 2 strong upper orbital bristles directed backwards: 3—6 lower orbitals directed inwards and standing closer together than the upper orbitals. Ocellar bristles very small. 3rd antennal segment broadened, somewhat angular apically. Head usually entirely black; sometimes frons and first two antennal segments brownish.

Dorsocentrals strongly developed, normally 4 + 2 clearly visible in profile (two being presutural). Acrostichals arranged in 6 irregular rows. Legs black or dark-brown, sometimes the tips of the front femora and the front tarsi are yellowish. Front tibiae and tarsi with outstanding hairs on their anterior edge.

Ratio of 2nd and 3rd costal segments (Fig. 36) about 4; 2nd and 4th about 5. Wing-tip between the ends of m_{1+2} and r_{4+5}. Veins brown: membrane more or less clear. Squama greyish or ochreous, with a black or dark-brown fringe. Wing-length about 2.3 mm.

♂ genitalia. Distance from the end of the aedeagal apodeme to the tip of the aedeagal hood 0.8 mm. Aedeagal apodeme more or less evenly curved downwards, heavily sclerotised. The strengthened part posterior to the attachment of the inner processes of the postgonites occupies $^1/_4$ of the whole apodeme. 9th sternite rather straight-sided, bearing a short indistinct hypandrial apodeme. The pregonites are as figured for *nigripes* (Fig. 2): postgonites larger than those figured for *nigripes* (Fig. 2). Aedeagal hood large, weakly sclerotised around its edges. Phallophore not clearly indented on its posterior edge in lateral view (compare *albipennis,* Fig. 1).

The basiphallus (Fig. 15c) consists of two rods, the left being obviously broader than the right. Mesophallus without any clearly defined "thorn" (contrast *distorta*): the right side forms a weakly sclerotised lobe. Distiphallus very short, clearly shorter than the basiphallus.

Ejaculatory bulb (Fig. 15a) moderately sclerotised, except along its distal edge, a little narrower than long: central channel visible, reaching almost to the distal edge. Stem fairly short, weakly sclerotised.

Larva. The larva may be compared with that of *distorta* as follows. For a more detailed description and figures consult KATO (1956).

Mandibles with 5 (rarely 4) alternating teeth (as figured for *distorta*). Paraclypeal phragma largely pale brown. Patches of bristle-like spines on the locomotory humps (Kriechwülsten) of the mesothorax, metathorax and all abdominal segments.

Front spiracles with 88—133 bulbs, distributed over the entire surface of the spiracle. Posterior spiracles much as figured for *distorta,* narrowly separated.

Biology. Mine on upperside of leaf. Eggs laid singly near the leaf-tip; the resulting larva produces a gradually broadening mine, heading towards the base

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Figs. 39—42. Larval parts of *Agromyza*: 39, *albipennis* Meigen; 40, *lucida* Hendel; 41, *hendeli* sp. nov.; 42, *phragmitidis* Hendel. a — mandibles; b — larval mouthparts; c — front spiracles; d — hind spiracles of the leaf. Frass particles fairly conspicuous, scattered. Zig-zag feeding lines visible. (Only one mine specimen was available, so I do not know if this is typical).

Pupation follows outside the mine. There is puparial dimorphism as in *distorta,* but not so strongly marked as in that species. KUWAYAMA (1950) noted the following important differences between the two types of puparia.

(In mm)	*Hibernant puparium*	*Non-hibernant puparium*
Mean length	2.598	2.855
Mean width	1.645	1.595
Mean height	1.542	1.385
Thickness of puparial skin	0.0294	0.0205
Colour	Dull black, rarely brownish black	Pale greenish brown, brown or dark-brown, rarely blackish, glossy.

KATO (1956) adds the following: "Hibernant puparium: Generally all the segments not polished as having many microscopic furrows or lumpy surface; second to fifth abdominal segments more or less subshiny, each having a distinct transverse keel girdling median position; sixth and seventh abdominal segments, each with weakly developed keels on both lateral sides, having several longitudinal and oblique keel-like wrinkles on dorsum: eighth abdominal segment generally without median keel or distinct wrinkles: anterior spiracles protruded rather laterad and the distal surface of each spiracle directed strongly or sometimes almost entirely laterad.

Non-hibernant puparium: Generally all the segments smooth and shiny, without any distinct keel or wrinkle; last three segments sometimes more or less subshiny according to the existence of microscopic furrows; anterior spiracles protruded rather ventrad and the distal surface of each spiracle directed strongly or sometimes almost entirely ventrad."

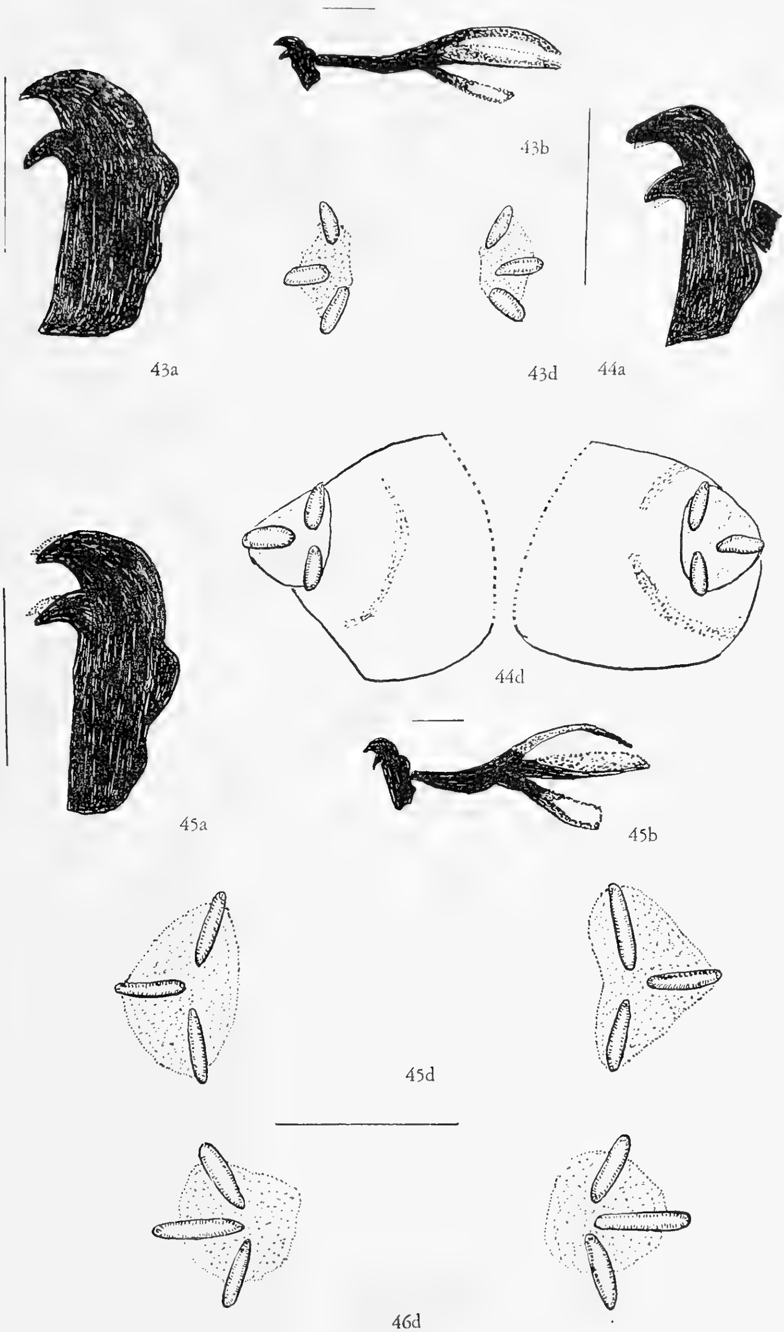
These differences correspond with those observed in the European *distorta.* In that species the differences are even more marked. KUWAYAMA also observes that the hibernant puparium "does not adhere closely to the rice-leaf", while the non-hibernant type does. This too is confirmed by my observation of *distorta.*

There are at least two generations. In Japan the first generation of larvae feed in June. Further details of the life-history are not known to me, though they are probably given in some of the Japanese papers listed by KATO (1956) in his synonymy. The flies were taken freely in June.

Material examined. In the HENDEL collection. ♂ (with preparation), type of the synonymous *Agr. oryzae* Hendel, ex *Oryza sativa,* Nikolsk-Ussurisk, Süd-Ussurigebiet, Siberia, 27.VII.28.

Distribution. Northern Japan (Hokkaido, Tohoku and Hokuriku provinces), East Siberia (South-Ussuri province).

Host plants. Gramineae, tribe Oryzeae: *Oryza sativa* L., *Zizania latifolia* Turcz.



Figs. 43—46. Larval parts of *Agromyza*: 43, *spenceri* sp. nov.; 44, *prespana* Spencer; 45, *graminicola* Hendel; 46, *baetica* sp. nov. a — mandibles; b — larval mouthparts; d — hind spiracles

Agromyza distorta Griffiths 1955

Agromyza distorta Griffiths, 1955, Ent. Gaz., vol. 6, p. 10—12.

Textfigures 14a, 14b, 14c, 25, 37, 47a, 47c, 47d, 47e, 47f

Frons very broad, 1.5—2 times the width of an eye at the level of the front ocellus, parallel-sided. Antennae clearly separated at their bases. In profile (Fig. 25) the cheeks and orbits clearly visible, forming a continuous ring around the eye. Eyes with scattered white hairs. Ratio of the eye-height to the height of the jowls 5—7; 4—5 strong orbital bristles, clearly differentiated into upper and lower orbitals: the upper directed backwards, the lower inwards. Ocellar bristles normal-sized, reaching beyond the bases of the 2nd pair of upper orbitals. 3rd antennal segment broadened apically, rather short, somewhat angulate at its apex. Colour of head entirely black, or at most the lunule and first antennal segment brown.

Dorsocentrals strongly developed (as *oryzae),* 4 + 1 or 4 + 2 clearly visible in lateral view, one or two presuturals being clearly developed. Acrostichals 8-rowed. Legs black, except for the yellow tips of the front femora. Front tibia with strong hairs on its anterior edges (though not so marked as in *oryzae*).

Ratio of the 2nd to 3rd costal segments 2.7—3; 2nd to 4th 4—5. Wing-tip between the ends of r_{4+5} and m_{1+2}. Veins brown: membrane strongly brownish tinged. Squama ochreous or dark grey with a dull black fringe. Wing length 2.5 mm.

♂ genitalia. Distance from the end of the aedeagal apodeme to the tip of the aedeagal hood 0.9 mm. Aedeagal apodeme heavily sclerotised, somewhat bent downwards; the strengthened part posterior to the attachment of the inner processes of the postgonites occupying a little less than $^1/_4$ of the whole. 9th sternite short and rounded (compare *nigripes,* Fig. 2), heavily sclerotised. Hypandrial apodeme short, its tip reaching $^1/_2$ of the length of the aedeagal apodeme. Pregonites large (compare *nigripes,* Fig. 2): postgonites larger than those figured for *nigripes* (Fig. 2), rounded. Aedeagal hood as for *nigripes,* but more weakly sclerotised around its edges. Phallophore as figured for *albipennis* (Fig. 1).

Basiphallus (Fig. 14c) consisting of two rods of moderate width: mesophallus asymmetrical: its left side developed into a black "thorn", while its right forms an ill-defined lobe of tissue. Distiphallus (Fig. 14b) very short, clearly shorter than the basiphallus.

Ejaculatory bulb (Fig. 14a) drop-shaped, weakly sclerotised, almost transparent in its distal $^1/_3$: central channel clearly visible, reaching to $^2/_3$ of the length of the bulb: distal edge delicately rounded. Stem fairly short.

Larva. The following description is partly based on HERING (1956) who gives a very detailed account of the larva.

Antennae and maxillary palpus small: longitudinal sclerite and mandibular abductor apodeme absent. Mandibles (Fig. 47a) long, with 5 alternating teeth: the upper two teeth longer than the lower three: right mandible higher than the left. Distinct mandibular adductor apodeme present. No filaments above the mandibles.

Labial sclerite slender: paraclypeal phragma strongly sclerotised.

Head bare. Prothoracic girdle consisting of about 8 rows of minute spines. Metathorax bare. Dorsal edge of abdomen bare: strong bands laterally on the metathorax and first three abdominal segments consisting of 14—18 rows of spines: bands of the following segments decreasing progressively. Metathorax and first three abdominal segments ventrally with a thick patch of elongate, bristle-like spines on their locomotory humps (Kriechwülsten). 8th segment laterally, 7th and 8th ventrally, and the anal region with small fine spines.

Front spiracles (Fig. 47c) large and circular, bearing 200—250 bulbs distributed over their whole surface: atrium short. Hind spiracles (Fig. 47d) projecting somewhat, narrowly separated from each other, with 3 small egg-shaped bulbs: adjacent bulbs forming an angle of about 90°.

Length (full-grown) about 5 mm.

Biology. Mine on upperside of leaf. Eggs laid singly near the edge of the leaf. The larva first produces a long narrow channel towards the leaf-tip, then turns and produces a large irregular blotch-mine. Frass particles scattered regularly throughout the mine. Zig-zag feeding lines visible. Often several mines coalesce to consume the whole leaf.

Pupation follows outside the mine. The winter puparia (Fig. 47e) are only weakly attached to the leaf (the ventral surface not being flat) and easily fall into the water.

The puparia are strongly dimorphic. The winter puparia (Fig. 47e) are black, thick-shelled, strongly arched dorsally and obviously hollowed ventrally: the hind end is very abruptly cut off. The summer puparium (Fig. 47f) is more elongate, red, thinner-shelled, of fairly normal shape for the group: dorsal edge only moderately arched: ventral surface flat: hind end less abruptly cut off. The same phenomenon occurs in *oryzae*, though to a lesser degree: detailed analyses by Japanese workers are summarised under that species.

This species attacks large *Glyceria* plants growing in the water. The highly modified front spiracles represent an adaptation to an aquatic environment (there are several other instances in the Agromyzidae of startling changes in the structure of the spiracles in species feeding on aquatic hosts). Nearly all the winter puparia must end up in the water, as they are only very loosely attached to the leaf. Furthermore I observed that one puparium (from which the type specimen later emerged) was situated on a leaf which could only have been reached by the larva crawling underwater. The patches of bristle-like spines on the ventral locomotory humps clearly are a device to assist the larva in gripping a surface. These are more strongly developed in *oryzae*.

Two generations. The larvae of the second generation are found in September.

Material examined. In the author's collection. Type ♂ (with preparation) Ash Vale, Surrey, 5.IX.53, ex *Glyceria maxima*: emerged 18.V.54.

In the Hering collection (Berlin). ♂ (with preparation), Aken, on the river Elbe, with summer puparium, but no further data.

Distribution. England, Germany. Apparently a rare species. Not common at the type locality.

Food plant. *Glyceria maxima* (Hartm.) Holmb.

Agromyza lunulata Sasakawa 1956

Agromyza lunulata Sasakawa, 1956, Sci. Rep. Saikyo Univ., Agr., vol. 8, p. 124—125.

This species was described from a single swept female. I have not attempted to include it in this paper. SASAKAWA (1956) states that it is allied to *distorta.* However until a male or the immature stages are found the question must remain open. The external characters of the type certainly resemble *distorta,* but the third antennal segment is clearly longer. Unfortunately no female of *distorta* is available yet for comparison.

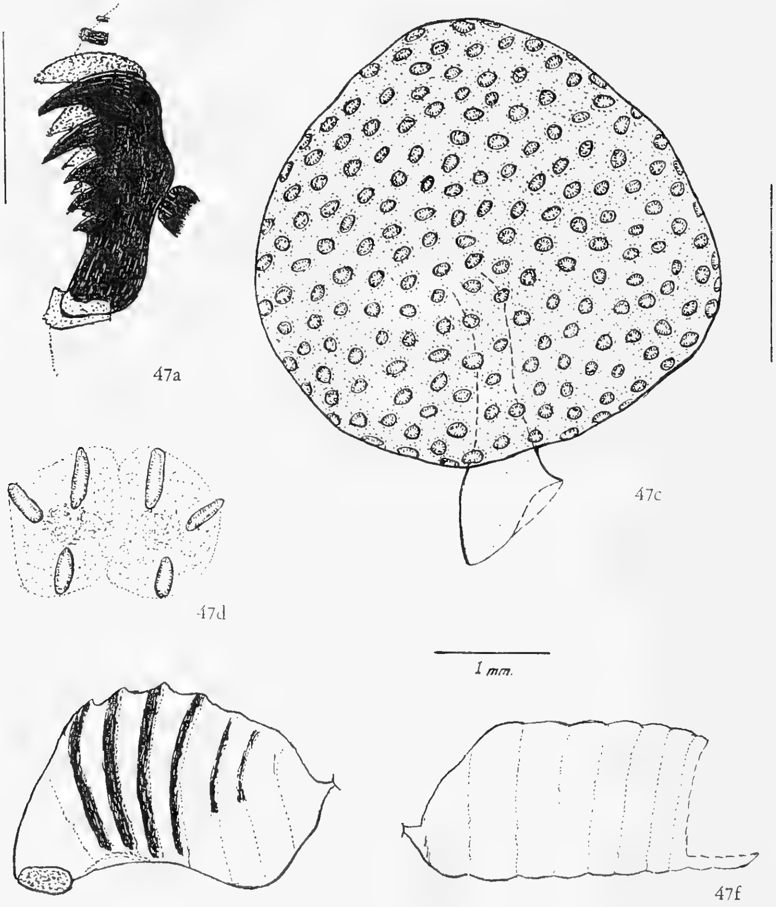


Fig. 47. Larval parts of *Agromyza distorta* Griffiths: a — mandibles; c — front spiracles; d — rear spiracles; e — winter puparium; f — summer puparium (with front spiracles missing)

The original description gives full details of the external morphology of the type with figures of the head and wing.

PARASITES

The majority of Agromyzid parasites belong to the Chalcid family Eulophidae and Braconids of the genus *Opius* and the tribe Dacnusini. Species of each of these groups occur as parasites of the *nigripes* group. There is no evidence of hyperparasitism.

One species of the Eulophidae has been bred freely from puparia of *Agromyza albipennis* Mg. on *Phalaris arundinacea.* These Chalcids are unfortunately not yet identifiable. The absence of Chalcid parasites from the majority of the species of the *nigripes* group is noteworthy. In the *Poëmyza* species, for instance, which also feed on Gramineae the Chalcids form numerically the greater part of the parasites.

Several *Opius* spp. occur freely here. These too are not yet identifiable, but this should be remedied soon, as Dr. MAX FISCHER of Vienna is working on the group, and has been sent much material bred from the Agromyzidae.

I can however give a reasonable account of the Dacnusini, which form the majority of the parasites of this group. Some records were included in my paper "Host Records of Dacnusini (Hym., Braconidae) from leaf-mining Diptera" in 1956. More can now be added. Mr. G. E. J. NIXON of the Commonwealth Institute of Entomology has been kind enough to assist me in identifying these species. All the specimens mentioned here have either been named by him, or by myself by comparison with specimens named by him.

Antrusa melanocera (Thomson)

In GRIFFITHS (1956) this species was recorded as bred from *albipennis, nigripes* and *distorta.* I can now add the following records.

Ex *Agromyza nigripes* Mg. on *Glyceria fluitans* and *G. maxima* collected at Ash Vale, Surrey, 5 & 6.IX, 15 examples emerged in Sept./Oct. and April/May. Ex *Agr. albipennis* Mg. on *Phalaris arundinacea,* same data and locality, 2 examples emerged 12.X and 14.III. Ex *Agr. distorta* Grif. on *Glyceria maxima*, same data and locality, one example emerged 3.X. Ex *Agr. lucida* Hd. ex *Glyceria maxima,* same date and locality, one example emerged 19.III.61. Ex *Agr. albipennis* Mg. on *Phalaris arundinacea*, Woodwalton Fen, Hunts., 22.VIII.60, one example emerged 4.IX.61.

These records add one further host, *Agr. lucida* Hd. The species is clearly common on *nigripes,* but is less frequent on the related *albipennis.* At the Ash Vale locality, where *distorta* and *lucida* are found feeding together with *nigripes* on *Glyceria maxima, Antrusa melanocera* has occurred on all three species. However only one example has been bred from *lucida,* so that it seems probable that *nigripes* represents the main host, from which I have bred about 25 specimens. The occurence of this species on *distorta* represents a clear case of disjunctive oligophagy, for it does not occur on the *Phragmites*-feeding species which are more closely related to *nigripes* than is *distorta.* This transference has clearly been facilitated by the fact that *distorta* occurs on the same food-plant as *nigripes.*

Antrusa spec. *a*

Four examples of another *Antrusa* species were bred from *Agr. lucida* Hd. on *Glyceria maxima,* Ash Vale, Surrey, 5.IX.60, emerged 27.III—7.IV.61.

These specimens differ from typical *melanocera* in the more striate sculpture of the petiole and the fewer hairs on tergite 3 + 4 and it is possible that they represent a distinct species. One specimen of the normal *melanocera* was also bred from the same host.

Dacnusa nydia Nixon

It has now become clear that this species, as formerly conceived, is composite. The true *nydia* is a parasite of *nigripes* though it is much less common than *Antrusa melanocera.* Three examples were recorded by GRIFFITHS (1956). Three more can now be recorded, bred from *Agr. nigripes* Mg. on *Glyceria maxima,* Ash Vale, Surrey, 5.IX.60, emerged 3.X.60 and March/April 1961.

Dacnusa sp. *a (nydia* group)

This species is represented by one specimen only bred from *Agr. phragmitidis* Hd. on *Phragmites communis,* Slapton, S. Devon, emerged April '55 (K. A. SPENCER).

Dacnusa spec. *b* (*nydia* group)

This species has been hitherto included under *nydia* but can be easily recognised by its possession of yellow tarsi with a contrasting black 5th segment, and its broader petiole. My records are as follows:

Ex *Agromyza hendeli* spec. nov. on *Phragmites communis,* Woodwalton Fen, Hunts., 23.VIII.60, 3 examples emerged 18—20.IX.60. Ex *Agr. phragmitidis* Hd. on *Phragmites communis,* Woodwalton Fen, Hunts., 28.IX.60, 5 examples emerged April/May '61. One example from the same host and food-plant, Slapton, S. Devon, emerged April '55 (K. A. SPENCER).

The species is clearly a common parasite of both the British *Phragmites*-feeding species, *hendeli* and *phragmitidis.*

Dacnusa cincta Haliday

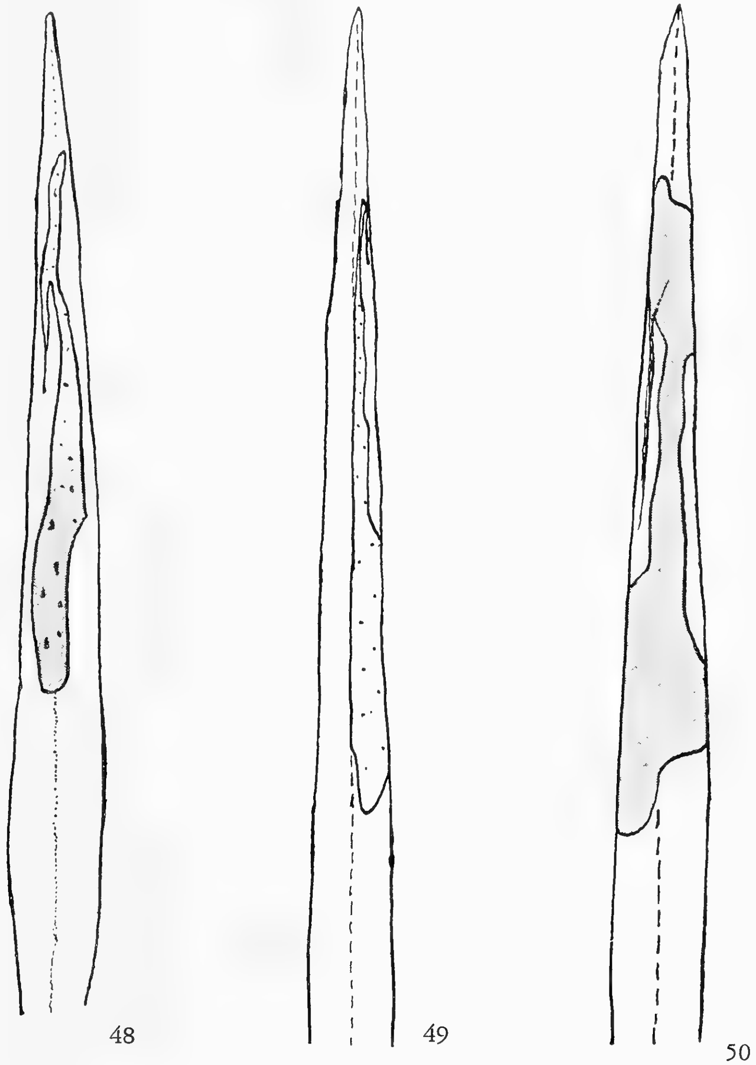
This large characteristic species has been bred from *Agr. lucida* on two occasions, the details being as follows:

Ex *Agromyza lucida* Hd. on *Deschampsia caespitosa,* Brookman's Park, Herts., 6.VIII.54, 4 examples emerged 1.IX.54 and 9—10.V.55. Ex *Agr. lucida* Hd. on *Glyceria maxima,* Ash Vale, Surrey, 5.IX.60, one example emerged 3.V.61.

Dacnusa pione Nixon

This is another large species related to *cincta,* of which only two Swedish examples have been hitherto known. I have now bred two specimens from *Agr. phragmitidis* Hd. on *Phragmites communis,* Woodwalton Fen, Hunts., 23.VIII.60 & 28.IX.60, emerged 10.VII.61.

The late emergence dates are noteworthy and suggest that the species may be single brooded. In captivity the vast majority of *Dacnusini* emerge before mid-May from overwintering puparia.



Figs. 48—50. Leaf-mines of *Agromyza*: 48, *albipennis* Meigen on *Phalaris arundinacea*; 49, *nigripes* Meigen on *Glyceria maxima*; 50, *lucida* Hendel on *Glyceria maxima* (natural size)

Dacnusa lugubris Nixon

Nixon (1945) records several examples of this species as having been bred by Hamm and Blair from "*Agromyza nigripes* on reeds". Judging from the late dates (September and October) on which the puparia were collected, these records probably refer to *Agr. phragmitidis* Hd., and I have listed this species as a parasite of that fly.

The species recorded in GRIFFITHS (1956) as *lugubris* from *Phytomyza pseudohellebori* Hendel has been re-examined by NIXON, who now states that it is definitely not the true *lugubris*. The species related to *lugubris* are a difficult group which is clearly in need of revision.

Dacnusa spec. *c* (*lugubris* group)

One example of a form near *lugubris* was bred from *Agr. nigripes* Mg. on *Glyceria maxima*, Ash Vale, Surrey, 5.IX.60, emerged 2.III.61. It is improbable that this is conspecific with the species bred from "reeds", referred to above as *lugubris*.

Dacnusa ninella Nixon

NIXON (1945) refers to this species three examples bred by HAMM from "*Agromyza nigripes* on reeds" from puparia taken in October near Oxford. It was bred together with *lugubris*. The host is probably *Agr. phragmitidis* Hd. and I have listed *ninella* as a parasite of that species.

Dacnusa spec. *d* (*lugubris* group)

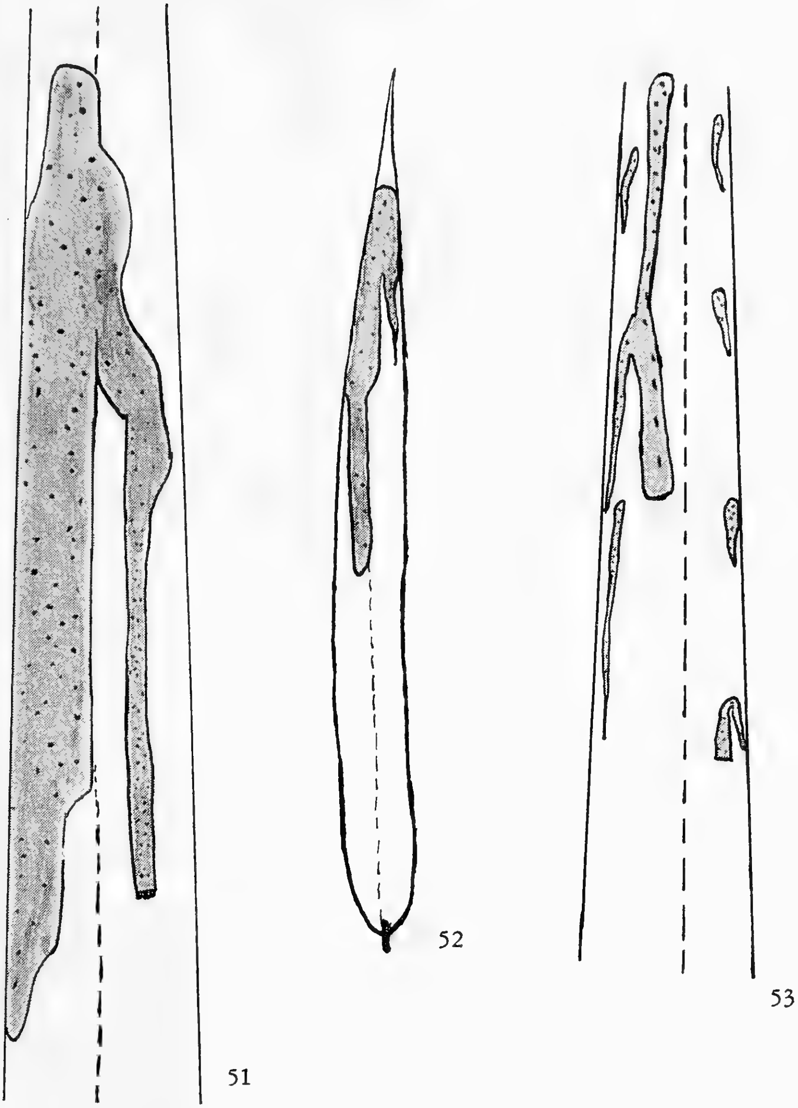
One example of an obviously distinct *Dacnusa* spec., probably referable to the *lugubris* group, was bred from *Agr. distorta* Grif. on *Glyceria maxima*, Ash Vale, Surrey, 5.IX.54, emerged 26.IV.55.

Dacnusa spec. *e*

One example of a new *Dacnusa* species was bred by SPENCER from *Agr. baetica* spec. nov. on *Phragmites communis*, Algeciras, S. Spain, 25.IV.55, emerged 25.V.55. As with most Dacnusini from the mediterranean area it is undescribed.

The following is the list of the known Dacnusine parasites from each species of the *nigripes* group.

Agromyza albipennis Meigen	*Antrusa melanocera* (Thomson)
A. nigripes Meigen	*Antrusa melanocera* (Thomson)
	Dacnusa nydia Nixon
	,, spec. *c* (*lugubris* group)
A. lucida Hendel	*Antrusa melanocera* (Thomson)
	,, spec. *a*
	Dacnusa cincta Haliday
A. hendeli spec. nov.	*Dacnusa* spec. *b* (*nydia* group)
A. phragmitidis Hendel	*Dacnusa* spec. *a* (*nydia* group)
	,, spec. *b* (*nydia* group)
	,, *pione* Nixon



Figs. 51—53. Leaf-mines of *Agromyza*: 51, communal mine of *phragmitidis* Hendel on *Phragmites communis* (compare also *spenceri* sp. nov. and *hendeli* sp. nov.); 52, *graminicola* Hendel on *Phragmites communis*; 53, *baetica* sp. nov. on *Phragmites communis* (with young mines). Natural size

	Dacnusa lugubris Nixon
	„ *ninella* Nixon
A. baetica spec. nov.	*Dacnusa* spec. *e*
A. distorta Griffiths	*Antrusa melanocera* (Thomson)
	Dacnusa spec. *d* (*lugubris* group)

The species with the widest range of hosts is *Antrusa melanocera* (see the discussion under that species). Of the other species *Dacnusa* spec. *b* occurs on both *hendeli* and *phragmitidis*, the two *Phragmites*-feeding species, while the other species of Dacnusini are recorded from one host only. It is probable however that some of the species bred from *phragmitidis* will also occur on *hendeli.*

Agromyza albipennis Mg. appears to have few parasites. The only Dacnusine which has been bred from it is *Antrusa melanocera,* and that is far commoner on *nigripes.* The flies can always be bred with the greatest of ease. The absence of parasite records from other species is of course due to the absence of material.

ACKNOWLEDGEMENTS

This paper could not have been written without the cooperation of several individuals and Museums in sending me material. I wish to express my thanks to the following: Professor Dr. E. M. HERING of the Humboldt University Museum in Berlin, Dr. M. BEIER of the Vienna Natural History Museum for the loan of HENDEL's material, Overlärare NILS RYDÉN of Hälsingborg, Sweden, Mr. K. A. SPENCER of Hampstead, London, Dr. J. T. NOWAKOWSKI of the Polish Academy of Sciences, Professor SASAKAWA of Kyoto Prefectural University, Japan, Mr. F. D. GOODLIFFE of Long Sutton, Hants., Dr. H. ANDERSSON of Lund University for the loan of a ZETTERSTEDT type, Dr. K. W. HARDE of the State Natural History Museum in Stuttgart for GROSCHKE's material and Mr. R. L. COE of the British Museum (Natural History) for the loan of a *prespana* paratype. My sister, Mrs. E. A. OSBORNE, drafted some of the drawings.

SUMMARY

1. The characters of the *nigripes* group of the genus *Agromyza* Fallén are defined. All the eleven Palaearctic species, including three, new to science, are described and also two new subspecies.

2. The male genitalia of all species and subspecies are described and figured for the first time.

3. The known larvae are described and figured: where larvae were not available, larval characters have been reconstructed as far as possible from the puparia. An attempt is made to rectify the considerable confusion which has reigned hitherto over the identification of the larvae, and in particular the true *nigripes* larva is described for the first time.

4. Details of the biology of all species are given as far as they are known.

5. The name *lucida* Hendel 1920 is removed from the well-known *Phragmites* species, to which it was wrongly applied by HENDEL himself, and returned to the original species. The *Phragmites*-feeder is redescribed as *hendeli* spec. nov.

6. Detailed records are given of the distribution of all species. Two species, *albipennis* and *phragmitidis*, extend right across the Palaeartic region to Japan: three other species, *nigripes, hendeli* and *lucida*, are wide-spread in temperate Europe. The known distribution of the other species is more restricted.

7. An attempt is made to clarify the host-relationship of *albipennis, nigripes* and *lucida,* which are recorded from many hosts.

8. Keys for the identification of adults and larvae are given.

9. Chapters on phylogenesis, host-relationship and previous workers' treatment of the group are included.

10. An account of the species of Dacnusini (Hym. Braconidae), parasitic on this group, is given.

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DEEL 106 AFLEVERING 3 1963

TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

INHOUD:

Tijdschrift voor Entomologie, deel 106, afl. 3. Gepubliceerd 15-V-1963

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COMPARATIVE MORPHOLOGY OF THE SALDIDAE AND MESOVELIIDAE (HETEROPTERA)[*]

BY

A. P. GUPTA

Department of Entomology, University of Idaho, Moscow, Idaho, U.S.A.

Contents

I. Introduction

There has been little agreement among heteropterists on the probable position of the Saldidae in the higher classification of the Heteroptera, and this family, more than any other, has been variously moved from one group to another. Recently, on the basis of his studies of the female genitalia of the Heteroptera, Scudder (1959) suggested that the Saldidae might be closely related to the Mesoveliidae. A comparative morphological study of these two families was, therefore, thought to be necessary to throw some light on the probable position of the Saldidae, and its relationship with the Mesoveliidae. Both alate and apterous forms of the two families have been studied and their morphology is compared and discussed.

In addition, two general aspects of the morphology of the Heteroptera have been considered namely, the interpretation of the head sclerites and the variation in the thoracic structure between apterous and macropterous forms of the two families.

II. Materials and methods

Saldula palustris (Douglas) was collected from the beach at Point Grey, Vancouver, B.C. *Aepophilus bonnairei* Sign. from Jersey, Channel Islands, was kindly supplied by Dr. G. G. E. Scudder of the University of British Columbia. *Mesovelia mulsanti* White from England and Holland were obtained from Mr. I. Lansbury (Hope Department of Entomology, Oxford) and Dr. R. H. Cobben

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[*]) Based in part on a thesis submitted in partial fulfilment of the requirements for the degree of Master of Science of the University of British Columbia, Vancouver, B.C.

(Wageningen, Netherlands), respectively. The alate specimens of *Mesovelia vittigera* Puton were obtained from the Musée Royal de L'Afrique Centrale, Tervuren, Belgium, and were originally collected in the Congo. Other specimens of the families belonging to the four higher taxonomic groups — Pentatomomorpha, Cimicomorpha, Amphibicorisae and Hydrocorisae — were also used for comparative study.

The external anatomy was studied both from dried and alcohol-preserved specimens. The material was boiled in 10% potassium hydroxide, passed through glacial acetic acid, stained in acid fuchsin, and cleared in creosote. Observations on the cephalic muscles of *Saldula* were made from specimens preserved in 70% alcohol, passed through different grades of alcohol, cleared in xylene and examined under polarized light.

All drawings were made by using a squared graticule eye piece, and are not made to the same scale.

III. COMPARATIVE DESCRIPTIONS

Head*)

Saldula palustris (Douglas) (Figs. 1—3)

Head short, broad, vertex well developed, with a lateral invagination near eye extending anteriorly to frons; coronal and ecdysial cleavage lines distinct in nymph, absent in adult; frons short, frontoclypeal sulcus absent; clypeal region relatively extensive, differentiated into postclypeus, anteclypeus and paraclypeus, cephalic portion of postclypeus with two lateral unpigmented areas; bucculae well developed; postgenal bridge short; mandibular plate absent, mandibular lever well developed, triangular (in nymph and adult); postocciput in the form of thin ring around occipital foramen, apparently differentiated into dorsal and lateral elements, lateral parts bearing paired condyles; labrum broad and flap-like, reaching distal end of second labial segment, epipharyngeal process absent; labium four-jointed, first segment thickest, third longest, being swollen proximally and tapering distally; antennae four-segmented with small intersegmental sclerites, first segment much thicker than rest, the whole beset with hairs, third and fourth segments also bearing stout bristles; eight to ten pairs of trichobothria present, scattered over vertex, frons, and postclypeus (nymph with four pairs, one pair on frons, two pairs on postclypeus and fourth pair on anteclypeus); compound eyes conspicuous, two ocelli present; two unpigmented areas present laterad of ocelli.

Aepophilus bonnairei Sign. (Fig. 4)

Similar to *Saldula* in essential parts, but differing in following features. Cephalic portion of postclypeus without two lateral unpigmented areas, paraclypeal region not as well defined as in *Saldula,* restricted to upper two thirds of anteclypeus; maxillary plate area well developed; bucculae not well developed; labrum

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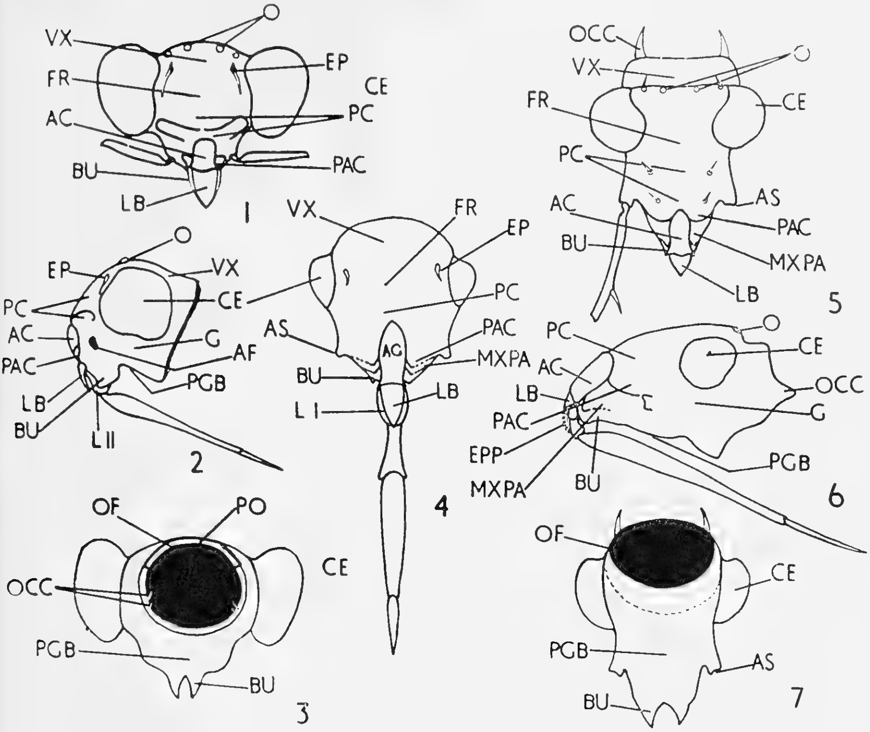
*) The terminology of parts follows that of SNODGRASS (1960).



Figs. 1—3. Head of *Saldula.* (1) dorsal (frontal) view; (2) lateral view; (3) ventral view. Fig. 4. Head of *Aepophilus bonnairei*, dorsal view. Figs. 5—7. Head of *Mesovelia mulsanti*: (5) dorsal view; (6) lateral view; (7) ventral view

reaching distal end of first labial segment, and not second as in *Saldula*; compound eyes not conspicuous, ocelli absent; postocciput not divided into dorsal and lateral elements; postgenal bridge longer than in *Saldula*; four pairs of trichobothria — one pair on frons, two pairs on postclypeus and one pair on anteclypeus.

Mesovelia mulsanti White (Figs. 5—7)

Head longer than in *Saldula*; vertex well developed, and overlapped by prothorax; coronal and frontal ecdysial cleavage lines indistinct in nymph and adult; frontoclypeal sulcus absent; clypeal region well developed, differentiated into postclypeus, anteclypeus and paraclypeus; maxillary plate area well developed, separated from paraclypeal region by a short genal sulcus; lower limit of maxillary plate area delimited by an indistinct line; bucculae poorly developed; mandibular plate absent, mandibular lever well developed, roughly quadrangular; labrum flaplike, with an epipharyngeal process extending almost to distal end of second labial segment; postgenal bridge longer than in *Saldula*; postocciput indistinguishable from occiput, and bearing two dorso-lateral condyles; labrum four-jointed; first segment thickest, third longest, being swollen on inner side proximally and tapering distally; antennae four-jointed with small intersegmental sclerites, first antennal segment thicker than rest, bearing a stout bristle lateromedially; three pairs of trichobothria, one pair on frons, two pairs on postclypeus (in the nymph one additional pair on anteclypeus); compound eyes inconspicous, ocelli rudimentary.

Mesovelia vittigera Puton

Similar to *M. mulsanti* but ocelli well developed.

Thorax

Saldula palustris (Douglas) (Figs. 8—13, 30—34)

Prothorax. Pronotum large, with anterior collar, posteriorly overlapping base of fore wings, callal area broad, dome-shaped and triangularly depressed in middle; episternum shorter than epimeron, forming a precoxal shelf, pleural sulcus and pleurodema distinct but short; trochantin short, very distinct in nymph; sternum differentiated into a transversely elongated presternum, a triangular basisternum, and a sternellum, furcal arms elongate, extending laterally to meet pleurodema.

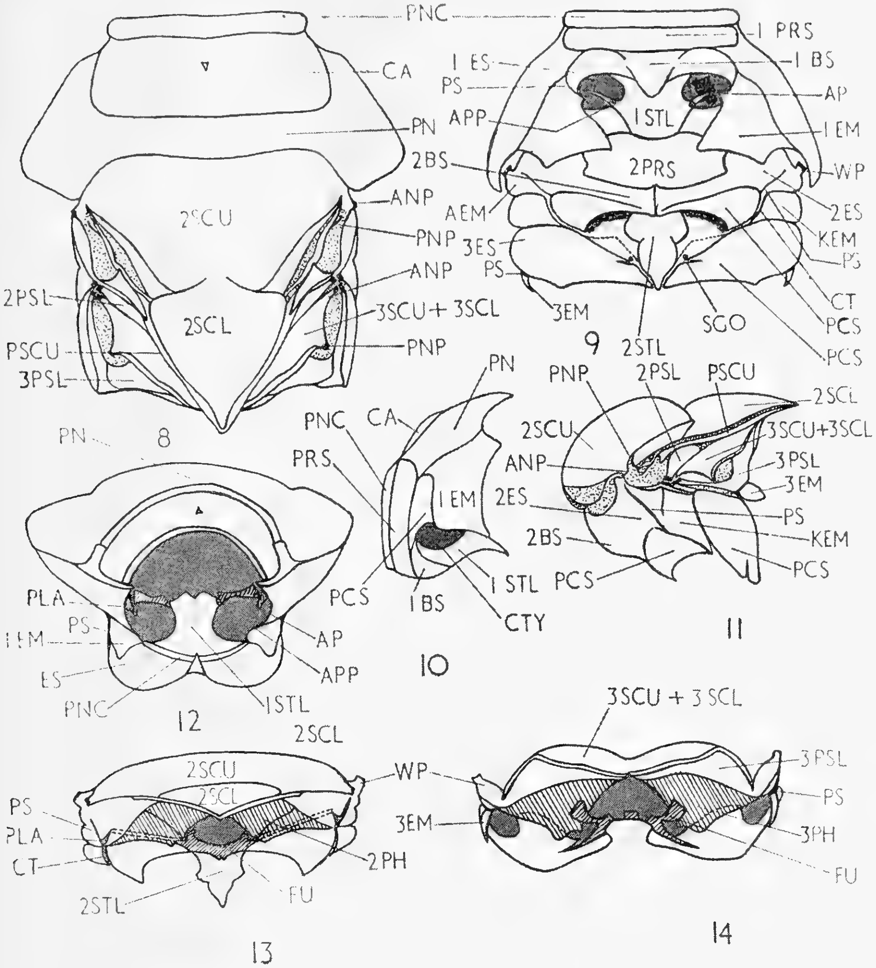
Mesothorax. Mesonotum differentiated into scutum and scutellum, with dividing sulcus incomplete, scutum secondarily divided into a median and two lateral areas, scutellum extending posteriorly over second abdominal segment, and apically pointed, parascutellum extending anterolaterally into scutoscutellar region, the latter being unequally sclerotized, postscutellum visible laterally; pleural sulcus distinct, short, pleurodema short, directed anteriorly; trochantin short; episternum forming precoxal shelves, epimeron divided into a dorsal anepimeron and a ventral katepimeron, the latter produced into a point at lower limit of coxal cleft; pleural wing process very distinct; basalar and subalar sclerites not distinguishable; sternum well developed, and divided into a presternum, a basisternum, and a sternellum, the latter extending posteriorly over metasternum; furca well developed, with furcal arms extending laterally and meeting pleurodema; phragma well developed.

Metathorax. Metanotum in the form of fused metascutum and scutellum, postscutellum well defined; pleural sulcus horizontal, and dorsal in position, pleurodema short; trochantin comparatively long; episternum broad, forming a large precoxal shelf, two precoxal shelves being approximated medially, epimeron small and dorsal in position; orifice of scent-apparatus located laterally; basalar and subalar sclerites indistinguishable; metapleural wing process lying forward in region of mesepimeron, and reinforced by processes from postscutellum and epimeron of mesothorax and postscutellum of metathorax; metasternum reduced to a small plate beneath mesoscutellum; furcal arms short, not reaching pleurodema; phragma very large.

Wings (Figs. 30, 31)

Fore wings differentiated into clavus, corium, embolium, and a membranous area, posterior end of clavus produced medially into a narrow triangular area along inner margin of membrane, membranous area with four cells.

Hind wings with distinct vannal and jugal folds, costa, subcosta and base of



Figs. 8—14. Thorax of *Saldula*: (8) dorsal view; (9) ventral view; (10) lateral view of prothorax; (11) lateral view of pterothorax; (12) internal view of prothorax showing pleurodema and apodemes; (13) internal view of mesothorax showing furca, phragmata and pleurodema; (14) internal view of metathorax showing furca, phragmata and pleurodema

radius fused, radius and media distally fused, base of media and cubitus in contact with distal median plate, two vannal veins in the vannal area, 2V with a thickened base, jugal lobe with single jugal vein; humeral plate well developed, first and second axillaries reduced, third axillary articulated both with proximal median plate and second axillary, two median plates (proximal and distal) present.

Legs (Figs. 32—34)

Coxae, especially those of hind leg, well developed, having only pleural and trochantinal articulations, hind coxa with inflected articular surface, proximal half with a coxal suture, internal ridge of suture continuous with inflection of articular surface, fore and middle coxae without coxal suture, distally coxae bearing anterior and posterior articular surfaces for articulation with trochanter, trochanter immovably articulated with base of femur; femora flattened laterally; hind tibia longer than hind femora, bearing stout bristles, proximal end with a distinct head bent toward femur; tarsi consisting of three tarsomeres, the basal the smallest, tarsomeres with bristles, pretarsus in the form of two claws.

Aepophilus bonnairei Sign. (Figs. 15—17)

Prothorax. Pronotum large with a pronotal collar; epimeron broader than episternum, precoxal shelf formed by both; pleural sulcus and pleurodema short; coxal cleft prominent, trochantin present; sternum differentiated into a basisternum and sternellum; furcal arms short.

Mesothorax. Mesonotum a triangular piece; pleural sulcus short (shorter than that of prothorax); trochantin present; sternum differentiated into a presternum, basisternum and sternellum, latter extending over metasternum (as in *Saldula*); furca not well developed.

Metathorax. Metanotum undifferentiated, shorter than pronotum and mesonotum; pleural sulcus dorsal in position; epimeron dorsal; pleurodema very short; episternum broad, forming a large precoxal shelf.

Legs. Coxae more or less like those of *Saldula*, no outer suture and inflection, anterior and posterior articular processes present, femora flattened laterally, hind tibiae longer than hind femora as in *Saldula*, tibiae with stout bristles at their distal ends, tarsi with three tarsomeres.

Two rudimentary mesothoracic wings present.

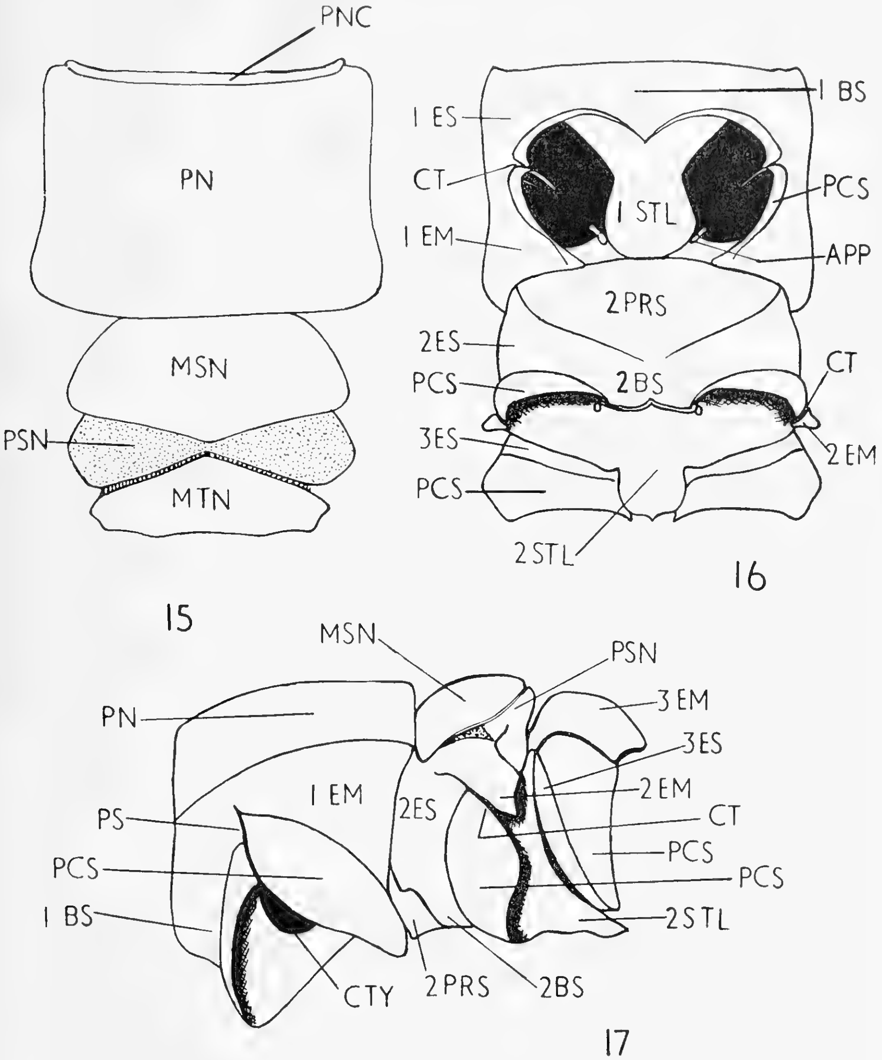
Mesovelia mulsanti White (Figs. 18—23)

Prothorax. Pronotum large, with a short collar; epimeron broader than episternum, precoxal shelf formed by both episternum and epimeron; pleural sulcus indistinguishable, a very short pleurodema present; trochantin present, very distinct in nymph; sternum differentiated into a basisternum and a sternellum; furcal arms (apophyseal apodemes) small, pointing ventro-posteriorly.

Mesothorax. Mesonotum undifferentiated; pleural sulcus indistinguishable, very short pleurodema present; episternum medially fused with basisternum; trochantin present; precoxal shelf formed by both episternum and epimeron; sternum differentiated into basisternum and sternellum; furcal arms (apophyseal apodemes) short, pointing posteriorly.

Metathorax. Metanotum undifferentiated; pleural sulcus indistinguishable; coxal cleft absent (present in prothorax and mesothorax); apophyseal apodemes short, pointing laterally; episternum fused with basisternum, forming a part of precoxal shelf; metasternum differentiated into basisternum and sternellum, latter fused with first abdominal sternite; single median orifice of scent apparatus present.

Legs. Coxae well developed, fore and middle coxae being swollen, articulation both pleural and trochantinal, hind coxae without coxal sutures on their outer



Figs. 15—17. Thorax of *Aepophilus bonnairei*: (15) dorsal view; (16) ventral view; (17) lateral view

surfaces; trochanter immovably attached to base of femur, femora flattened laterally, fore and middle femora with more stout bristles than hind femora, hind tibiae with stout bristles, middle tibiae with combs at their distal ends, three tarsomeres, pretarsus in the form of claws, latter provided with pseudoaroliae (parempodium).

Mesovelia vittigera Puton (Figs. 24—29)

Prothorax. Pronotum with anterior collar, posteriorly overlapping bases of fore and hind wings, pronotum with a wide callal area, the latter with two laterally located depressions; epimeron broader than episternum; pleural sulcus short, pleurodema very short; trochantin present; sternum as in *M. mulsanti.*

Mesothorax. Mesonotum differentiated into scutum and scutellum, the latter not extending posteriorly over second abdominal segment as in *Saldula*; postscutellum present; sternopleural region the same as in *M. mulsanti.*

Metathorax. Metascutum and scutellum fused, median part extending over second abdominal segment; postscutellum distinguishable; pleurosternal region the same as in *M. mulsanti.*

Wings (Figs. 28, 29)

Fore wings with clavus, corium, an indistinct embolium, bases of costa, subcosta, radius fused, distal ends of fused costa, subcosta and radius, and media and cubitus form a stigma, rest of wing membranous, but without cells.

Hind wings without jugal fold, vannal fold present, bases of costa, subcosta, radius and media fused, radius and media distally fused, two vannal veins present.

Legs. As in *M. mulsanti.*

Abdomen

Saldula palustris (Douglas) (Figs. 35—39, 45, 46, 50)

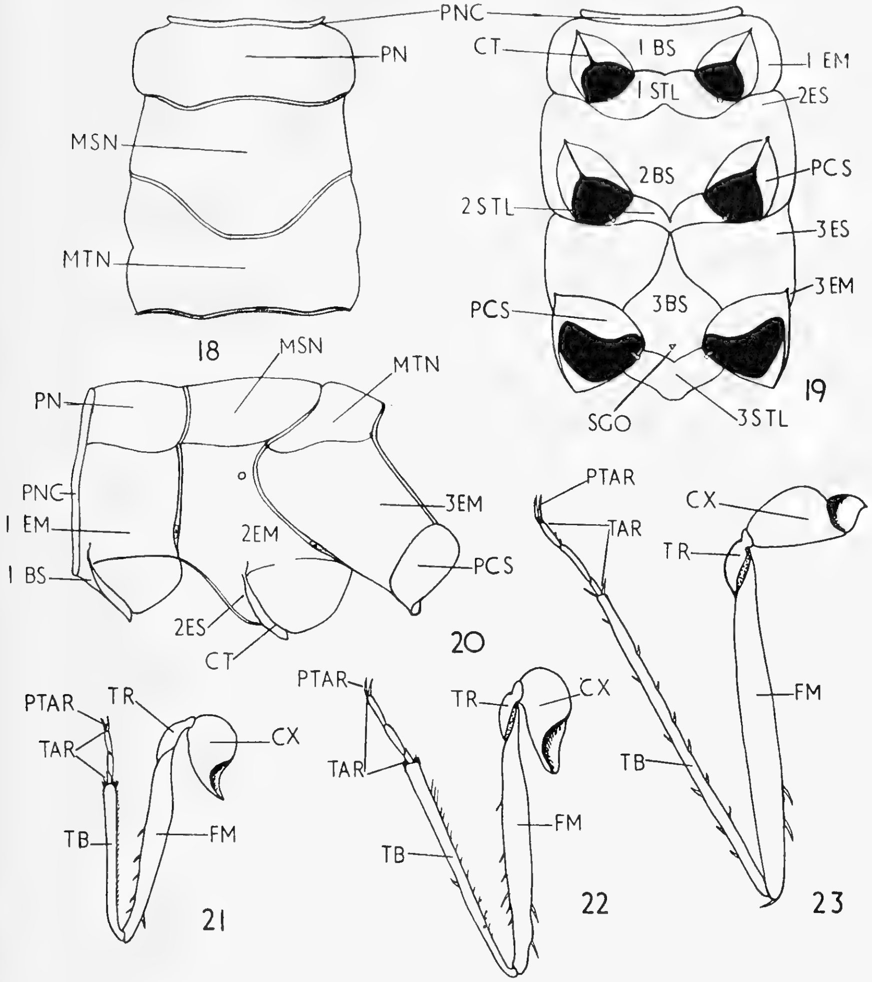
Abdomen with ten segments. Terga of segments two to eight differentiated into dorsal median plates and lateral paratergites, tergum of first segment not complete medially, in the male posterior margin of second paratergite modified into a granulated convex lobe; conjunctiva between second and third paratergite forming beneath the anterior margin of third paratergite a fold with a concave anterior margin, the latter being beset with stout setae; this together with convex lobe of second paratergite forms, during copulation, grasping mechanism in male; remnants of orifices of abdominal scent-glands present at posterior margin of third tergite.

Sternum of first segment rudimentary and indistinguishably fused with partially membranous sternum of second segment; seven pairs of spiracles present on lateral margins of sterna two to eight.

Female genitalia (Figs. 36—39)

Previous descriptions: EKBLOM (1926); LESTON (1956); SCUDDER (1959).

First gonapophyses joined by membrane, elongate, tapering and split longitudinally with serrate dorsal tips, rami sclerotized; first gonocoxa fused with ventral part of eighth paratergite; ninth tergum without separate paratergite; gonangulum triangular, its anterior limbs being fused with first ramus, and posterior side with ninth tergum, ventral angle of posterior side articulating in a notch on middorsal side of second gonocoxa, thus forming a fulcrum on which the latter pivots; second gonapophyses broader than first, sclerotized and united except at apices, the latter being truncate; second gonocoxa elongate and thickened dorsally; gono-



Figs. 18—20. Thorax of *Mesovelia mulsanti*: (18) dorsal view; (19) ventral view; (20) lateral view. Figs. 21—23. Legs of *Mesovelia mulsanti*: (21) fore leg; (22) middle leg; (23) hind leg

placs broad, curved and free distally, united proximally by partially sclerotized membrane; spermatheca single, with an oval bulb or receptacle, and an elongated spermathecal tube; the latter communicating with vagina, a muscular pump with a single flange present between receptacle and main part of duct; wall of vagina lined internally with wrinkled chitinous intima, and strenghtened by a sclerotized ring.

Male genitalia (Figs. 45, 46, 50)

Previous descriptions: Ekblom (1926); Marks (1951); Pruthi (1925).

Aedeagus differentiated into phallosoma and endosoma, the latter being further divisible into conjunctiva and vesica; proximal part of phallosoma wide and membranous, distal part being narrow, heavily sclerotized and bent over proximal part, mouth of phallosoma located ventro-laterally and confined to its distal half, two minute posteriorly-directed appendages located one on each side of the anterior end of mouth, base of phallosoma supported by an inverted Y-shaped sclerite, with its upper limb fused with junction of basal plates; dorsal half of conjunctiva sclerotized, forming a curved sclerite with its two ends produced into lateral "wings" on either side of mid-dorsal line, distal end of conjunctiva containing two pairs of dorsolaterally located appendages, anterior pair smaller than posterior one, ventral wall of conjunctiva containing near mouth of phallosoma a V-shaped structure with two pairs of processes projecting anteriorly from inner angle of V, inner pair being smaller than outer; vesica narrow, coiled, and in close contact with ejaculatory duct; ejaculatory reservoir located at junction of conjunctiva and vesica; basal plates completely fused in middle line, forming horseshoe-shaped structure; capitate processes attached on to ends of basal plates; parameres long, sickle-shaped, and pointed at apices, proximal ends being broader and curved for muscle attachment.

Aepophilus bonnairei Sign. (Fig. 47)

Abdomen with ten segments. Terga two to eight differentiated into median tergites and lateral paratergites; first tergum fused with second; clasping organ present in second and third segments.

First sternum rudimentary and indistinguishably fused with partially membranous second sternum; seven pairs of spiracles on segments two to eight.

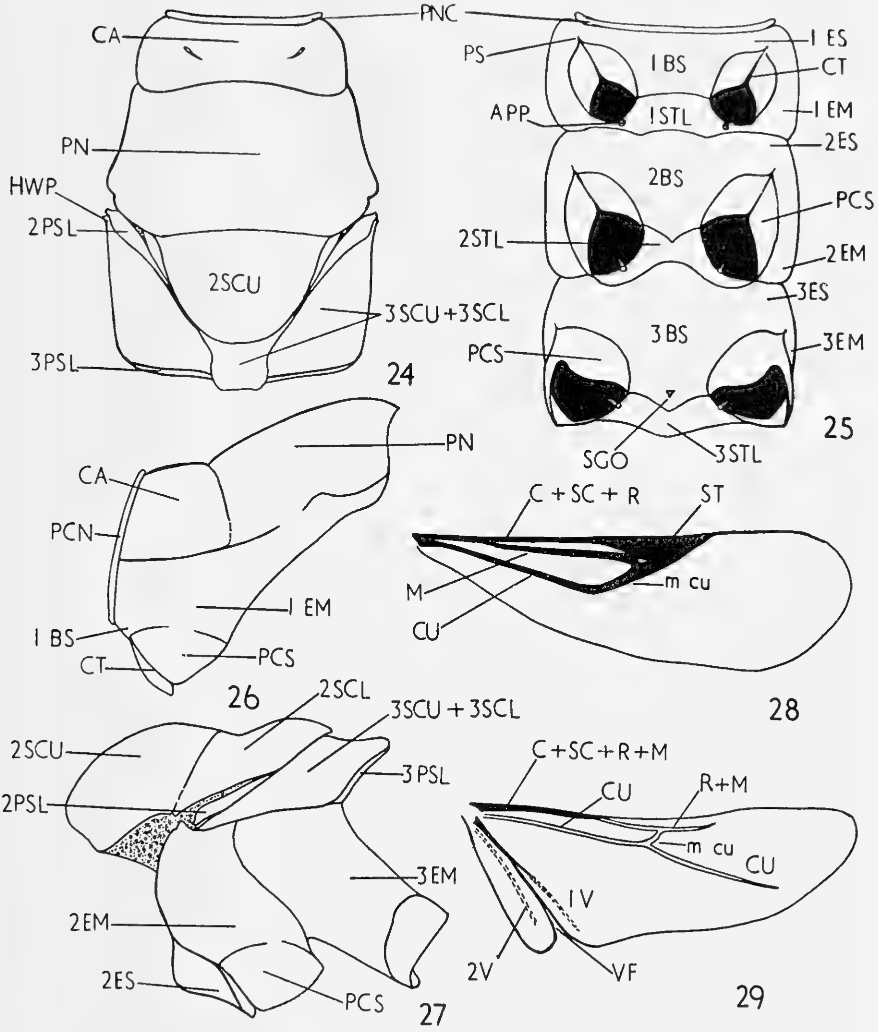
Female genitalia. More or less as in *Saldula palustris.*

Male genitalia (Fig. 47). Aedeagus differentiated into a phallosoma and endosoma, the latter with two appendages projecting out of mouth of phallosoma, base of phallosoma membranous, distal part narrow and heavily sclerotized, bent over proximal part, base of phallosoma supported by an L-shaped sclerotized structure, horizontal limb being fused with junction of basal plates; dorsal part of endosoma presents a sclerotized structure; basal plates completely fused and like those in *Saldula.*

Mesovelia mulsanti White (Figs. 40—44, 48, 49, 51)

Abdomen with ten segments. Terga of segments two to eight in female and two to seven in male differentiated into dorsal median tergites and lateral paratergites; orifice of abdominal scent-gland in middle of fourth tergum; clasping organ in male absent.

First sternum indistinguishably fused anteriorly with metasternellum and posteriorly with second sternum; seven pairs of spiracles present on segments two to eight; anterior margin of seventh sternum produced anterolaterally in mid-line as a long apodeme; two circular patches of black setae present on eighth sternum in male.



Figs. 24—27. Thorax of *Mesovelia vittigera*: (24) dorsal view; (25) ventral view; (26) lateral view of prothorax; (27) lateral view of pterothorax. Figs. 28—29. Wings of *Mesovelia vittigera*: (28) fore wing; (29) hind wing

Female genitalia (Figs. 41—44)

Previous description: Ekblom (1926); Neering (1954); Pendergrast (1957); Scudder (1959).

First gonapophyses joined by membrane, elongate, tapering and split longitudinally, with serrate tips; rami sclerotized and interlocking; first gonocoxa fused with eighth paratergite; gonangulum triangular, its posterior side also fused with an inflection between eighth and ninth terga; second gonapophyses elongate, sclerotized, laciniate, united except at tips; second gonocoxa elongate; gonoplacs triangular, sclerotized, curved and attached to second gonocoxae; spermatheca single with an accessory fecundation canal.

Male genitalia (Figs. 48, 49, 51)

Previous description: EKBLOM (1926); PRUTHI (1925).

Aedeagus differentiated into phallosoma and endosoma, the latter being further divisible into conjunctiva and vesica; proximal part of phallosoma membranous, distal part heavily sclerotized and bent over proximal part; a triangular sclerotized area present in mid-dorsal part of conjunctiva, proximally conjunctiva produced into sclerotized appendages projecting from mouth of phallosoma; vesica narrow and short, in close contact with ejaculatory duct; two ejaculatory reservoirs distinguishable; basal plates completely fused in middle line, forming a horseshoe-shaped structure; capitate processes attached laterally; parameres hook-like, pointed at apices, proximal ends being broader for muscle attachment.

Mesovelia vittigera Puton

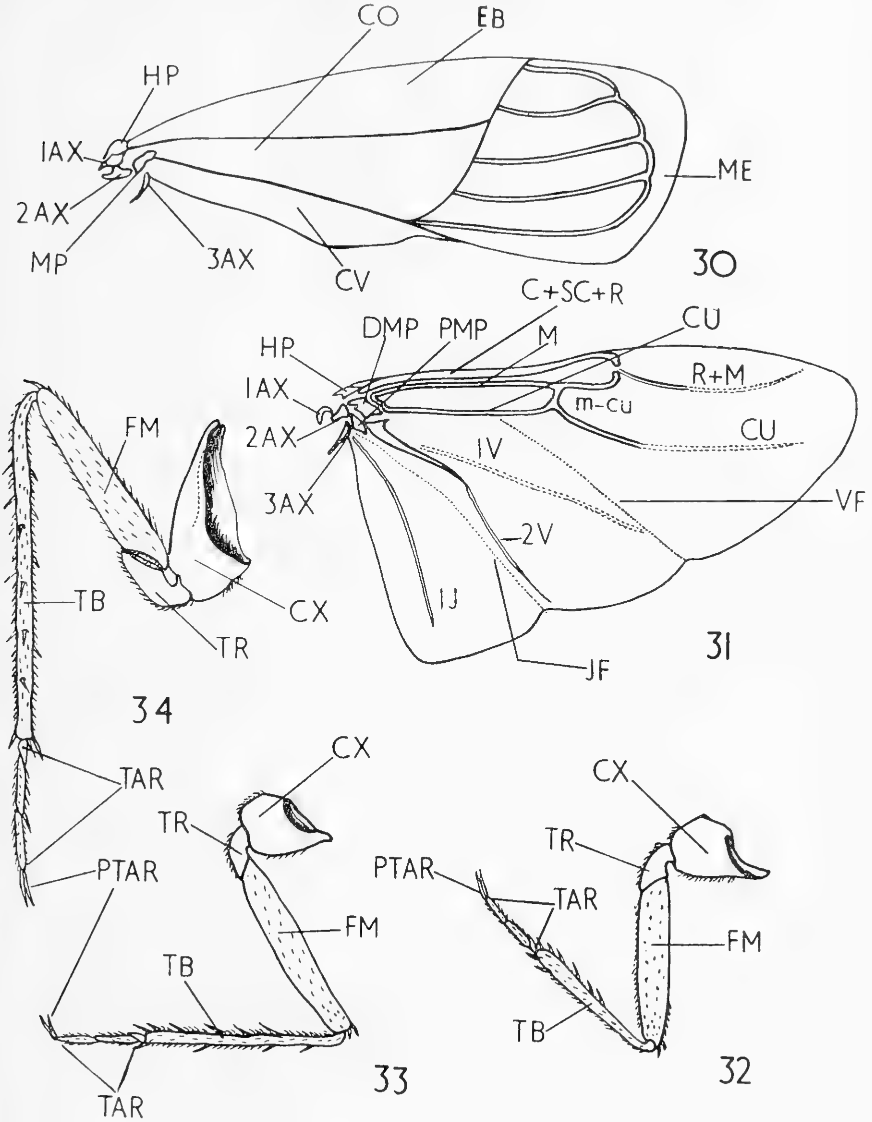
Abdomen very similar to that of *M. mulsanti.*

IV. MORPHOLOGICAL CONSIDERATIONS AND COMPARISONS

Head

Saldula palustris (Douglas). In the adult insect, on the anterodorsal part of the head capsule, the position of the frontal ecdysial cleavage line can be recognized by the position of the two pits; these are found on each side of the vertex along the frontal ecdysial cleavage line in the nymph. These two lateral pits are not homologous with the pretentoria of Cicadellidae (SPOONER, 1938). They have no counterparts in other Heteroptera as far as is known, and the name epicranial pits is here suggested for these structures. It should be mentioned that the frons is not always delimited laterally by the ecdysial cleavage line, for SNODGRASS (1960) states, "they vary greatly in their extent and position in different insects." He suggested the name cephalic apotome for the part cut out at ecdysis by the ecdysial cleavage line.

In *Saldula* the fronto-clypeal sulcus is absent, and consequently there is no external demarcation between the frons and the clypeus. The positions of the antafossae or the mandibular levers are often used as landmarks to delimit the frontal and clypeal areas (SPOONER, 1938). However, in *Saldula* they are situated cephalad and so are perhaps unreliable. These areas can be distinguished, however, by muscle attachment; the dilator muscles of the sucking pump are attached to the clypeus internally (SNODGRASS, 1935). SNODGRASS (1960) stated that the cibarium has often been called the 'pharynx' although it lies outside the mouth. He further stated that this cibarium has become the sucking pump of the liquid-feeding insects. It is evident, therefore, that the term pharyngeal pump is in-



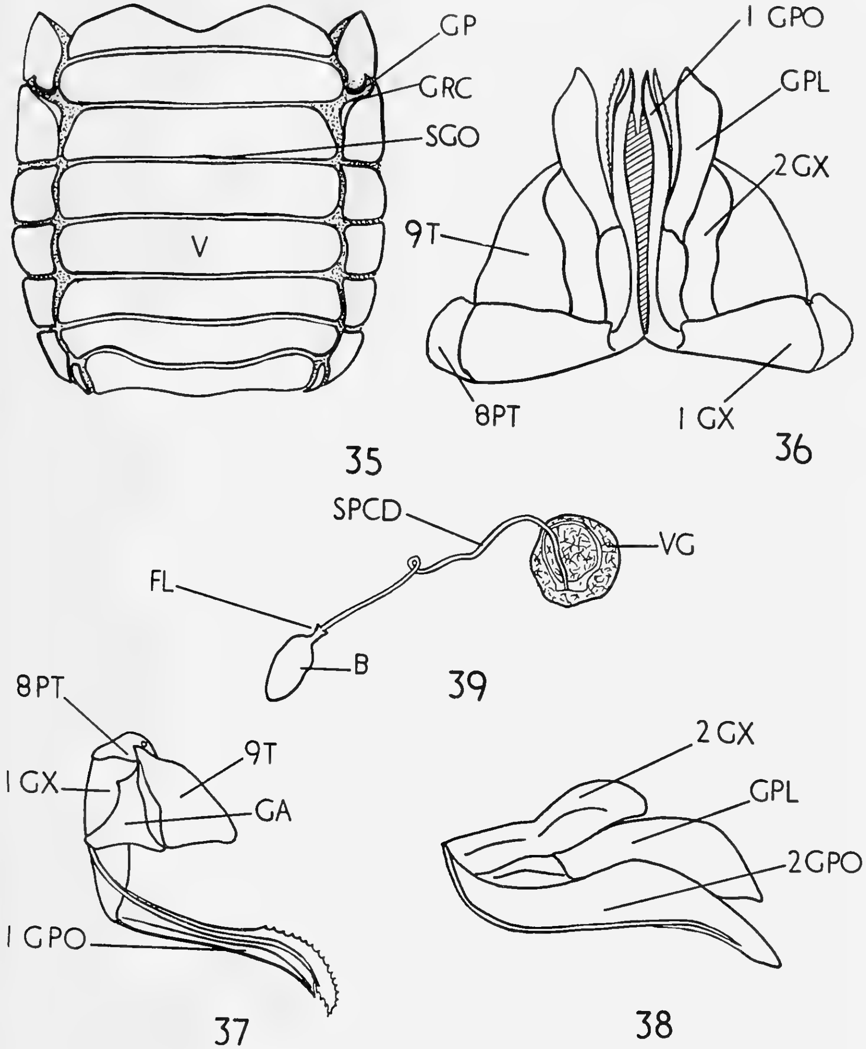
Figs. 30—31. Wings of *Saldula*: (30) fore wing; (31) hind wing. Figs. 32—34. Legs of *Saldula*: (32) fore leg; (33) middle leg; (34) hind leg.

accurate. In *Saldula* the criterion of the muscle attachment has been used to delimit the frontal and the clypeal areas, although it is realized that this procedure is open to some criticism. For example, FERRIS (1944), DU PORTE (1946), and PARSONS (1959) have criticized the criterion of muscle attachment for the identification of the sclerites. The latter in her account of *Gelastocoris* used the frontal ganglion as landmark to delimit the point of attachment of the dilator muscle of the food-pump. She recognized two sets of muscles: cibarial, which lie posterior to the frontal ganglion and attach on the clypeus, and pharyngeal muscles, which lie posterior to the frontal ganglion and attach on the frons. In this she followed MARKS (1959). PARSONS (1959), however, suggests, "that the muscle posterior to the frontal ganglion could come to insert on a cibarial portion of the food-pump, or that cibarial muscles might shift their insertions to the pharyngeal portion." She further quoted MARKS (1959) and stated that the position of the frontal ganglion also varies relative to the muscles from one species to another. It is evident then that an interpretation based on the position of the frontal ganglion is neither reliable. In the present study, therefore, in the absence of any alternative, the criterion of muscle attachment has been adopted to delimit the frontal and the clypeal portions of the head capsule. Examination shows that the dilator muscles of the sucking pump attach to a definite part of the head capsule, and so it is probably correct to interpret this area as the clypeus. EKBLOM (1926) states that in *Saldula saltatoria* (Lat.), "the forehead forms in front a transverse ridge where it limits the clypeus." This ridge would appear to be merely the posterior margins of the unpigmented postclypeal areas. In *Saldula*, therefore, as in other Heteroptera, the clypeus appears to be differentiated into a postclypeus, which is united with the frons, a distinct anteclypeal region, and two paraclypeal lobes.

The anteclypeus is a clearly defined area, and appears externally as a convex lobe, its internal concavity together with its lateral invaginations form a supporting base for the food-pump. To the cephalic margin of the anteclypeus is attached the flap-like labrum.

The paraclypeal lobes are well defined areas on each side of the anteclypeus; they extend caudad up to half the length of the latter. They are clearly visible in both the nymph and the adult, and appear to have no internal muscle attachment. The homology of the paraclypeal lobes in the Hemiptera is very controversial, and has been the subject of much debate. SMITH (1892) and WEBER (1929) considered them to be homologous with the mandibular plates. SNODGRASS (1935) also mentions, "that these paraclypeal lobes appear to be the mandibular plates of the Homoptera," but he himself doubted their mandibular origin in the Homoptera in the absence of any embryological evidence. EKBLOM (1926) and COBBEN (1960) designated these lobes in *Saldula saltatoria* as "laminae maxillares" and "maxillare Platten" respectively. PARSONS (1959) stated that the paraclypeus in *Gelastocoris* is wholly inflected within the head. However, most authors consider the paraclypeal lobes as parts of the clypeus. MUIR & KERSHAW (1911, 1912) regarded them as "extensions of the clypeus", and confirmed that "they have no relation to the mandibles." SFOONER (1938) stated that the paraclypeal lobes are undoubtedly parts of the clypeus. MACGILL (1947) referred to these two lobes in *Dysdercus intermedius* Distant as juga.

It is usually not possible to trace the mandibular plates in the Heteroptera since there is no sulcus between the mandibular plate area and the gena. It is, therefore, advisable to consider the whole area of the head capsule between the eye and the points of attachment of the mouthparts as the genal area; if mandibular plate area need to be recognized, it is suggested that it be defined as the ventro-anterior area of the gena to which the mandible articulates.



Figs. 35—39. Abdomen and female genitalia of *Saldula*: (35) dorsal view of abdomen of male; (36) ventral view of female terminalia; (37) first gonocoxa and associated parts; (38) second gonocoxa and associated parts; (39) spermatheca

In mandibulate insects the maxillae are usually attached to the ventral part of the postocciput (Snodgrass, 1935). It does not appear to be necessary to recognize a maxillary plate area despite the fact that such an area is usually described in the hemipterous head. Maxillary plates are absent in the primitive orthopteran type of the head, and usually cannot be defined by sulci in the hemipterous head.

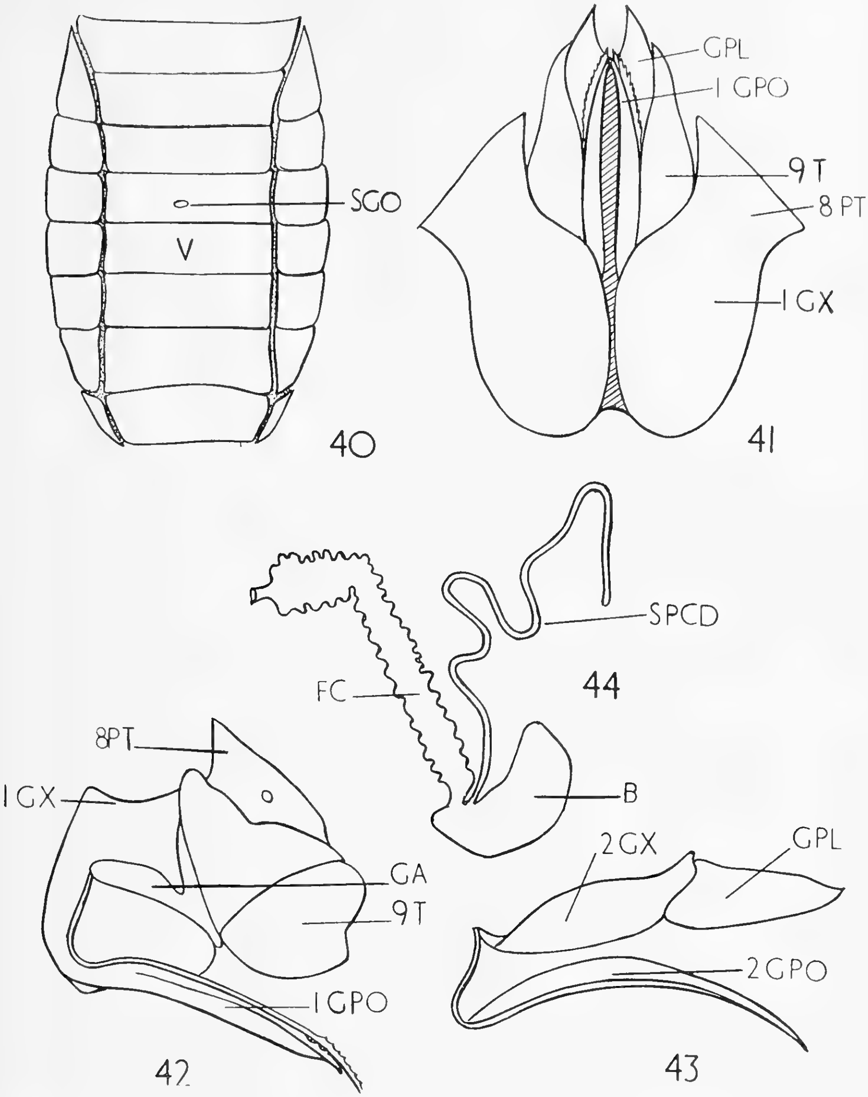
The origin of what is herein termed the postgenal bridge has been a problem in the past. Many authors claim that the ventral region of the head is formed by the fusion ventrally of the maxillary plates, the area considered to be equivalent to the postero-ventral part of the gena anterior to the point of articulation of the labium. MACGILL (1947) referred to the ventral area of the head in *Dysdercus intermedius* as a "large median ventral sclerite interpolated between the labium and the foramen magnum." However, she made no comment regarding its origin. PARSONS (1959), like most earlier authors, adopted the term "gula" but noted that perhaps it is not a true gula. SNODGRASS (1960) has recently considered the ventral sclerites of the head in insects, and has concluded that they are not homologous in all groups, and thus cannot in all be termed a "gula". He mentioned three distinct processes which may result in the formation of ventral sclerites of the head in insects: in the first, a hypostomal bridge may be formed between the occipital foramen and the base of the labium by the ventral fusion of two hypostomal lobes as in the Diptera. The hypostomal bridge, he stated, is continuous dorsally with the postocciput. The second modification, according to SNODGRASS, is the ventral fusion of two postgenal lobes forming a postgenal bridge between the occipital foramen and the base of the labium, as in *Vespula maculata*. When this is the case, the hypostomal bridge is replaced by the postgenal bridge, which differs from the former in not being continuous dorsally with postocciput. He thus regarded the ventral plate in *Notonecta* and *Naucoris* as the postgenal bridge since it is continuous with the postgenae and not with the postocciput. The third process described by SNODGRASS is the ventral fusion of the lower ends of the postocciput to form a median plate, which may become extended distally as in Coleoptera. This median plate is the true gula, and is continuous proximally with the postocciput.

In *Saldula* as in *Notonecta* and *Naucoris*, the ventral plate seems to be formed by the fusion ventrally of the postgenae. However, a developmental study of this region is badly needed to determine whether or not the homology accepted in the present study is really the correct one. This study should include a consideration of the origin of the bucculae. These structures, which apparently serve to support the rostrum during feeding, are interpreted as the ventral extensions of the areas anterior to the point of attachment of the labium. Since they often extend posterior to the rostrum, this interpretation is perhaps incorrect.

Thorax

The prothorax in *Saldula* is more or less of a generalized type seen in other Heteroptera in that it shows no differentiation into separate sclerites. The presence of the dome-shaped callal area does not seem to be a constant feature in the Saldidae, for DRAKE & CHAPMAN (1958) stated that a callus is absent in the genus *Saldoida*.

Of the three thoracic segments, the mesothorax in *Saldula* is the most developed. This agrees with WEBER'S (1930) thesis that in the Hemiptera the fore wings are the principal organs of flight. Both the mesoscutellum and mesosternum are well developed. TAYLOR (1918) stated that in the Heteroptera the mesothoracic sternum is indistinguishably fused with the pleura. This is true in *Saldula*, and it is because of this fusion that the limits of the pleural and sternal sclerites cannot

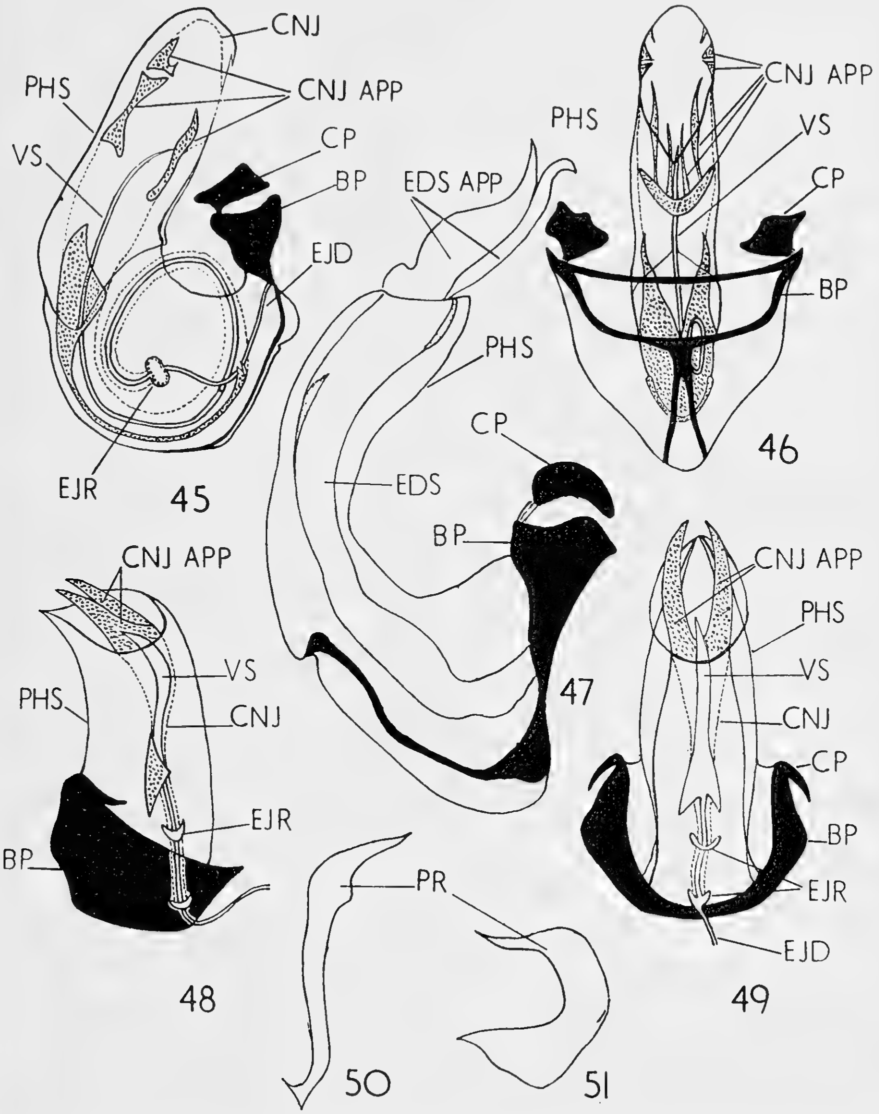


Figs. 40—44. Abdomen and female genitalia of *Mesovelia mulsanti*: (40) dorsal view of abdomen of female; (41) ventral view of female terminalia; (42) first gonocoxa and associated parts; (43) second gonocoxa and associated parts; (44) spermatheca

be clearly defined. The fusion of the sternopleural sclerotizations is also seen in the metathorax. Brindley (1934) figured the thorax of *Saldula pilosella* (Thomson), and labeled the anterior and posterior areas of the mesosternum BS2 (basisternum of mesothorax) and BS3 (basisternum of metathorax), and left the middle area unnamed. If the location of the apophyseal pits is taken as the landmark in delimiting the sternal plates, her interpretation appears to be inaccurate with respect to the mesosternum. According to the interpretation given, the areas which she called BS2 and BS3 are merely the mesothoracic, presternum and sternellum respectively. The basisternum of the metathorax in *Saldula* is a small plate, and lies beneath the mesosternellum, with the metasternal apophyseal pits lying on each side of it. This can be seen if the mesothorax and the metathorax are pulled apart. This structure is most clear in the nymph. Thus what BRINDLEY considered as the basisternum of the metathorax is evidently the sternellum of the mesothorax.

The pleural sulcus of the metathorax is horizontal, and lies on the margin of the pleura, so much so that the epimeron occupies a dorsal position, and is attached to the lateral margin of the metascutellum. According to TAYLOR (1918), the horizontal position of the pleural sulcus seems to be a general feature in the Heteroptera. BRINDLEY (1934) stated that this horizontal position is characteristic of the aquatic bugs because of the enlarged coxae, which extend behind rather than from beneath the thorax. LARSEN (1945) mentioned a horizontal pleural ridge in *Salda muelleri* (Gmelin). The upper forward margin of the metapleuron extends forwards beneath the posterior margin of the mesopleuron, and terminates in the metapleural wing process in the region of the mesepimeron. TAYLOR (1918) mentioned that similar condition is seen in the Nabidae, Gerridae and Berytidae. However, the metapleural wing process in *Saldula* is peculiar in that it is also supported by processes from the mesepimeron and the metascutellum, and lies in the region of the mesothorax. The large precoxal shelves of the metapleuron seem to be associated with the greatest development of the hind coxae.

In the fore wing, the corium is secondarily divided into a marginal embolium. DRAKE and CHAPMAN (1958) also mentioned an embolium in the genus *Saldoida.* In the interpretation of the veins of the hind wing of *Saldula* the criterion of the axillaries and their association with particular veins has been adopted. Thus the veins in association with the distal median plate have been designated as the media and cubitus, the former together with the radius seem to be very much approximated toward the costa and subcosta. It may be mentioned here that different degrees of fusion of the costa, subcosta, and radius occur also in the Miridae, Lygaeidae, Phymatidae, Mesoveliidae, and Piesmidae (HOKE, 1926). DRAKE and DAVIS (1958) have figured the hind wing of the piesmid *Miespa splendida* Drake, and have shown the cubitus in the same position as in *Saldula.* HOKE (1926) has studied the venation of the hind wings of the Heteroptera in detail. She followed the COMSTOCK-NEEDHAM system, and divided the wing into four areas: the costal area with costa, subcosta, radius and media 1 and 2; medial area with media 3 and 4; cubital area with cubitus and first anal, and the anal area with the remaining anal veins. On comparison, it becomes obvious that her cubital area in *Salda bouchervillei* Prov. (= *coriacea* Uhler) and *Saldula pallipes* (F.) (= *separata* Uhler) should really be interpreted as the vannal area, and thus it appears that the vein which she designated as cubitus is probably one of the vannal veins (Table I). Although she has omitted the consideration of the axillaries in her interpretation, she has figured them in the two saldids she studied, and it is evident that her cubitus is not in association with the distal median plate, which it should be according to the interpretation (SNODGRASS, 1935) adopted in the present study. Since many of the veins of the adult wing in the Heteroptera are without a corresponding trachea (HOKE, 1926) the inter-



Figs. 45—46 and 50. Male genitalia of *Saldula*: (45) lateral view of aedeagus and associated structures; (46) frontal view of aedeagus and associated structures; (50) paramere Fig. 47. *Aepophilus bonnairei*: lateral view of aedeagus and associated parts. Figs. 48—49 and 51. Male genitalia of *Mesovelia mulsanti*: (48) lateral view of aedeagus and associated parts; (49) frontal view of aedeagus and associated parts; (51) paramere

pretation of the adult veins seems to be more reliable if based on the associated axillaries. Very little information is obtained by studying the position of the trachea in the nymph. A reinterpretation of the wing venation of the Heteroptera based on the association of veins with axillaries is thus needed.

TABLE I. INTERPRETATION OF THE VEINS OF THE HIND WING

HOKE	GUPTA
Costa	Costa
Subcosta	Subcosta
Radius	Media
r-m	m-cu
Media 1 plus 2	Cubitus
Cubitus	Vannal 1
Anal 1	Vannal 2
Anal 2	Jugal 1

Abdomen

DRAKE and HOTTES (1951) stated that "the hardened and plate-like and roughened lobe of the first paratergite together with the "peg-like" or "spine-like" organs of the second paratergite form the stridulatory organ in the Saldidae. LESTON (1957), however, stated that the granulated plate and the pegs were actually situated on the second and third paratergites respectively, and not on the first and second as indicated by DRAKE and HOTTES. LESTON also stated that the organ functions not as a stridulator but as clasping mechanism in the male during copulation. Examination of the organ in *Saldula* has revealed, however, that one small modification is needed in LESTON's description; the pegs are located actually on a fold of the conjunctiva underneath the anterior margin of the third paratergite and not on the anterior margin of the paratergite itself.

In the male genitalia, the sclerotized curved structure in the base of the conjunctiva probably acts as a guiding mechanism for the vesica, which passes along the ventral surface of this sclerite; the vesica is then directed on to the V-shaped structure in the ventral wall of the conjunctiva and is thus everted. PRUTHI (1925), in his account of the male genitalia of *Chiloxanthus pilosus* (Fall.) and *Salda littoralis* (L.) did not mention the conjunctival appendages, the ejaculatory reservoir, and the capitate processes. The latter, according to MARKS (1951), are secondary developments in the Heteroptera, and mark the original points of attachment of the parameres to the basal plates. EKBLOM (1926) also failed to notice the ejaculatory reservoir and the capitate processes.

PRUTHI (1925) mentioned that the aedeagus in *Mesovelia* is not differentiated into phallosoma and endosoma, but examination of *Mesovelia mulsanti* has shown that the phallosoma, conjunctiva and vesica are distinguishable. EKBLOM (1928) figured a drawn-out endosoma with its two appendages in his account of *Mesovelia furcata.*

COMPARISONS

Head

On comparing the head structures of the two families, it is found that *Saldula* and *Mesovelia* resemble each other in a number of features namely, the well developed vertex, the indistinct coronal and frontal ecdysial cleavage lines in the adult, the well developed clypeal regions, the absence of the frontoclypeal sulci, the four-jointed labium, the antennae, and in the possession of four pairs of cephalic trichobothria in the nymphs. However, these similarities lay not in characters of great taxonomic importance in the group. There are a number of important features in which they are quite distinct (Table II). It should be mentioned that although *Aepophilus bonnairei* appears to resemble *Mesovelia* more than *Saldula,* in respect of the most important taxonomic characters (that is, the shape of the mandibular lever, the presence of epicranial pits, and the absence of epipharyngeal process), *Aepophilus* is exactly like *Saldula.* It is evident that the two families, the Saldidae and Mesoveliidae, show more differences than resemblances in their head structures, and thus it is concluded that in the head structure they are distinct morphologically. The epicranial pits are a feature which appears to be confined to the Saldidae and can thus be regarded as a character by which this family can be separated from all other Heteroptera. However, other genera must be examined to ascertain that these structures are actually a constant feature in the family.

Thorax

In respect to the thoracic structures we also find that the Saldidae and the Mesoveliidae show certain resemblances, particularly in the pronotal collar, callal area with its median or lateral depressions, precoxal shelf, trochantin, and fused metascutum and scutellum, well developed coxae, flattened femora, and three tarsomeres, etc., but they exhibit distinct differences (Table II) which outweigh the resemblances. A preliminary examination of some of the families of the four higher taxonomic groups of the Heteroptera, namely Pentatomomorpha, Cimicomorpha, Amphibicorisae and Hydrocorisae, revealed that the structure of the mesonotum and the metasternum in the various families are of either Saldula-type (the mesosternum projecting over the metasternum) or Mesovelia-type (the mesosternum not projecting over the metasternum). Examination also revealed that, with the exception of the Amphibicorisae, the three groups possess both types (GUPTA, in press). This indicates that if the above mentioned taxa are natural groups, the structure of the thorax is of little value in distinguishing the suprafamilial categories.

Abdomen

On comparing the structure of the female genitalia, the aedeagus, the presence of ejaculatory reservoir, paratergites, and the seven pairs of abdominal spiracles, the two families are found to be very similar, but it is evident that other characters indicate that they are taxonomically distinct (Table II).

From the foregoing study it is evident that the Saldidae and the Mesoveliidae are not closely related as suggested by the comparative morphological study of the female genitalia; they are quite distinct in other morphological features.

COMPARISON OF ALATE AND APTEROUS (AND BRACHYPTEROUS) FORMS IN THE SALDIDAE AND MESOVELIIDAE

From the comparative morphology of the alate and the apterous forms in both the Saldidae and the Mesoveliidae, it was found that these two groups show distinct structural differences, particularly in the thorax (Table III). Insects with flight possess well developed flight muscles and correlated with them an elaborate thoracic structure, while those with limited or no flight have reduced flight muscles, and consequently less developed thoracic structure. Flight in insects is effected by two sets of muscles, the direct and the indirect. The indirect muscles include the dorsal longitudinal muscles and the dorso-ventral muscles. The direct muscles are attached to wing bases or wing sclerites and include principally the basalar, the subalar and the muscles of the axillaries.

According to LARSEN (1945), the principal muscles are present in *Saldula*, and accordingly, as one would expect, the apodemes and the internal margin of the pronotal collar are well developed in the prothorax. The longitudinal muscles, running from the first phragma to the second phragma in the pterothorax, mainly produce the arching of the nota, and thus raising the notal processes relative to the pleural processes, act as depressors of the wing. And since these muscles are important in flight, the phragmata in *Saldula* are well developed. Similarly the development of the furca seems to be correlated with the development of the direct muscle, m. furca-pleuralis (of LARSEN). By the same token, the absence of another direct muscle, m. coxa-subalaris (of LARSEN) both in the mesothorax and the metathorax is correlated with the absence of the subalar sclerites in the pterothorax. The lateral oblique muscle, m. mesonoti secundus (of LARSEN) is well developed in the mesothorax of *Saldula*, but is absent in the metathorax. This can be explained on the basis of WEBER's thesis that in the Heteroptera the fore wings are principal organs of flight, and thus the mesothorax is more developed than the metathorax. It is evident from the foregoing that the morphological differences are the reflections of the functional differences in the alate and the apterous forms. Unfortunately, no account of the musculature of *Mesovelia* is available for comparison, but the structural differences in the thorax of *Mesovelia vittigera* and *M. mulsanti* could also be explained on a functional basis. This study has also revealed that the sternal region in the alate and the apterous forms shows very little difference, and thus perhaps the dorso-ventral muscles are not of great importance in the flight of these insects.

On comparing the alate and the apterous forms of both families, it is found that the ocelli are rudimentary or absent in the apterous forms, but are present in the alate forms. Accompanied with this presence of the ocelli in the alate forms, are well developed compound eyes, which are not so conspicuous in the apterous forms. Such correlated presence or absence of certain structures has also been reported in the Lygaeidae (SCUDDER, personal communication). It is likely that perhaps an alate insect needs more perfect visual apparatus than an apterous one, and probably the ocelli supplement the compound eyes in their visual perception. It is also possible that the presence of the ocelli in the alate forms and its absence in the apterous may be due in part to a genetic linkage with some other character affected by the loss of flight.

The systematic position of the Saldidae and the Mesoveliidae, based on their morphology, has been considered elsewhere (GUPTA, in press).

TABLE II. DIFFERENCES IN THE STRUCTURES OF HEAD, THORAX AND ABDOMEN

Parts	Saldidae	Mesoveliidae
	HEAD	
(1) Postclypeus.	(1) Cephalic portion of postclypeus with two lateral unpigmented areas (absent in nymph): absent in *Aepophilus*	(1) No such unpigmented areas present.
(2) Paraclypeal region	(2) Well defined in *Saldula*; not so in *Aepophilus*.	(2) Not well defined.
(3) Bucculae.	(3) Well developed in *Saldula*; not so in *Aepophilus*.	(3) Not well developed.
(4) Postgenal bridge.	(4) Short in *Saldula*; longer in *Aepophilus*.	(4) Longer than in *Saldula*.
(5) Mandibular lever.	(5) Triangular both in *Saldula* and *Aepophilus*.	(5) Roughly quadrangular.
(6) Postocciput.	(6) Differentiated into dorsal and lateral portions in *Saldula*; not so in *Aepophilus*.	(6) Not so differentiated.
(7) Maxillary plate area.	(7) Not developed dorsally in *Saldula*; developed dorsally in *Aepophilus*.	(7) Developed dorsally.
(8) Labrum.	(8) Without epipharyngeal process both in *Saldula* and *Aepophilus*.	(8) With epipharyngeal process.
(9) Cephalic trichobothria.	(9) Eight to ten pairs in adult *Saldula*; four pairs in *Aepophilus*.	(9) Three pairs in the adult.
(10) Compound eyes.	(10) Conspicuous in *Saldula* not so in *Aepophilus*.	(10) Not so conspicuous as in *Saldula*.
(11) Ocelli.	(11) Present in *Saldula*; absent in *Aepophilus*.	(11) Rudimentary in *Mesovelia mulsanti*; present in *M. vittigera*.
(12) Epicranial pits.	(12) Present both in *Saldula* and *Aepophilus*.	(12) Absent.
	THORAX	
(13) Scutellum (mesoth.).	(13) Extends over second abdominal segment in *Saldula*; not so in *Aepophilus*.	(13) Does not extend over abdomen.
(14) Parascutellum (mesothorax).	(14) Present in *Saldula*; absent in *Aepophilus*.	(14) Absent.
(15) Pleural sulcus (mesothorax).	(15) Distinct but short in both.	(15) Indistinguishable in both.

(16) Epimeron (mesoth.).	(16) Divided into dorsal anepimeron and ventral katepimeron.	(16) Not so divided in both.
(17) Sternum (mesoth.).	(17) Sternellum extending over metasternum in both.	(17) Sternellum not extending over metasternum.
(18) Coxal cleft (metathorax).	(18) Present in both.	(18) Absent in both.
(19) Pleural sulcus (metathorax).	(19) Present and dorsal in both.	(19) Absent in both.
(20) Orifice of scent apparatus.	(20) Two, located laterally.	(20) One, median in position.
(21) Fore wings.	(21) Differentiated into clavus, embolium and membranous part.	(21) Mostly membranous.
(22) Hind wings.	(22) With jugal fold.	(22) Without jugal fold.
(23) Base of media.	(23) Not fused to costa, subcosta and radius.	(23) Fused to costa, subcosta and radius.
(24) Tibial comb.	(24) Absent in both.	(24) Fore and middle tibiae with combs at distal ends.
(25) Pseudo-aroliae (parempodium).	(25) Absent.	(25) Present.

ABDOMEN

(26) Apodeme in sternum VII.	(26) Absent.	(26) Present.
(27) Clasping organ.	(27) Present.	(27) Absent.
(28) Aedeagus.	(28) Differentiated into phallosoma, conjunctiva and vesica in *Saldula*; in *Aepophilus*, into phallosoma and endosoma only.	(28) Differentiated into phallosoma, conjunctiva and vesica.
(29) Base of phallosoma.	(29) Supported by an inverted Y-shaped structure in *Saldula*; by L-shaped structure in *Aepophilus*.	(29) Absent.
(30) Conjunctiva.	(30) Dorsal half sclerotized into a curved structure in both.	(30) Present.
(31) Ejaculatory reservoir.	(31) One.	(31) Two.
(32) Parameres.	(32) Sickle-shaped.	(32) Hook-like.

TABLE III. DIFFERENCES IN THE ALATE AND APTEROUS (BRACHYPTEROUS) FORMS IN THE SALDIDAE AND THE MESOVELIIDAE

Parts	Alate form	Apterous (brachypterous) form
	Saldula palustris	*Aepophilus bonnairei*
(1) Callal area.	(1) Present.	(1) Absent.
(2) Furcal arms.	(2) Well developed.	(2) Not well developed.
(3) Mesoscutellum.	(3) Extends over the abdomen.	(3) Does not extend over the abdomen.
(4) Ocelli.	(4) Present.	(4) Absent.
	Mesovelia vittigera.	*Mesovelia mulsanti.*
(1) Callal area.	(1) Present.	(1) Rudimentary.
(2) Mesonotum.	(2) Differentiated into mesoscutum and scutellum, the former being overlapped by the posterior part of the pronotum.	(2) Mesonotum undifferentiated.
(3) Metanotum.	(3) Median part extending over abdomen.	(3) Does not extend over abdomen.
(4) Ocelli.	(4) Present.	(4) Rudimentary.

KEY TO LETTERING OF FIGURES

A	— anal vein
AC	— anteclypeus
AEM	— anepimeron
AF	— antafossae
ANP	— anterior notal wing process
AP	— apodemes
APP	— apophyseal pits
AS	— antennal tubercle
AT	— antenna
1 AX	— first axillary
2 AX	— second axillary
3 AX	— third axillary
B	— spermathecal bulb
BP	— basal plates
1 BS	— basisternum of prothorax
2 BS	— ,, ,, mesothorax
3 BS	— ,, ,, metathorax
BU	— bucculae
C	— costa
CA	— callus
CE	— compound eye
CL	— clypeus
CNJ	— conjunctiva
CNJ APP	— conjunctival appendages
CO	— corium
CP	— capitate processes
CT	— coxal cleft
CU	— cubitus
CV	— clavus
CX	— coxa
DMP	— distal median process
EP	— epicranial pit
EDS	— endosoma
EDS APP	— endosomal appendages
EJD	— ejaculatory duct
EJR	— ejaculatory reservoir
1 EM	— epimeron of prothorax
2 EM	— ,, ,, mesothorax
3 EM	— ,, ,, metathorax
EPP	— epipharyngeal process
1 ES	— episternum of prothorax
2 ES	— ,, ,, mesothorax
3 ES	— ,, ,, metathorax
FC	— fecundation canal
FL	— flange of pump
FM	— femur
FR	— frons
FU	— furca
FWP	— fore wing process
G	— gena
GA	— gonangulum
GP	— granular plate of clasping organ
GPC	— concavity of clasping organ
GPL	— gonoplac
1 GPO	— first gonapophysis
2 GPO	— second gonapophysis
1 GX	— first gonocoxa
2 GX	— second gonocoxa
HP	— humeral plate
HWP	— hind wing process
J	— jugal vein
JF	— jugal fold
KEM	— katepimeron
L	— labium
LB	— labrum

M — media
ME — membrane
MP — median plate
MSN — mesonotum
MTN — metanotum
MXPA — maxillary plate area
N — notum
O — ocellus
OC — occiput
OCC — occipital condyle
OF — occipital foramen
PAC — paraclypeus
PC — postclypeus
PCS — precoxal shelf
PG — postgena
PGB — postgenal bridge
2 PH — phragma of mesothorax
3 PH — ,, ,, metathorax
PHS — phallosoma
PHS APP — phallosomal appendages
PLA — pleurodema
PMP — proximal median plate.
PN — pronotum
PNC — pronotal collar
PNP — posterior notal wing process
PO — postocciput
PR — paramere
1 PRS — presternum of prothorax
2 PRS — ,, ,, metathorax
PRSC — prescutum
PS — pleural sulcus
PSCU — parascutellum
2 PSL — postscutellum of mesothorax
3 PSL — ,, ,, metathorax
PSN — postnotum
PT — paratergite
PTAR — pretarsus
R — radius
SC — subcosta
2 SCL — mesoscutellum
3 SCL — metascutellum
2 SCU — mesoscutum
3 SCU — metascutum
SGO — scent gland orifice
SPCD — spermathecal duct
ST — stigma
1 STL — sternellum of prothorax
2 STL — ,, ,, mesothorax
T — tergum
TAR — tarsus
TB — tibia
TN — trochantin
TR — trochanter
1 V — first vannal vein
2 V — second vannal vein
VF — vannal fold
VG — vagina
VS — vesica
VX — vertex
WP — pleural wing process

V. ACKNOWLEDGMENTS

A part of this work was done while in receipt of a research grant from the National Research Council of Canada, in the Department of Zoology, University of British Columbia, Canada. I am thankful to Dr. G. G. E. SCUDDER for his help during the progress of the work. Dr. C. J. DRAKE of the United States National Museum kindly identified the species of *Saldula.* I am grateful to Dr. W. F. BARR and Mr. A. R. GITTINS for reading the manuscript and giving me the benefit of their criticisms.

Furthermore, I am indebted to the Nederlandsche Entomologische Vereeniging (Netherlands Entomological Society) which kindly accepted this paper for publication.

VI. SUMMARY

The systematic position of the Saldidae is controversial. SCUDDER (1959) suggested a close relationship between the Saldidae and the Mesoveliidae, based on his studies of their female genitalia. The morphology of these two families has been studied to throw some light on their probable relationship. It was found that these two families are distinct morphologically. Their systematic position has been considered elsewhere (GUPTA, in press).

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"Mosely (1932) says...." or "(Mosely, 1932)".

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DEEL 106 AFLEVERING 4 1963

TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

INHOUD:

R. STRAATMAN. — Observations on migration in certain Australian Lepidoptera, pp. 197—199.

Tijdschrift voor Entomologie, deel 106, afl. 4. Gepubliceerd 15-V-1963

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OBSERVATIONS ON MIGRATION IN CERTAIN AUSTRALIAN LEPIDOPTERA

BY

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In Australia several species of Lepidoptera are known to have migratory habits. WILLIAMS (1930) lists the following.

Catopsilia pomona pomona Fabr.
C. crocale Cramer
C. pyranthe pythias Waterhouse & Lyell
Appias paulina ega Boisduval
Anaphaeis java teutonia Fabr.
Delias nigrina Fabr.
D. harpalyce Donovan
Terias smilax Donovan
Danaus plexippus L.
D. chrysippus petilia Stoll.
D. hamata hamata Macleay
D. affinis affinis Fabr.
Acraea andromacha Fabr.
Vanessa cardui kershawi McCoy
Badamia exclamationis Fabr.

The author had an opportunity to make a few observations on migration of Lepidoptera which may prove to be of some value for other students. These observations were made in the area between Ingham and Tully in north-eastern Queensland (17—18° S.L.) in the years 1960—1961. The rainy season in those years was unusually dry.

Towards the middle of March, 1961, *Badamia exclamationis* Fabr., a Hesperid well known for its migratory habits, appeared in increasing numbers, flying constantly in a north-north-westerly direction. The migration reached its peak in the second half of April; a rough count yielded a total of 85—100 specimens per minute crossing a stretch of approximately 80 yards of the main road, about one mile from the sea shore between Ingham and Tully. Very few were seen feeding at this site, but on the same day and again later in the month, in areas near rain forests overgrown with *Lantana* many thousands of specimens were seen feeding at flowers or drinking from moist sandy river banks, while many others were resting on the underside of leaves. At Ingham several specimens were caught in a light trap, suggesting that they were still active after nightfall. By the end of April their numbers had decreased considerably, and from then on, only odd specimens were seen, feeding actively but not migrating. No specimens were seen mating or ovipositing and no larvae were found. Of a few specimens caught in June, females were somewhat predominant. It is not known, whether these specimens, which were slightly worn, were hibernating.

The butterfly *Danaus hamata* Macleay was also abundant in the same area of north-eastern Queensland. This species has a wide distribution in the Indo-Malayan and Australian regions where it is represented by several races. From mid-February odd specimens were seen flying consistently in a north-north-westerly direction. Their number increased slowly but steadily, and their flight reached a peak by mid-April. Rough counts made in April yielded a total of 55 to 65 specimens per minute passing over a stretch of about 70 yards of road near Ingham. On several occasions specimens were also taken in a light trap. A few specimens of *Euploea eichhorni* Staudinger and *E. corinna corinna* Macleay, were included in these flights.

At Forest Beach, 12 miles east of Ingham, these butterflies were seen flying towards the land from high over the sea, but on reaching the shore they dropped to near ground level where many were found resting on scrubs and mangroves. Little or no feeding was observed. At Mission Beach, 17 miles northeast of Tully where rain forest grows near the beach, thousands of specimens were found in the late afternoon clustering on small twigs, generally in clearings of the rain forest sheltered from the wind. In the morning large numbers were observed feeding on *Lantana* flowers and others were gathered around puddles on the road.

As the season advanced, the number of migrating specimens decreased slowly, although as late as June odd specimens were still flying in a north-north-westerly direction. When migration was in progress, neither mating nor oviposition was observed nor were any larvae found.

The first report about migratory flights of Australian butterflies comes from Captain COOK, who mentions that at Thirsty Sound, on the East Coast of New South Wales, he found an incredible number of butterflies "so that for the space of three or four acres the air was so crowded with them that millions were to be seen in every direction at the same time that every branch and twig was covered with others that were not upon the wing". In "Survey of the Coasts of Australia", Captain KING reports that at Cape Cleveland as well as at other places where he landed, "the air was crowded with a species of butterfly, a great many of which were taken", and which he thought to belong to the same species recorded by Captain COOK in Thirsty Sound. He further reports that this species was described by Macleay as *Euploea hamata.* (Both reports are mentioned by McKEOWN, 1944).

In the second half of June, at Forest Beach near Ingham, many thousands of Danaid butterflies were found clustering on dry branches of the "paper-bark tree", *Melaleuca leucodendron*, which grows in and around swamps, about half a mile from the sea shore. The dry conditions had caused the swamps to dry up, making observations easy. Other specimens were found sheltering on the underside of dry *Pandanus* and other leaves. Most specimens were *Danaus hamata*, the majority of which were females, but there was a small percentage of two other species: *Euploea eichhorni* Staud. and *Hypolimnas bolina nerina* Fabr. During the warmer hours of the day many butterflies could be disturbed by walking beneath the trees, but *Hypolimnas bolina* remained inactive resting head downwards and antennae folded between the wings. As soon as the disturbed Danaidae started to fly they were attacked by birds, identified as the masked wood-swallow (*Artamus personatus*), which caught the butterflies in a swooping flight, consuming the bodies but dropping the wings. Large quantities of wings on the ground suggested that many butterflies had been destroyed by the birds. When a bird missed its prey, the butterfly dropped to the ground, usually remained motionless for several minutes and then escaped by slowly walking along the ground to take shelter in grass. Those which flew up again were often caught. Fryer (1913) and Williams (1927) recorded similar bird attacks on migrating *Danaus hamata septentrionis* and on *Euploea* species, by the drongo, *Dicrurus leucopygialis* and by a wood-swallow *Artamus fuscus*, in Ceylon. A well-known theory suggests that the representatives of the family Danaidae which usually are slow fliers, besides being conspicuously marked, would be distasteful to birds. It seems likely now that Danaidae are distasteful only to some species of birds or that they lose their distasteful properties while hibernating. Other Lepidoptera were collected in the same area by beating dry *Pandanus* leaves, which form dense, tent-like shelters around the trunks. Two species of Nymphalidae, *Hypolimnas bolina nerina* Fabr. and *H. alimena lamina* Fruhst. and one of Pieridae, *Catopsilia pomona* Fabr., were found in small numbers scattered throughout the area.

When disturbed the Nymphalids were quite inactive, generally dropping to the ground where they either remained motionless or sometimes flew a short distance. *Catopsilia* butterflies also flew only briefly before taking cover again. In these species both sexes were present. None was seen feeding or flying, unless disturbed, and their inactivity suggests that they were hibernating.

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Mosely, M. E., 1932. "A revision of the European species of the genus Leuctra (Plecoptera)". Ann. Mag. Nat. Hist., ser. 10, vol. 10, p. 1—41, pl. 1—5, figs. 1—57.

Text references to this list might be made thus :

"Mosely (1932) says...." or "(Mosely, 1932)".

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DEEL 106 AFLEVERING 5 1963

TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

INHOUD:

Tijdschrift voor Entomologie, deel 106, afl. 5. Gepubliceerd 15-V-1963

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SUPPLEMENT OP DE NAAMLIJST VAN DE IN NEDERLAND AANGETROFFEN THYSANOPTERA

DOOR

C. J. H. FRANSSEN & W. P. MANTEL

Instituut voor Plantenziektenkundig Onderzoek, Wageningen

In 1962 publiceerden wij in dit tijdschrift een beredeneerde naamlijst van in Nederland aangetroffen Thysanoptera. Intussen zijn er weer een aantal soorten bijgekomen, waaronder één geheel nieuwe, die onlangs door TITSCHACK (1962) beschreven werd. Veel van het ons ter beschikking staande materiaal werd verzameld door de heer P. VAN UDEN, die daardoor een belangrijke bijdrage heeft geleverd tot de kennis van de Nederlandse fauna.

Alvorens tot de behandeling van de nieuwe soorten over te gaan, moeten eerst een drietal correcties in de oorspronkelijke lijst worden aangebracht. Als soort no. 40 noemden wij *Odontothrips loti* Haliday; daarbij staat onder meer vermeld, dat in de collectie DOEKSEN 17 ♀ en 2 ♂ werden aangetroffen onder de naam *Odontothrips ulicis* Haliday. Wij hielden de betreffende dieren toen voor *O. loti* Haliday, doch achteraf blijkt het door DOEKSEN verzamelde materiaal te behoren tot de soort *Odontothrips cytisi* Morison, die nieuw is voor Nederland.

Onder de nummers 45 en 46 worden twee vertegenwoordigers van het geslacht *Rhopalandrothrips* genoemd, namelijk *consociatus* Targ.-Tozz. en *obscurus* Targ.-Tozz. Laatst genoemde soort, die door Dr. H. PRIESNER op naam was gebracht, is een synoniem van *consociatus*.

Tenslotte vermeldden wij onder no. 89 *Haplothrips juncorum* Bagnall. Deze determinatie is niet juist geweest; een zekere determinatie is echter niet mogelijk wegens het ontbreken van mannetjes.

Het aantal van 106 soorten in de naamlijst is hiermede teruggebracht tot 104, doch met de 22 hieronder te behandelen nieuwe tripsen, zijn er thans 126 soorten van Nederland bekend.

Veel dank zijn wij verschuldigd aan Prof. Dr. H. PRIESNER en Prof. Dr. E. TITSCHACK voor het verifiëren van het door ons gedetermineerde materiaal.

De opgesomde soorten zijn macropteer, tenzij anders vermeld.

TEREBRANTIA

AEOLOTHRIPINAE

Aeolothrips ericae Bagnall
Maastricht: 1.VIII.1962, 4 ♀ op *Genista pilosa* L. en 1 ♀ op *Reseda lutea* L.
Forma *meulleri* Priesner
Nunhem: 5.VI.1961, 3 ♀ op *Vicia cracca* L.; Haelen: 21.VII.1961, 7 ♀ op *Sarothamnus scoparius* (L.) Wimm. (leg. P. VAN UDEN); Kessel-Eik: 22.V.1962, 1 ♀ op *Cerastium arvense* L. (leg. P. VAN UDEN) en 3 ♀ op *Sarothamnus sco-*

parius (L.) Wimm.; 29.V.1962, 5 ♀ op *Sarothamnus scoparius* (L.) Wimm.; Neer: 29.V.1962, 2 ♀ op *Sarothamnus scoparius* (L.) Wimm. (leg. P. VAN UDEN).

Aeolothrips manteli Titschack
In totaal werden 68 stuks en 1 larve verzameld in de Amsterdamse waterleidingduinen te Vogelenzang (gem. Bloemendaal). Alle dieren werden gevonden op *Anchusa officinalis* L. met uitzondering van 1 ♀, dat werd aangetroffen op een *Verbascum*-soort. Het mannetje is nog niet bekend (FRANSSEN & MANTEL, 1963).

Aeolothrips propinquus Bagnall
Natuurreservaat „de Hamert": 30.VII.1962, 1 ♀ op *Echium vulgare* L.; Maastricht: 1.VIII.1962, 1 ♀ op *Echium vulgare* L.

Anaphothripina

Aptinothrips elegans Priesner
Deze aptere soort werd gevonden in de Amsterdamse waterleidingduinen te Vogelenzang (gem. Bloemendaal). Het mannetje is nog niet van Nederland bekend (FRANSSEN & MANTEL, 1963).

Thripina

Iridothrips mariae Pelikan
Al het materiaal werd verzameld te Venlo op *Typha latifolia* L. in 1962: 22.V, 3 ♀, 29.V, 5 ♀, 24.VII, 5 ♀ en 3 ♂, 6.VIII, 12 ♀ en 2 ♂.

Odontothrips cytisi Morison
Wageningen: 9.V.1937, 17 ♀ en 2 ♂ op *Sarothamnus vulgaris* Wimm. (coll. DOEKSEN); Kessel-Eik: 22.V.1962, 116 ♀ en 3 ♂ op *Sarothamnus scoparius* (L.) Wimm. en 1 ♀ op *Betula*-species; 29.V, 71 ♀ op *Sarothamnus scoparius* (L.) Wimm.; Venlo: 22.V.1962, 1 ♀ op *Typha latifolia* L. (leg. P. VAN UDEN); Tiel: 23.V.1962, 3 ♀ op *Typha latifolia* L. (leg. P. VAN UDEN); Neer: 29.V.1962, 76 ♀ op *Sarothamnus scoparius* (L.) Wimm. (leg. P. VAN UDEN) en 1 ♀ op *Sorbus aucuparia* L. (leg. P. VAN UDEN).

Odontothrips meliloti Priesner
Heel en Panheel: 1.IX.1958, 2 ♀ op *Melilotus officinalis* (L.) Lamk.; Venlo 10.VII.1962, 8 ♀ en 3 ♂ op *Melilotus officinalis* (L.) Lamk. (leg. P. VAN UDEN).

Odontothrips phaleratus Haliday
St. Odiliënberg: 21.VII.1961, 4 ♀ en 1 ♂ op grassen.

Taeniothrips kratochvili Pelikan
Er werd één brachypteer wijfje verzameld te Wolvega (FRANSSEN & MANTEL, 1962).

Thrips alni Uzel
Al het materiaal van deze soort werd in 1962 verzameld te Kessel-Eik op *Alnus incana* (L.) Moench.: 22.V, 36 ♀, 29.V, 18 ♀, 2.VII, 111 ♀ en 54 ♂.

Thrips minutissimus L.
Al ons materiaal behoort tot de forma *obscura* Coesfeld. Bloemendaal: 17.V.1961, 2 ♀ op *Anchusa officinalis* L. en 6.VI.1961, telkens één ♀ op *Anchusa officinalis* L. en op grassen; Wolvega: 8.VI.1961, 1 ♀ op grassen (Franssen & Mantel, 1962 en 1963).

TUBULIFERA

Cryptothripina

Cryptothrips nigripes O. M. Reuter
Forma brachyptera
Haelen: 25.VI.1962, 1 ♀ en 3 ♂ achter schors van *Malus*-species (leg. P. van Uden).
Forma macroptera
Haelen: 25.VI.1962, 4 ♀ achter schors van *Malus*-species (leg. P. van Uden).

Haplothripini

Haplothrips-species
Wolvega: 22.VI.1961, 1 ♀ op grassen (Franssen & Mantel, 1962).

Neoheegeria verbasci Osborn
Haelen: op *Verbascum*-species, 21.VII.1961, 111 imagines en 425 larven; 14.VIII.1961, 19 imagines, 149 larven, 22 voorpoppen en 109 poppen; Wellerlooi: 2.VII.1962, 7 ♀ en 5 ♂ op *Verbascum*-species.

Xylaplothrips subterraneus J. C. Crawford
Wageningen: 25.XI.1960, 71 imagines op bollen van een *Lilium*-species.

Phlaeothripina

Hoplandrothrips bidens Bagnall
Kesteren: 23.VIII.1961, 1 ♀ op *Symphoricarpos rivularis* Suksd. (leg. P. van Uden).

Hoplandrothrips williamsianus Priesner
Kesteren: 23.VIII.1961, 2 ♀ op *Symphoricarpos rivularis* Suksd. (leg. P. van Uden).

Phlaeothrips annulipes O. M. Reuter
Wolvega: 25.V.1961, 1 ♀ op grassen (Franssen & Mantel, 1962).

Poecilothrips albopictus Uzel
Forma brachyptera
Wageningen: 9.VI.1962, 32 ♀ achter schors van *Fagus sylvatica* L. (leg. R. COBBEN).
Forma macroptera
Wageningen: 9.VI.1962, 15 ♀ achter schors van *Fagus sylvatica* L. (leg. R. COBBEN).

Cephalothripina

Cephalothrips monilicornis O. M. Reuter
Forma aptera
Bloemendaal: op grassen, 6.VI.1961, 9 ♀, 16.VI.1961, 2 ♀ en 1 larve, 12.VII. 1961, 2 imagines, 10.VIII.1961, 20 imagines, 8.VI.1962, 16 imagines.
Forma macroptera
Bloemendaal: 10.VIII.1961, 1 ♀ op grassen.

Hoplothripina

Hoplothrips longisetis Bagnall
Lichtenvoorde: 31.X.1961, 2 ♀ achter schors van *Quercus*-species (leg. P. VAN UDEN); Aerdenhout: 26.I.1962, 1 ♀ achter schors van *Quercus*-species.

Hoplothrips ulmi F.
Forma brachyptera
Bleiswijk: 28.VIII.1961, 6 ♀ en 2 ♂ achter schors van *Prunus avium* L. (leg. P. VAN UDEN).
Forma macroptera
Grollo: 10.VI.1961, 2 ♀ op grassen onder *Ulmus carpinifolia* Gled.; Bleiswijk: 28. VIII.1961, 5 ♀ achter schors van *Prunus avium* L. (leg. P. VAN UDEN).

SUMMARY

A supplement is given to the list of Thysanoptera (*Tijdschrift voor Entomologie*, 1962, vol. 105, p. 97—133). The material has been collected in 1961 and 1962 by Mr. P. VAN UDEN and both the authors of this paper. Up to now 126 species have been found in the Netherlands.

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DEEL 106 AFLEVERING 6 1963

TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

INHOUD:

Tijdschrift voor Entomologie, deel 106, afl. 6. Gepubliceerd 19-VIII-1963

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PARADOXOSOMATIDAE FROM BORNEO (DIPLOPODA, POLYDESMIDA)

BY

C. A. W. JEEKEL

Zoölogisch Museum, Amsterdam

INTRODUCTION

In comparison with the numbers of Paradoxosomatidae*) known to occur in Java or Sumatra, remarkably few species of this family have been recorded from Borneo. In all, the faunistic list of the island included the following species:

Orthomorpha beaumontii (Le Guillou)
Orthomorpha coarctata (Sauss.)
Orthomorpha rotundata Att.
Orthomorpha borneona Att.
Orthomorpha kuekenthali (Att.)
Pratinus fasciatus (Att.)
Euphyodesmus gracilis Att.
"*Strongylosoma*" *nodulosum* Att.

Of these species, *O. beaumontii* was described in 1841 in a way which rendered its identity and relationship largely a matter of speculation. Similarly, "*S.*" *nodulosum,* because of having been based on a female specimen, always remained a species of doubtful status. *O. coarctata*, finally, is a circumtropical ubiquist, which probably does not belong to the autochthonous fauna of the island. In reality, therefore, there remained but five species to show us the particularities of the Paradoxosomatid fauna of Borneo.

That this small number of species represented a negligible portion of the local fauna was revealed to me by the study of a rather large amount of material of Paradoxosomatidae from Borneo which I found in various lots of unidentified millipeds received in loan from the Museums of Bogor, Leiden, and Stockholm. The collections under consideration cover the eastern, central and western parts of Borneo and were made in particular by Dr. A. W. NIEUWENHUIS, in the course of several Dutch Borneo Expeditions of some sixty years ago, by Dr. E. MJÖBERG during the middle twenties and, more recently, by Mr. A. M. R. WEGNER. For the loan of these valuable collections I am very much indebted to the authorities of the above mentioned Museums, and in particular to Miss A. M. BUITENDIJK † (Leiden), Mr. L. J. M. BUTOT (Bogor) and Dr. R. MALAISE (Stockholm).

My thanks are also due to Dr. M. VACHON (Paris) for enabling me the re-examination of the type specimen of *Orthomorpha beaumontii.*

The present study not only multiplies the number of known species but also shows that Borneo has a Paradoxosomatid fauna which, although having general

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*) The name Paradoxosomatidae Daday, 1889, has priority over Strongylosomatidae, Cook, 1895.

southeast Asiatic features, is characterized by a large percentage of endemic genera. In fact, the examination of the material under report has revealed the existence of several generic categories not recognised previously. Especially the species hitherto referred to *Orthomorpha* upon closer study have proved to belong to various groups of questionable interrelationship. In order to arrive at a better taxonomy, it has been deemed necessary to separate generically these groups from *Orthomorpha*.

The possibility that some of the proposed generic names in the future will prove to have only subgeneric value has, of course, to be left open. For the present it seems better to refrain from a more refined taxonomy in a group where so many forms apparently await discovery.

For similar reasons I have abstained from using a trinary nomenclature. In general, the decision by previous authors on what constitutes a subspecies appears to have been influenced by the degree of morphological differentiation rather than by genetic and geographical coherence. In the present paper several instances can be found where morphologically very similar forms occur in one locality. Not seldom the differences between such forms, to be looked upon as "good" species, are less significant than those between two forms which may represent geographically vicarious populations. I have mentioned, as a rule, the possibility of subspecific relationship where necessary.

With the present additions the list of Paradoxosomatidae of Borneo reads as follows:

DESCRIPTIONS

Kalimantanina gen. nov.

Generic diagnosis. — 20 segments. Poreformula normal. Head without particulars; labrum tridentate. Antennae rather long.

Segments moderately (♀) or rather strongly (♂) constricted. Prosomites with fine cellular structure, somewhat dull. Waist of moderate width, strongly longitudinally ribbed in the dorsal half of the segments, finely and rather widely striate in the ventral half dorsad of the sternal level. Metatergites shining, hairless or with few hairs, without sculpture. Transverse furrow distinct but not very deeply impressed, finely longitudinally striate, present from the 5th segment onwards. Pleural keels well developed in a number of segments in the anterior half of the body.

Lateral keels rather weakly developed, posteriorly rounded on nearly all segments and projecting behind the posterior margin of the metasomite only in the 2nd segment, or, eventually, also very slightly in the 18th and 19th segments. Keels of 2nd segment well below the level of those of the next segment.

Sternites with moderately to well developed cross-impressions, longer than wide (♂) or about as long as wide (♀), rather weakly to moderately setiferous. Sternite of 5th segment of ♂ with a well developed, distally laminate process between the anterior legs. Sternite of 6th segment of ♂ somewhat modified: only its anterior part somewhat raised above the ventral surface of the metasomal ring. Sternite of 7th segment of ♂ with on each side a latero-anterior sublongitudinal ridge-like protuberance. Sternite of 8th segment of ♂ not modified. Legs rather long; the distal part of the tibiae and the tarsi of at least some of the anterior legs of the ♂ with brushes.

Gonopods with coxa of moderate size, straight-cylindrical, with the distal end slightly bent caudad; latero-anterior side of the distal end with a setiferous area. Prefemur somewhat elongate, almost in one line with the femur and laterally well demarcated from that joint, the demarcation oblique on the longitudinal axis of the femur. Femur straight, well developed, about as long as coxa or somewhat longer. Postfemur not demarcated. Spermal channel running more or less straight along the anterior or medio-anterior side of the femur towards the base of the solenomerite. Solenomerite long, flagelliform, arising from the anterior side of the distal end of the femur. From the medio-anterior side of the femur, more or less near the base of the solenomerite, or from the solenomerite itself, directly mesad of the course of the spermal channel, arises a rather long, lanceolate or spiniform process. Tibiotarsus springing from the posterior side of the distal end of the femur, well developed, distinctly demarcated from the femur. Tibiotarsus consisting of a simple, more or less circular solenophore without accessory processes, curving into a posterior direction. Both lamina medialis and lamina lateralis well developed, sheathing the solenomerite for its greater part.

Type-species. — *Kalimantanina ruficeps* spec. nov.

Range. — Borneo.

Number of species. — Five.

Remarks. — In a previous paper (JEEKEL, 1953), in connection with the description of a new species, I have discussed already the heterogeneity within the genus *Sundanina* Att. In particular I then questioned the dominant taxonomic value previously attributed to the presence of one or more femoral processes in the gonopods of the species of that genus. When the general structure of the gonopods is taken into consideration, fundamental diversities are encountered which seem to exclude the possibility that the species of *Sundanina* really represent a monophyletic unity.

On account of the presence of a femoral process the species of *Kalimantanina* could have been referred to *Sundanina* in the broad sense of ATTEMS. However, pending a revision of the latter genus it seems more convenient to separate at once the homogeneous group of presently described Bornean species. As a matter of fact, there seems to exist no particular relationship between *Kalimantanina* and any of the known species of *Sundanina*. The genus is, however, closely related to *Borneonina* gen. nov.

Key to the species. — In general morphology the species of *Kalimantanina* are extremely similar. For their separation we have to rely mainly on the characters of the male gonopods.

1. Femoral process of gonopods arising well proximad of the base of the solenomerite and projecting scarcely distad of the base of the tibiotarsus ... . *K. decolorata* spec. nov.
— Femoral process arising from the base of the solenomerite, or from the solenomerite proper 2
2. Dorsum and sides of the somites black; head and anal valves of a contrasting reddish brown colour 3
— Dorsum and sides of the somites black, except the lateral keels and an area dorsad of these which are white. Head and anal valves not contrasting in colour 4
3. Femur of gonopods about as long as the coxa. Femoral process arising from the solenomerite. Tarsal brushes of the ♂ absent in the legs of the posterior half of the body .... *K. ruficeps* spec. nov.
— Femur about one and a half times as long as coxa. Femoral process arising just proximad of the base of the solenomerite. Tarsal brushes of the ♂ absent only in the last two pairs of legs .... *K. hirtitarsus* spec. nov.
4. Femur of gonopods about as long as the coxa. Femoral process spiniform. White area above the lateral keels about as broad as the keels .... *K. albonigra* spec. nov.
— Femur about one and a half times as long as coxa. Femoral process lanceolate. White area dorsad of the lateral keels only half as wide as the keels .... *K. ocellata* spec. nov.

Kalimantanina ruficeps spec. nov.

Material. — East Borneo: Pajan River (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 2 ♂, (2 ♀).

Colour. — Head reddish brown, very dark in the vertigial part. Antennae brownish yellow, the 6th joint growing very dark, almost blackish brown, towards the end. 7th joint also very dark, but the distal portion and the 8th joint whitish. Collum and subsequent segments black, the poriferous keels very dark brown around the pore. Ventral portion of somites brownish gray. Sternites and legs dirty pale yellow. Anal segment black, the tail growing brownish yellow towards the end. Valves and anal scale reddish brown.

Width. — Holotype ♂ 2.5 mm, other ♂ 2.6 mm; ♀ 3.2 mm and 3.4 mm.

Head and antennae. — Labrum narrowly and moderately emarginate. Clypeus rather weakly convex, moderately impressed towards the labrum. Lateral sides hardly emarginate. Surface of head shining, with some irregular wrinkles. Clypeal part of headplate rather dispersedly setiferous, a few bristles on the frontal part and two on the vertex. Antennal sockets separated by slightly more than the diameter of one socket or by about three fifths of the length of the 2nd antennal joint. Postantennal groove shallow, the wall in front moderately prominent. Vertex moderately convex, not demarcated from the frontal area. Sulcus moderately impressed, with some transverse wrinkles, reaching downward to about the upper level of the sockets. Antennae not particularly slender. Length of joints decreasing very slightly from the 2nd to the 5th, the 6th joint somewhat more distinctly shorter than the 5th, about two thirds of the length of the 2nd. Joints of subequal width, the 6th very slightly thicker than the others. Antennal joints moderately to rather densely setiferous.

Collum. — (fig. 1—2). Sligthly narrower than the head, subsemicircular in dorsal outline. Anterior border evenly rounded, posterior border widely and rather weakly emarginate. Lateral sides rather widely rounded. Surface smooth and shining, longitudinally as well as transversely moderately convex; a few hairs may be present. Lateral and latero-anterior border with a fine marginal rim, gradually disappearing towards the middle of the anterior border.

Body segments. — Metatergites mostly hairless. Transverse furrow present up to the 17th segment, extending laterad to about halfway the dorsal delimitation of the lateral keels in most segments. Sides rugulose and dispersedly granulate up to the 4th segment, only weakly rugulose from the 5th segment onwards. Pleural keels present up to the 7th segment, totally absent from the 8th segment onwards. Up to the 4th segment these keels are represented by complete ridges which are posteriorly produced into a well developed angular lappet projecting behind the posterior margin of the somites. From the 5th segment onwards the pleural keels are present only on the posterior half of the segments and the posterior lappet becomes smaller, projecting very slightly behind the margin of the somite in the 5th segment only.

Lateral keels. — (fig. 1—4). 2nd segment somewhat wider than the collum. The keels anteriorly somewhat shouldered at the base, the anterior and posterior edges rounded, the posterior edge projecting slightly behind the border of the segment. Marginal rim rather weakly developed. 3rd and 4th segments of subequal width, slightly narrower than the 2nd. The keels anteriorly widely, posteriorly somewhat more narrowly rounded, ventrally demarcated only in their posterior half. 5th segment distinctly wider than the 4th. Keels from the 5th segment onwards anteriorly and posteriorly widely rounded, especially in the poreless segments. Poriferous keels somewhat more prominent. Only in the 18th and 19th segments the keels have a minute acutely angular posterior edge, which, however,

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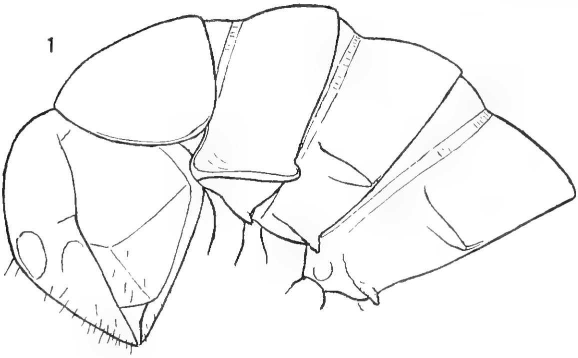

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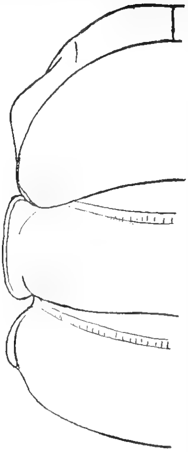

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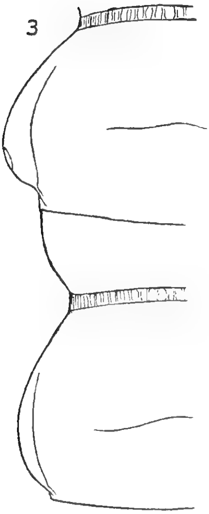

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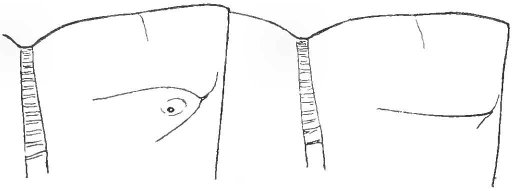

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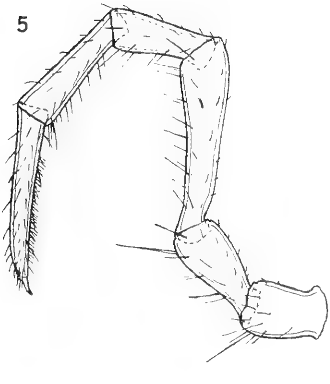

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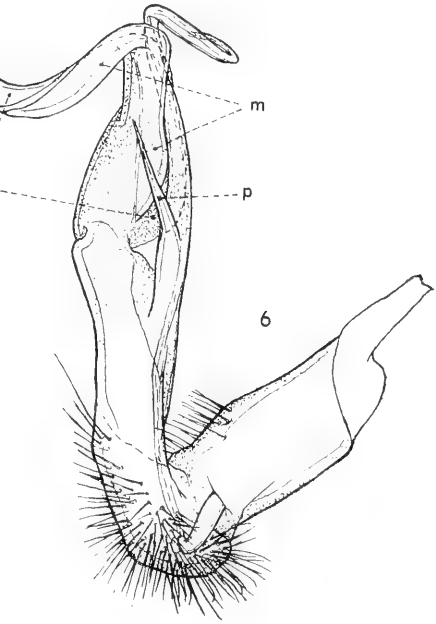

does not project behind the margin of the segments. Dorsal furrow of keels narrow, not reaching the waist. Seen from the lateral side the poreless keels have their dorsal margin slightly concave, the poriferous keels are somewhat convex. Poreless keels ventrally demarcated only near the posterior end, poriferous keels in the posterior half. Pores lateral, in a slight excavation, somewhat more near the ventral demarcation of the keels.

Sternites and legs. — Sternites of middle segments one and one third times as long as broad, rather weakly setiferous. Cross impressions rather wide, not sharply impressed. Sternite of 5th segment with a parallel-sided process directed cephaloventrad and projecting slightly before the anterior border of the sternite. End of process rounded and indistinctly bilobate by a very weak median incision, the anterior side densely set with short bristles. Behind the process a rather deep transverse furrow; between the posterior legs a normal longitudinal impression. Sternite of 6th segment posteriorly not raised above the ventral level of the metasomite; the anterior portion widely transversely concave and slightly longitudinally convex. Legs (fig. 5) moderately to, in tarsi, rather densely setiferous Tarsi and distal end of tibiae of the anterior legs with ventral brushes, which are rapidly thinning out in the subsequent legs and are absent in the legs of the second half of the body. Length of joints: $3>6>5>4 = 2>1$.

Anal segment. — Tail rather broad at its base, dorsoventrally rather thick, of moderate length. The sides rather strongly and straight converging; before the end a well developed lateral setiferous tubercle, the end truncate and scarcely emarginate. Anal segment with a very slight transverse depression at the base of the tail. Ventral side of tail somewhat concave. Valves with narrow rims, the setae on small tubercles. Scale triangular, the end truncate, the sides weakly concave. The setiferous tubercles at the posterior edges rather close to each other, projecting very weakly.

Gonopods. — (fig. 6). Femur of about the same length as the coxa. Femoral process (*p*) spiniform, arising from the solenomerite. Tibiotarsus relatively well developed, curving somewhat mesad and caudad, then proximad, and, finally, somewhat laterad.

Female. — In the tube containing the males of *ruficeps* and the holotype of *ocellata* there were two female specimens, obviously belonging to *Kalimantanina* and with some doubt referable to the former of the two species. These two ♀ differ from the ♂ of *ruficeps*, aside from the usual secundary sexual characters like the modifications of the sternites of the anterior segments, the brushes of the legs, etc., in the following particulars. Colour either faded or not fully developed: except for a very fine black middorsal stripe, entirely pale brownish yellow. The antennae have the distal half of the 6th and the proximal part of the 7th joint dark brown. Antennae somewhat more slender than in the ♂, the 6th

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Fig. 1—6. *Kalimantanina ruficeps* spec. nov. — 1: left side of the head and the four anterior segments of the holotype ♂, lateral view. 2: left side of the head and the three anterior segments of the holotype ♂, dorsal view. 3: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 4: the same, lateral view. 5: leg of the 7th segment of the holotype ♂. 6: right gonopod of the holotype ♂, medial view. p: femoral process; l: lamina lateralis; m: lamina medialis. (The solenomerite has moved out of its natural position) joint being as wide as the proximal joints. Body segments comparatively less constricted in the waist, resulting in a more robust aspect of the animals. Pleural keels as in the ♂, but missing from the 7th segment onwards. The lateral keels are somewhat more prominent than in the ♂; the posterior edges of the keels of the 17th segment are minute but acutely angular. Sternites about as long as broad. Legs scarcely more slender than in the ♂.

Kalimantanina hirtitarsus spec. nov.

Material. — East Borneo: without nearer location (Coll. Dr. E. Mjöberg, Mus. Stockholm), 1 ♂ (holotype).

Differing from *ruficeps* in the following characters.

Colour. — On the whole a little darker, probably because of a somewhat better

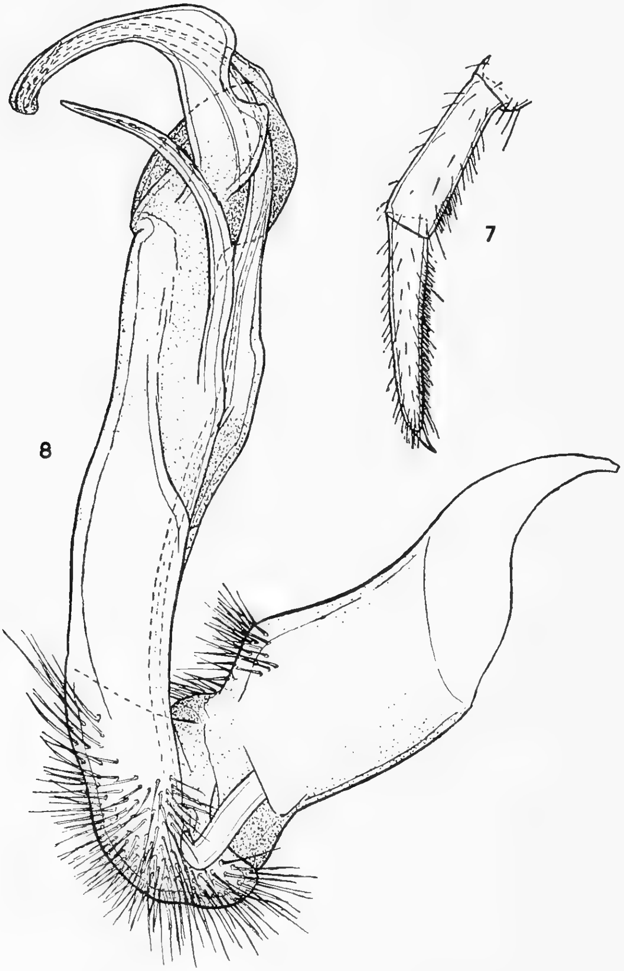

Fig. 7—8. *Kalimantanina hirtitarsus* spec. nov. — 7: tibia and tarsus of the leg of the 7th segment of the holotype ♂. 8: right gonopod of the holotype ♂, medial view

state of preservation. In the body segments only the venter is brownish gray. The end of the tail dark brown.

Width. — 3.1 mm.

Head and antennae. — Vertigial sulcus running downward nearly to the lower level of the antennal sockets.

Sternites and legs. — Legs (fig. 7) with tarsal and distal tibial brushes rather dense, gradually thinning out in the legs of the second half of the body, but absent only in the two ultimate pairs.

Gonopods. — (fig. 8). Femur about one and a half times as long as coxa. Femoral process serrulate, arising from the base of the solenomerite. Tibiotarsus relatively smaller than in *ruficeps*, curving medio-distad, caudad and a little proximad, and finally, latero-distad. Lamina medialis with an anterior emargination.

Female. — Unknown.

Remarks. — On the whole this species is so similar to *ruficeps*, that it might as well be regarded as a geographical race of the latter. However, as compared to the other species of the genus the differences in the gonopods of *ruficeps* and *hirtitarsus* are quite significant, and a specific treatment seems fully justified.

Kalimantanina ocellata spec. nov.

Material. — East Borneo: Pajan River (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 1 ♂ (holotype). East Borneo: without nearer location (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 3 ♂, 1 ♀.

Differing from *ruficeps* in the following characters.

Colour. — Head very dark brown, with only the labral area somewhat paler. Antennae dark castaneous, the distal part of the 7th and the 8th joints whitish. Groundcolour of collum and body segments very dark brownish gray to black. Lateral sides of collum and of the metasomites of the subsequent body segments with rather large, rather sharply demarcated, white spots, comprising the lateral keels and an area dorsad of these of about half the dorso-ventral width of a poriferous keel. Medial side of these spots rounded. Ventral side of body segments dark. Sternites yellowish; the legs brownish yellow, with the tarsi in the distal half shading to dark brown. In a few pairs of anterior legs the dark colour extends over the whole length of the tarsus and over the distal portion of the tibia. Anal segment dark brownish gray to black, valves and scale paler brown.

Width. — Holotype 3.2 mm, paratypes ♂ 3.0, 3.4 and 3.4 mm; allotype ♀ 3.8 mm.

Head and antennae. — Frontal area of head sometimes demarcated from vertex by a weak depression. Vertigial sulcus running downward to about the upper level of the antennal sockets, or continued below that level by a slight longitudinal impression.

Collum. — Posterior border at each side dorsad of the lateral roundings with a weak notch.

Body segments. — Pleural keels present up to the 7th segment, almost completely absent on the 8th. The posterior lappets projecting behind the posterior margins up to the 6th segment.

Lateral keels. — (fig. 9). Somewhat more prominent than in *ruficeps* or *hir-*

titarsus; the keels of the poreless segments have the posterior edges distinctly more narrowly rounded, they are ventrally demarcated in their posterior half. Keels of the 18th and 19th segments as in *ruficeps.*

Sternites and legs. — Sternites one and a half times longer than broad. Cross-impressions somewhat deeper. Sternal process of 5th segment with the sides weakly converging in the distal direction. Brushes of tibiae and tarsi as in *hirtitarsus*: absent only in the last two pairs of legs.

Anal segment. — Sides of tail somewhat less converging distally; the end somewhat more distinctly emarginate.

Gonopods. — (fig. 10). Femur about one and a half times as long as coxa, widening distad. Femoral process arising from the base of the solenomerite, elongate, laminate and more or less curving in a spiral. Tibiotarsus curving medio-distad, caudad and finally laterad and a little distad.

Female. — In the 5th to the 7th segments the pleural keels are somewhat less strongly developed than in the ♂. Sternites slightly longer than broad. The legs comparatively a little shorter than in the ♂.

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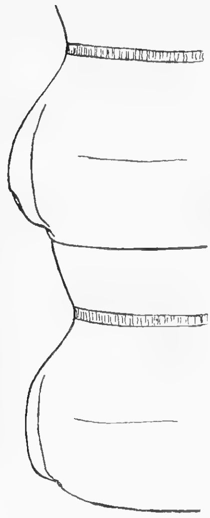

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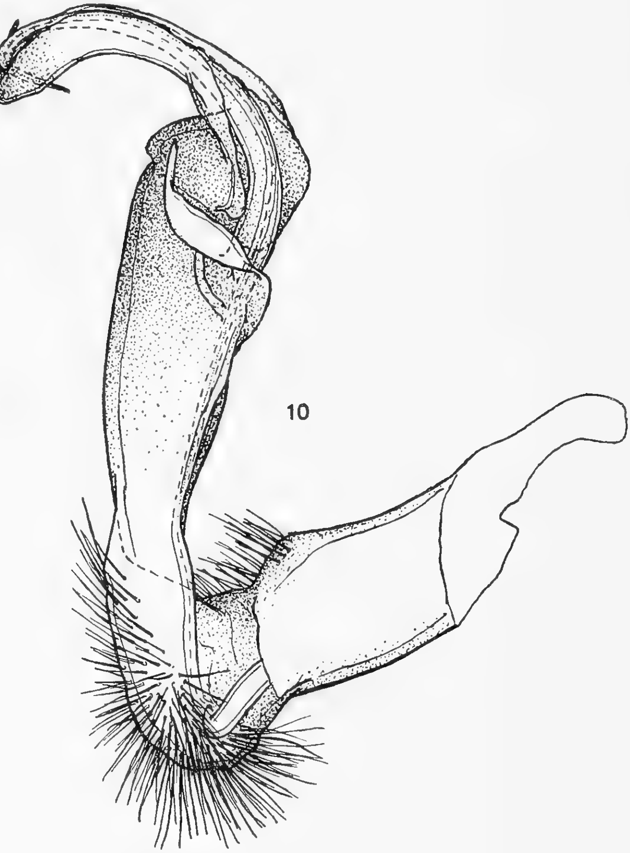


Fig. 9—10. *Kalimantanina ocellata* spec. nov. — 9: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 10: right gonopod of the holotype ♂, medial view

Remarks. — The gonopods in the three male paratypes are almost identical with those of the holotype. The telopodite, however, is slightly tortuous towards the lateral side, so that the femoral process slightly projects caudad of the femur.

Kalimantanina albonigra spec. nov.

Material. — East Borneo: Mt. Tibang, 1700 m (Coll. Dr. E. Mjöberg, Mus. Stockholm), 1 ♂ (holotype). East Borneo: without nearer location (Coll. Dr. E. Mjöberg, Mus. Stockholm), 1 ♂.

Differing from *ruficeps* in the following characters.

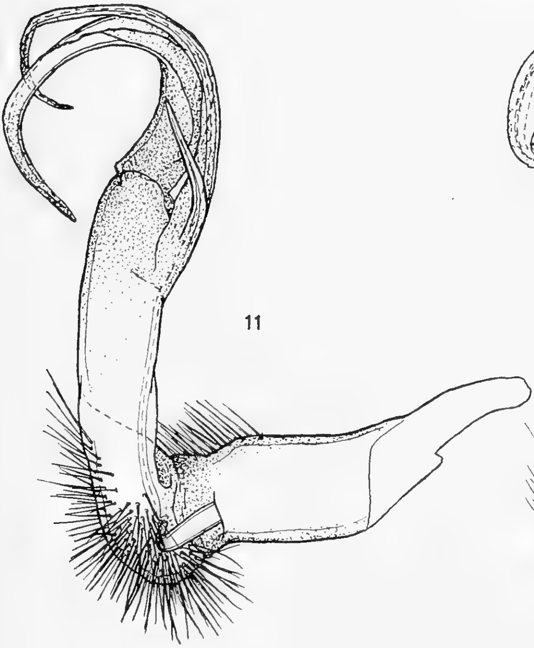
Colour. — As in *ocellata,* but the white lateral spots of the collum and metasomites are comparatively larger and embrace the keels and an area dorsad of these of about the dorso-ventral width of a poriferous keel. Legs paler: yellowish white.

Width. — Holotype 2.9 mm, paratype 2.7 mm.

Head and antennae. — Vertigial sulcus running downward to just below the upper level of the antennal sockets.

Collum. — Posterior border dorsad of the lateral roundings very weakly emarginate.

Body segments. — Pleural keels as in *ocellata.*



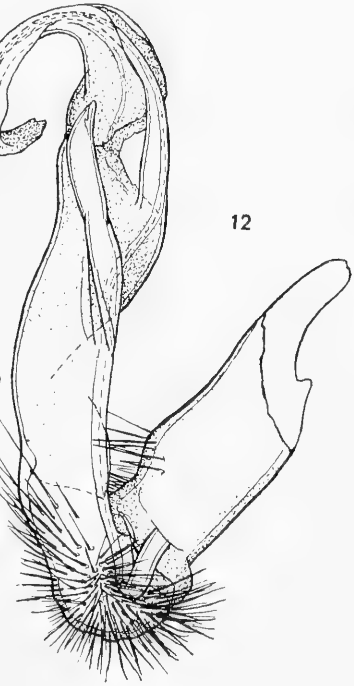


Fig. 11. *Kalimantanina albonigra* spec. nov. — right gonopod of the holotype ♂, medial view. (The solenomerite has moved out of its natural position). Fig. 12. *K. decolorata* spec. nov. — right gonopod of the holotype ♂, medial view

Lateral keels. — As in *ocellata*.

Sternites and legs. — Sternites and sternal process of the 5th segment as in *ocellata*. Brushes of tibiae and tarsi as in *hirtitarsus* and *ocellata*.

Anal segment. — Tail as in *ocellata*.

Gonopods. — (fig. 11). Femur and coxa of subequal length. Femoral process arising from the basal part of the solenomerite proper, spiniform. Tibiotarsus curving medio-distad, caudad and, finally, cephalo-proximad and somewhat laterad.

Female. — Unknown.

Remarks. — A similar remark as was made regarding the relationship between *ruficeps* and *hirtitarsus* applies to *ocellata* and *albonigra*. These two species also are very similar in colour and general morphology, although the gonopods are differing importantly. In this respect it is interesting to note the similarity of the gonopods of *albonigra* and *ruficeps*, two species otherwise rather disjunct.

A form closely related to *albonigra* was represented in the collection by a single male specimen from East Borneo (Coll. Dr. E. Mjöberg, Mus. Stockholm). It has a width of 2.3 mm, thus being considerably smaller than *albonigra*, and differs furthermore in the gonopods. In these the femur is relatively smaller than in *albonigra* and the tibiotarsus is making a wider curve. The rather poor state of preservation of the animal and the absence of an exact locality renders a description of this form useless.

Kalimantanina decolorata spec. nov.

Material. — West Borneo: Bungan River, July, 1894 (Borneo Exped., Coll. Dr. A. W. Nieuwenhuis, Mus. Leiden), 1 ♂ (holotype). East Borneo: Mahakkam River, Blu-u, November, 1898 (Borneo Exped., Coll. Dr. A. W. Nieuwenhuis, Mus. Leiden), 1 ♂.

Differing from *ruficeps* in the following characters.

Colour. — Possibly faded or not fully developed. Entirely pale brownish yellow. In the holotype only the 6th and a part of the 7th joints of the antennae dark brown. The paratype has the proximal joints also brown.

Width. — Holotype 2.9 mm, paratype 3.0 mm.

Head and antennae. — Vertigial sulcus running downward to just below the upper level of the antennal sockets.

Collum. — As in *albonigra*.

Body segments. — Pleural keels as in *ocellata*.

Lateral keels. — More prominent than in *ruficeps* and thus more resembling those of *ocellata* except that the lateral margins when seen from the dorsal side are somewhat less rounded. On the other hand the posterior edges are more pronounced and rather narrowly rounded; in the keels of the 18th and 19th segments the posterior edges are minutely angular and projecting a little behind the posterior margin of the segments.

Sternites and legs. — Sternites as in *ocellata;* the sternal process of the 5th segment as in *ruficeps* but more distinctly bilobate at the distal end. Brushes of tibiae and tarsi as in *ocellata*.

Anal segment. — Sides of tail somewhat more concave at the base, scarcely converging in the distal part. The end more distinctly emarginate than in *ocellata*.

Gonopods. — (fig. 12). Femur about one and a half times as long as coxa. Femoral process elongate-laminate, slightly constricted in the middle, arising about halfway the femur and thus distinctly proximad of the base of the solenomerite. Tibiotarsus comparatively small, curving medio-distad, caudad, proximad, and, finally, cephalad and somewhat laterad.

Female. — Unknown.

Remarks. — Future collecting may show whether the specimen from Blu-u, which differs from the type specimen only by the colour of the antennae, belongs to a distinct subspecies.

Borneonina gen. nov.

Generic diagnosis. — 20 segments. Poreformula normal. Head without particulars; labrum tridentate. Antennae rather long.

Segments rather strongly constricted. Prosomites with fine cellular structure, somewhat dull. Waist rather broad, strongly longitudinally ribbed in the dorsal half, finely and rather widely striate in the ventral half dorsal of the sternal level. Metatergites shining, hairless or with very few hairs, without sculpture. Transverse furrow distinct but not deeply impressed, finely longitudinally striate, present from the 4th segment onwards. Pleural keels present on a number of anterior segments.

Lateral keels weakly developed, posteriorly rounded in nearly all segments, projecting behind the posterior margin of the metasomite in the 2nd segment only. Keels of 2nd segment well below the level of those of the next segment.

Sternites longer than wide, scarcely to dispersedly setiferous, with moderately developed cross impressions. Sternite of 5th segment with a well developed, distally laminate process between the anterior legs. Sternite of 6th segment somewhat modified only in the posterior part. Sternite of 7th segment with on each side a latero-anterior sublongitudinal ridge-like protuberance. Legs rather long, without distinct tibial or tarsal brushes.

Gonopod-coxa of moderate size, straight-cylindrical, latero-distal surface with a setiferous area. Prefemur rather short, almost in one line with the femur and laterally well demarcated from that joint, the demarcation almost transverse on the longitudinal axis of the femur. Femur straight, well developed, somewhat longer than the coxa. Postfemur weakly demarcated. Spermal channel running straight along the medio-anterior side of the femur towards the base of the solenomerite. Solenomerite rather short, flagelliform, arising from the anterior side of the distal end of the femur. From the medio-anterior side of the distal end of the femur, mesad of the course of the spermal channel arises a rather long, lanceolate process. Tibiotarsus arising from the posterior side of the distal end of the femur, comparatively small, distinctly demarcated from the femur. Tibiotarsus consisting of a simple solenophore, straight with only the distal end curving a little cephalad. Lamina medialis and lamina lateralis both present, the latter more strongly developed than the former, sheathing the greater part of the solenomerite.

Type-species. — *Borneonina retrorsa* spec. nov.

Range. — Borneo.

Number of species. — One.

Remarks. — The general morphology of this genus is in close agreement with that of *Kalimantanina. Borneonina* is separated particularly because of the different shape of the tibiotarsus of the gonopods. In *B. retrorsa* the tibiotarsus is notably smaller than in *Kalimantanina*, and it is curved in a direction opposite to that found in the latter genus. There seems to exist no particular relationship between *Borneonina* and any of the previously described species of *Sundanina.*

Borneonina retrorsa spec. nov.

Material. — West Borneo: Bungan River, July, 1894 (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 1 ♂.

Colour. — Probably faded. Pale brownish yellow, with on each side on keel-level a continuous brownish longitudinal band of the width of the poriferous keels. There is also an indication of the presence of a continuous middorsal brownish band, apparently widest in the middle of the pro- and metasomites.

Width. — 2.1 mm.

Head and antennae. — Labrum narrowly and rather weakly emarginate. Clypeus moderately convex, moderately impressed towards the labrum. Lateral sides scarcely emarginate. Surface of head smooth and shining. Clypeus and frons rather dispersedly setiferous, vertex with two setae. Antennal sockets separated by slightly more than the diameter of a socket, or by three fifths of the length of the 2nd antennal joint. Postantennal groove shallow, the wall weakly prominent. Vertex moderately convex, not demarcated from the frontal area. Sulcus rather weakly impressed, reaching downward to the upper level of the antennal sockets. Antennae not particularly slender. Length of joints decreasing very slightly from the 2nd to the 6th, the 6th joint about three quarters of the length of the 2nd. Joints of subequal width, the 6th a little thicker than the others. Antennal joints moderately to rather densely setiferous.

Collum. — (fig. 13—14). Slightly narrower than the head, subreniform in dorsal outline. Anterior border very weakly rounded in the middle, somewhat more strongly so towards the sides. Posterior border widely and weakly emarginate, somewhat convex laterally. Lateral sides rather widely rounded, caudally with a weak indication of a blunt posterior edge. Surface smooth and shining, longitudinally as well as transversely moderately convex; a few hairs present. Lateral and latero-anterior border with a fine marginal rim, disappearing gradually towards the middle.

Body segments. — Metatergites mostly hairless. Transverse furrow present from the 4th to the 18th segment, but weakly impressed on the 4th. Furrow reaching to almost one third from the dorsal demarcation of the lateral keels in most segments. Sides somewhat rugulose and dispersedly granular up to the 4th segment, smooth and almost without wrinkles from the 5th onwards. Up to the 4th segment the pleural keels are well developed ridges, which are posteriorly produced into an angular lappet which projects weakly behind the posterior margin of the somites. On the 5th and the 6th segments there is only a very weak indication of the presence of pleural keels near the posterior margin of the somites.

Lateral keels. — (fig. 13—16). 2nd segment scarcely wider than the collum.

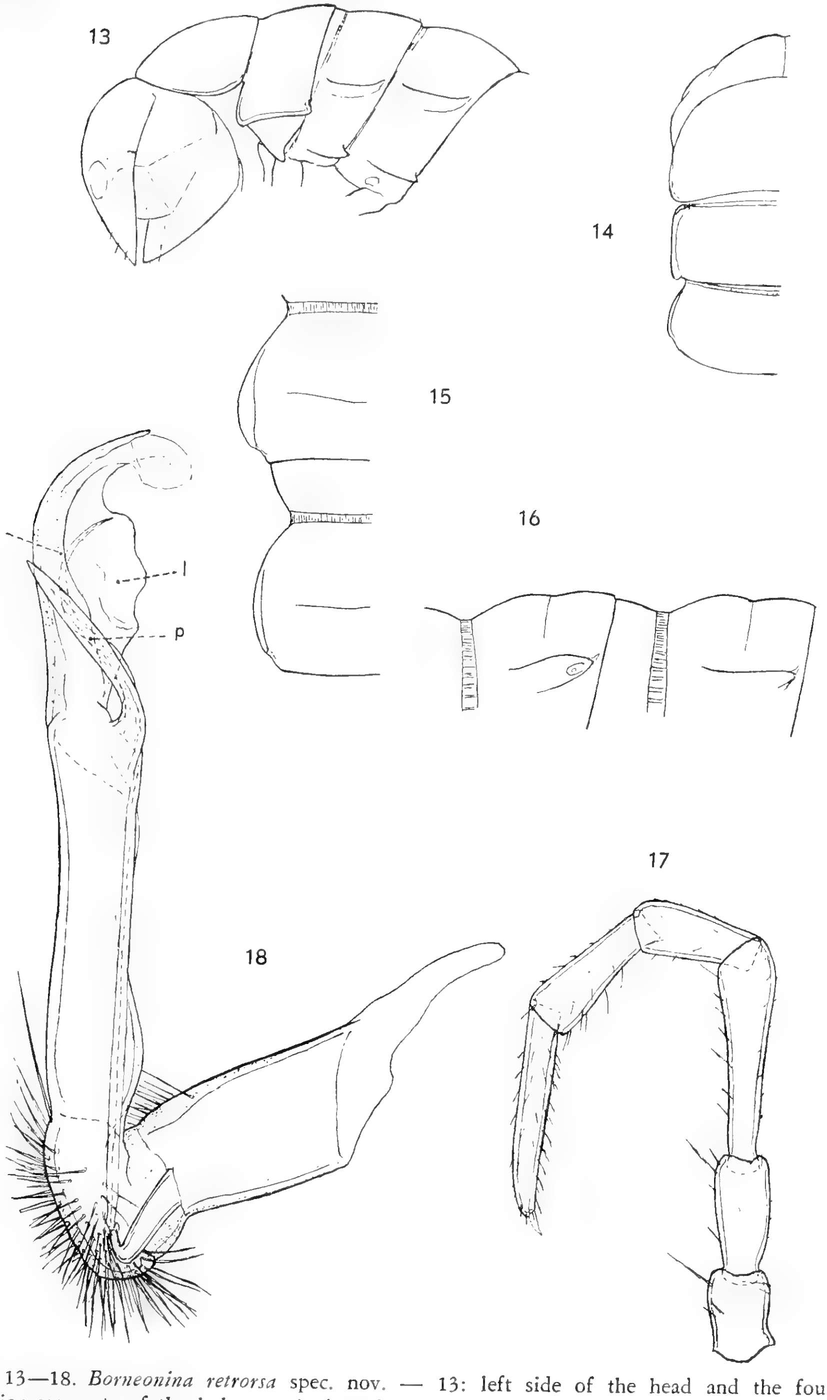


Fig. 13—18. *Borneonina retrorsa* spec. nov. — 13: left side of the head and the four anterior segments of the holotype ♂, lateral view. 14: left side of the head and the three anterior segments of the holotype ♂, dorsal view. 15: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 16: the same, lateral view. 17: leg of the 7th segment of the holotype ♂. 18: right gonopod of the holotype ♂, medial view. p: femoral process; l: lamina lateralis; m: lamina medialis

The keels anteriorly somewhat shouldered at the base, the anterior and posterior edges rounded, the posterior edge projecting slightly behind the border of the segment. Marginal rim rather weakly developed. 3rd and 4th segments of subequal width, slightly narrower than the 2nd. The keels anteriorly widely rounded, posteriorly somewhat more narrowly rounded. Ventrally they are demarcated only in their posterior half. 5th segment distinctly wider than the 4th. Keels from the 5th segment onwards anteriorly and posteriorly widely rounded, especially in the poreless segments. Poriferous keels somewhat more prominent. In the posterior half of the body the posterior edges of the poriferous keels become slightly more prominent and in the 18th and 19th segments they are minutely rectangular. Dorsal furrow of keels narrow, not reaching the waist. Seen from the lateral side the poreless keels have their dorsal demarcation slightly concave, the poriferous ones are weakly convex. Poreless keels ventrally demarcated only near the posterior end, poriferous keels in the posterior half. Pores lateral in a slight excavation, a little more near the ventral demarcation of the keels.

Sternites and legs. — Sternites $1^1/_3$ × as long as broad, mostly sparsely setiferous. Cross impressions distinct but not deep. Process of the sternite of the 5th segment with the sides parallel at the base, slightly convergent in the distal half. The process directed cephalo-ventrad and projecting slightly before the anterior border of the sternite. End of process rounded and deeply incised medially, without a brush of short setae, but normally setiferous. Behind the process a rather deep transverse furrow; between the posterior pair of legs a normal longitudinal impression. Sternite of 6th segment with a wide cross impression, the longitudinal impression caudally widening triangularly. Sternite of 8th segment without particulars. Legs (fig. 17) rather long; weakly to, in tarsi, moderately setiferous. Anterior legs somewhat more densely setiferous but none of them with brushes. Length of joints: $3 > 6 > 5 > 4 = 2 > 1$.

Anal segment. — Tail rather broad at the base, dorso-ventrally rather thick. The sides moderately converging, straight; before the end a well developed lateral setiferous tubercle. End of tail straight-truncate. Dorsal side of tail without a transverse depression, ventral side somewhat concave. Valves with narrow rims, the setae on small tubercles. Scale trapezoidal; the setiferous tubercles low and not projecting.

Gonopods. — (fig. 18). Femur about one and a half times as long as coxa. Lamina lateralis with an irregular margin.

Female. — Unknown.

Dajakina gen. nov.

Generic diagnosis. — 20 segments. Poreformula normal. Head without particulars. Antennae of moderate length to rather long.

Segments rather weakly to rather strongly constricted. Waist distinctly ribbed. Metatergites shining, hairless, without sculpture. Transverse furrow present from the collum or from the 5th segment onwards. Pleural keels weakly developed in a few anterior segments.

Lateral keels weakly developed. Only those of the 2nd segment projecting slightly behind the border of the metasomite, and situated well below the level of those of the 3rd segment.

Sternites longer than or as long as wide, moderately to rather weakly setiferous, with moderately developed cross impressions. Sternite of 5th segment of ♂ without process. Legs of moderate length to rather long. At least a few of the anterior legs of the ♂ with tarsal brushes.

Gonopod-coxa rather long, straight-cylindrical, the latero-distal surface with a setiferous area. Prefemur somewhat elongate, slightly oblique on the axis of the femur and laterally well demarcated from that joint, the demarcation almost transverse on the longitudinal axis of the femur. Femur almost straight, well developed, somewhat shorter than the coxa. Postfemur not demarcated. Spermal channel running along the medial side of the femur towards the base of the solenomerite, the latter arising from the anterior side of the distal end of the femur. Solenomerite of moderate length, flagelliform. Tibiotarsus arising from the posterior side of the femoral end, moderately developed, distinctly demarcated from the femur. Tibiotarsus consisting of a simple solenophore curving widely in a posterior direction. Lamina medialis and lamina lateralis well developed, sheathing the solenomerite for its greater part. Lamina medialis with a laminate process just proximad of the terminal end of the tibiotarsus.

Type-species. — *Dajakina oculata* spec. nov.

Range. — Borneo.

Number of species. — Two.

Remarks. — The erection of this genus, which besides the type-species also includes *Orthomorpha rotundata* Att., may be regarded as a first step towards a subdivision of the species so far included in the genus *Orthomorpha* Bollm. into natural categories. These species all agree in having a relatively simple gonopod structure, in which, for instance, the tibiotarsus is represented by a solenophore without or with very small secondary processes.

The simple structure of the gonopods and the fact that the gonopod characters in this group obviously belong to the more stable, which are subject only to minor changes in the course of speciation, have somewhat obscured the heterogeneity of *Orthomorpha*. However, several generic categories may be recognised when non-gonopod characters as well as the smaller details of the gonopods, such as the course of the spermal channel, the development of the laminae medialis and lateralis of the tibiotarsus, etc., are taken into consideration.

A more extensive discussion on the mutual affinities of the species of *Orthomorpha* is given in connection with the redescription of *O. beaumontii* (Le Guillou).

The genus *Dajakina* may be distinguished by a combination of characters of which must be mentioned: the weakly developed lateral keels, the weakly developed pleural keels, the absence of a sternal process in the 5th segment of the male, the lack of a sharply demarcated postfemur in the gonopods, the what may be called "normal" development of the laminae medialis and lateralis of the tibiotarsus of the gonopods and the conformation of the tip of the tibiotarsus. Little can be said of the relationship of the genus, apart from the general remark that it belongs to the *Orthomorpha-Pratinus* complex. The peculiar emarginations of the posterior borders of the segments occurring in the type-species of the genus remind of a similar structure described for *Sundanina spini-*

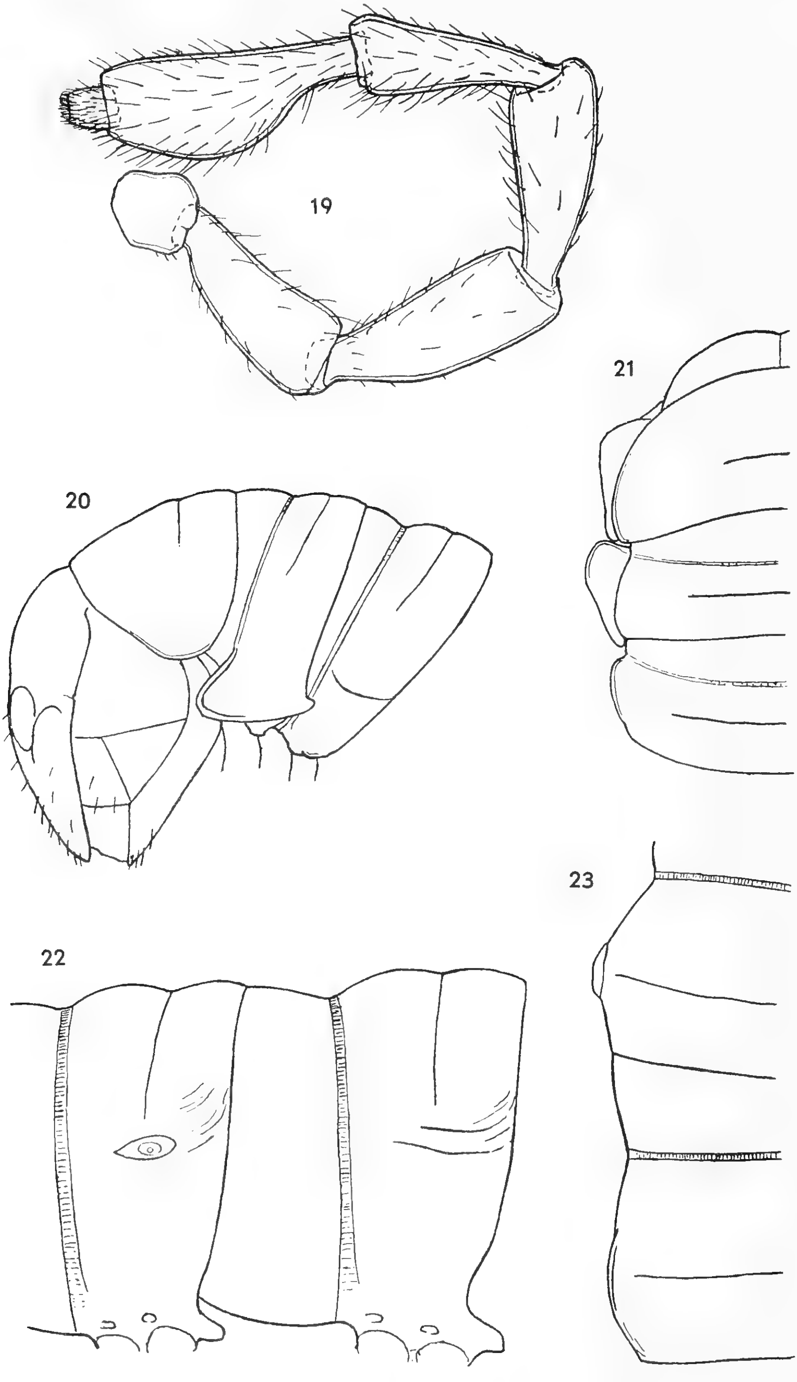


Fig. 19—23. *Dajakina oculata* spec. nov. — 19: antenna of the holotype ♂. 20: left side of the head and the three anterior segments of the holotype ♂, lateral view. 21: the same, dorsal view. 22: left side of the 10th and 11th segments of the holotype ♂, lateral view. 23: the same, dorsal view

pleura Carl from Birma and *Sundanina emarginata* Jeekel from Tonkin. In particular *S. emarginata* seems to come rather close to *D. oculata*, in the shape of these emarginations as well as in characters of the gonopods. In fact, it may be more closely related to *D. oculata* than to the type-species of the genus *Sundanina* and may represent the nearest relative of *D. oculata* outside Borneo. On the other hand it seems to have sufficient characteristic features not to be united in the same genus with that species.

Key to the species. — Contrary to the condition in *Kalimantanina* or *Arthrogonopus*, the species of *Dajakina* can hardly be separated on their gonopod characters. Other features, on the other hand, such as the shape of the lateral keels and various secondary sexual characters of the males provide ample possibilities for specific distinction.

1. Lateral keels of poriferous segments represented by low, more or less eye-shaped protuberances which are sharply demarcated on all sides. Transverse furrow of metatergites present from the collum to the 18th segment. Posterior borders of the 8th to the 18th segments of the ♂ with emarginations in the lower half of the sides and behind the sternites. Legs of the ♂, except the last two pairs, with tarsal brushes. Width of ♂ 4.0 mm .... *D. oculata* spec. nov.

— Lateral keels of poriferous segments low but normally ridge-like, only dorsally sharply demarcated by a furrow. Transverse furrow of metatergites present from the 5th segment onwards. Posterior borders of segments not emarginate. Tarsal brushes of ♂ present only in a few anterior pairs of legs. Width of ♂ 2.5 mm .... *D. rotundata* (Att.)

Dajakina oculata spec. nov.

Material. — West Borneo: Sambas, October, 1893 (Borneo Exped., Coll. Dr. Hallier, Mus. Leiden), 1 ♂.

Colour. — Possibly either faded or not fully developed: entirely pale brownish yellow. The distal part of the 6th and the proximal part of the 7th joints of the antennae dark brown.

Width. — 4.0 mm.

Head and antennae. — Labrum narrowly and rather deeply emarginate, tridentate. Clypeus rather weakly convex, moderately impressed towards the labrum. Lateral sides scarcely convex. Surface of head moderately shining, somewhat irregularly rugulose in the clypeal part. Clypeal and frontal part of headplate moderately to rather dispersedly setiferous, vertex with two bristles. Antennal sockets separated by three quarters of the diameter of one socket, or by about one third of the length of the 2nd antennal joint. Postantennal groove shallow, the wall in front of it moderately prominent. Vertex moderately convex, demarcated from the frontal area by a slight depression. Sulcus moderately impressed, with some transverse wrinkles, reaching downward to just below the upper level of the antennal sockets. (The lower end of the sulcus is marked by two minute contiguous tubercles. However, this may be an anomalous structure since the frontal area of the specimen studied was injured). Antennae (fig. 19) rather long, though not particularly slender. Length of the 2nd to the 5th joints subequal, the 6th joint notably longer. Width of the 2nd, 3rd and 4th joints subequal, the 5th joint somewhat narrower, the 6th conspicuously ventrally inflated. Antennal joints sparsely to moderately setiferous.

Collum. — (fig. 20—21). Narrower than the head, subreniform in dorsal outline. Anterior border weakly rounded in the middle, slightly more strongly so towards the lateral sides, laterally very weakly emarginate. Posterior border widely and very weakly emarginate in the middle, weakly convex towards the sides. Lateral sides rather widely rounded. Surface shining and somewhat uneven, a moderately impressed transverse furrow at one third from the posterior border. Surface hairless, weakly longitudinally and moderately transversely convex. Lateral and latero-anterior border with a fine marginal rim gradually disappearing towards the middle.

Body segments. — Rather weakly constricted. The waist rather narrow dorsally, somewhat widening laterally; dorsal half rather finely but distinctly longitudinally ribbed, ventral half, above the level of the sternites, finely striate. Prosomites

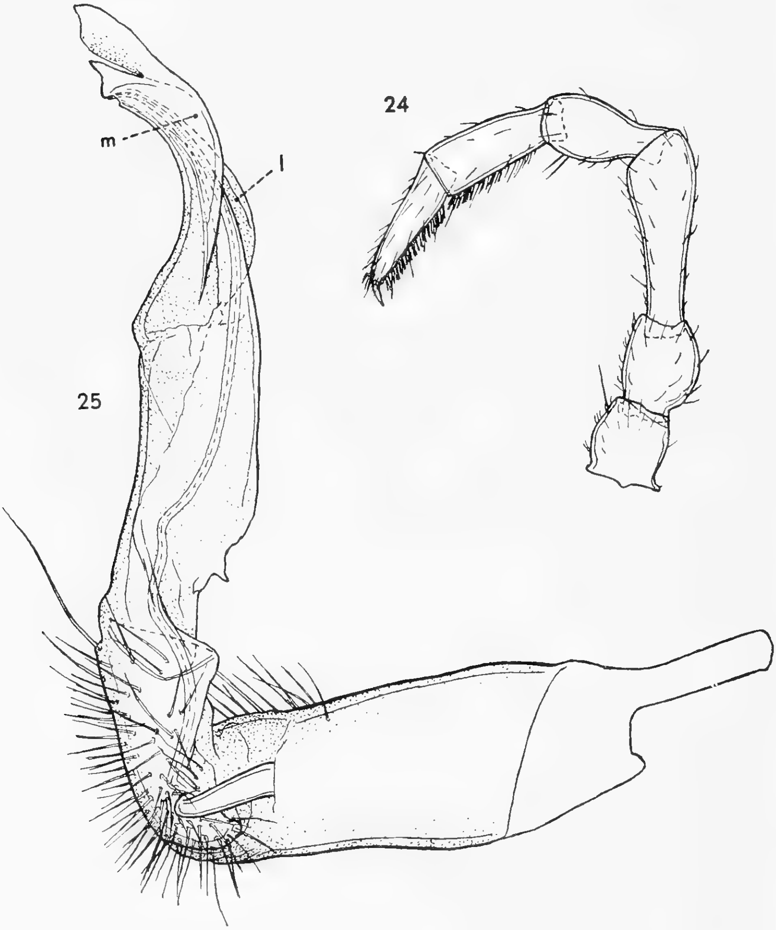


Fig. 24—25. *Dajakina oculata* spec. nov. — 24: leg of the 7th segment of the holotype ♂. 25: right gonopod of the holotype ♂, medial view; lamina lateralis; m: lamina medialis

with fine cellular structure, rather dull. Transverse furrow present on all segments up to the 18th, rather sharply and rather deeply impressed and in most segments almost reaching the dorsal delimitation of the lateral keels. Sides with fine and moderately dense granulation in all segments. Pleural keels up to the 4th segment represented by weak, curved, somewhat granular ridges on a slight swelling. On the 5th segment only a swelling is visible. From the 8th to the 17th segments, and also, though weakly, in the 18th segment, the posterior border of the metasomites in the ventral half of the sides as well as ventrally behind the sternites is rather strongly emarginate. As a consequence the posterior margin of these segments at the level of the stigmata appears rather strongly produced posteriorly, the produced part being somewhat inflated.

Lateral keels. — (fig. 20—23). 2nd segment distinctly wider than the collum. The keels anteriorly shouldered, their anterior edge rather widely, their posterior edges narrowly rounded; the posterior edge projecting a little caudad of the border of the segment. Marginal rim present only in the anterior half of the keels. 3rd and 4th segments of subequal width, distinctly narrower than the 2nd. The keels anteriorly somewhat more narrowly rounded than posteriorly. They are demarcated, dorsally only, by a narrow furrow. 5th segment distinctly wider than the 4th. Keels of poriferous segments represented by low eye-shaped protuberances, sharply demarcated on all sides. In posterior segments these protuberances become more elongate towards the anterior side. Pores lateral, in a slight excavation, almost in the middle of the keels. None of the keels angular. Poreless keels somewhat less prominent than the poriferous, represented by low, rather short longitudinal ridges, dorsally and ventrally demarcated by furrows, which do not reach the waist. Behind the keels some irregular wrinkles curving upwards.

Sternites and legs. — Sternites one and a half times longer than broad, moderately setiferous. Cross impressions well developed, rather wide, not sharply impressed. 5th segment without sternal process, but with a normal cross impression. Sternites of the 6th, 7th and 8th segments without particulars, except that in the 6th segment the sternite is slightly more concave between the posterior legs. Legs (fig. 24) of moderate length in the anterior part of the body, becoming distinctly more elongate in the posterior part. All legs distinctly incrassate, rather weakly to moderately setiferous. Dense ventral brushes are present on the distal part of the tibiae and on the tarsi of most of the legs. Brushes, in particular those of the tibiae, thinning out in the legs of the posterior part of the body, almost absent in the legs of the 17th and completely absent in the legs of the 18th segment. Brushes consisting of typically penicillate hairs. Length of the joints of the legs: $3>5>6>4>2>1$.

Anal segment. — Tail rather broad and thick and rather long. Sides not converging, even a little concave, before the end a weak lateral tubercle. End truncate and scarcely emarginate. No dorsal transverse depression at the base of the tail. Ventral side of tail hardly concave. Valves with narrow but rather high rims, the setae on small tubercles. Scale triangular, the posterior edge rounded, the sides almost straight. Setiferous tubercles low, not projecting.

Gonopods. — (fig. 25). Femur at the anterior side near the base with some notches. Tibiotarsus curving weakly in a posterior and somewhat medial direction.

Female. — Unknown.

Remarks. — A species very closely related to *oculata* was represented by two female specimens from East Borneo: Blu-u, Mahakkam River, November 1898 (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden). These females differ from *oculata* in particular by the shape of the lateral keels of the 2nd segment. In these the anterior edge is acutely angular, the lateral margin straight and the posterior completely absent. The two specimens are notably smaller than *oculata,* having a width of 3.3 mm and 3.1 mm, respectively. The antennal sockets are separated by somewhat more than the diameter of one socket. The antennae are of moderate length, the 6th joint has a quite normal shape. The transverse furrow is absent in the metatergites of the three anterior segments. The posterior borders of the segments lack the emarginations as described for *oculata.* The legs are of moderate length and width, and the tail is somewhat shorter than in *oculata.*

Considering the characteristic shape of the poriferous keels these female specimens must be closely related to *oculata.* It seems likely therefore that the peculiar structure of the 6th antennal joint, the emarginations of the posterior borders of the metasomites and the incrassate legs described here for *oculata* are secondary sexual characters of the male.

Dajakina rotundata (Att.)

1931 *Orthomorpha* (*O.*) *rotundata* Attems, Zoologica, Stuttg., vol. 30, fasc. 3/4, p. 116, fig. 175.

1937 *Orthomorpha* (*O.*) *rotundata,* Attems, Tierreich, vol. 68, p. 64, fig. 78.

Distribution. — West Borneo: Lebang Kara, Nanga Serawei.

Remarks. — The gonopods of this species, which was not represented in the collection under report, appear to be almost identical with those of *oculata.* Aside from some minor details they seem to differ only in the somewhat stronger curved tibiotarsus and the comparatively slightly shorter femur. In view of these scarcely significant differences it is highly interesting to note the important dissimilarities in the external morphology of the two species.

D. rotundata is a much smaller species than *oculata*, the width being 2.5 mm, as against 4.0 mm. The antennae are said to be of moderate length and width; no statement was made on the structure of the 6th joint, so that this joint probably lacks the conspicuous inflation described for *oculata.* The lateral keels of the poriferous segments were described as being small, short and dorsally demarcated by a furrow, which is not conform with the peculiar structure in *oculata.* Furthermore, the transverse furrow of the metatergites is present only from the 5th to the 18th segments in *rotundata.* The characteristic emarginations of the posterior border of the metasomites are not mentioned in the description of *rotundata.* Finally, contrary to the condition found in *oculata*, the legs of *rotundata* are stated to be long and slender, with the tarsal brushes present only in the anterior legs.

In all, the differences between *oculata* and *rotundata* reveal to what remarkable extent the non-gonopod characters may diverge evolutionally, without this divergence being paralleled by an important structural alteration in the gonopods.

Arthrogonopus gen. nov.

Generic diagnosis. — 20 segments. Poreformula normal. Head without particulars; labrum tridentate. Antennae rather long.

Segments moderately (♀) to rather strongly (♂) constricted. Prosomites with fine cellular structure, somewhat dull. Waist of moderate width (♂) to rather narrow (♀), strongly longitudinally ribbed in the dorsal half, finely and rather widely striate in the ventral half dorsad of the sternal level. Metatergites shining, hairless or with very few hairs, without sculpture. Transverse furrow distinct but not deeply impressed, finely longitudinally striate, present from the 5th segment onwards. Pleural keels well developed on a number of anterior segments.

Lateral keels rather weakly developed. In nearly all segments posteriorly rounded or minutely angular in a number of segments of the posterior half of the body. Only the keels of the 2nd segment projecting behind the posterior margin of the segment; eventually also the keels of the 19th segment very slightly projecting behind the margin. Keels of 2nd segment well below the level of those of the next segment.

Sternite with moderately developed cross impressions, longer than wide (♂) or about as long as wide (♀), moderately to rather weakly setiferous. Sternite of 5th segment of ♂ with a well developed process between the anterior legs. Sternite of 6th segment of ♂ somewhat modified: a little excavated especially in the posterior part. Sternite of 7th segment of ♂ with on each side a weak callous protuberance before the gonopod opening. Sternite of 8th segment of ♂ without particulars. Legs rather long; without tibial or tarsal brushes in the ♂.

Gonopods with coxa of moderate size to rather small, almost straight-cylindrical; latero-anterior side of the distal end with a setiferous area. Prefemur rather short, slightly oblique on the longitudinal axis of the femur and laterally well demarcated from that joint, the demarcation almost transverse on the longitudinal axis of the femur. Femur almost straight, well developed, somewhat longer than the coxa. In the basal half the femur has two laminate crests on the medial side. Postfemur laterally sharply demarcated. Spermal channel running along the medial side of the femur. In the basal part it runs along the posterior laminate crest towards the posterior side of the femur; more distally it runs towards the anterior side of the femur. At the medio-posterior side of the distal end of the femur a small femoral process or knob may be present. Solenomerite of moderate length, flagelliform, arising from the medio-anterior side of the distal end of the postfemur. Tibiotarsus springing from the posterior side of the distal end of the postfemur, distinctly demarcated from that joint. Tibiotarsus moderately to rather weakly developed, consisting either of a simple semicircular solenophore without accessory processes or of a solenophore which on the lateral side gives rise to a comparatively well developed secondary process. Lamina medialis absent, lamina lateralis well developed. Solenomerite not sheathed by, but closely applied to the medial side of the tibiotarsus.

Type-species. — *Arthrogonopus edentulus* nov. spec.

Range. — Borneo.

Number of species. — Four.

Remarks. — Besides the three new species described in this paper, this new genus also includes the one previously known as *Orthomorpha borneona* Att. These four species are even more disjunct from the group of typical species of *Orthomorpha* than the two united under *Dajakina.* They are characterised especially by the absence of a lamina medialis in the tibiotarsus of the gonopods, by the two laminate crests of the basal part of the femur of the gonopods and by the weakly developod lateral keels of the metasomites. In the structure of the tibiotarsus and its relationship to the solenomerite as well as in the weakly developed lateral keels the new genus approaches the Sumatran species of *Sundanina* and the species of *Opisthodolichopus* Verh. like *O. javanicus* (Att.), but *Arthrogonopus* may be distinguished from these by the sharply demarcated postfemur of the gonopods.

Key to the species. — The species of *Arthrogonopus* have a quite monotonous external morphology. The characters of diagnostic value are found mainly in the gonopods.

1. Colour of the last two pairs of legs not differing from that of the others. Gonopods with a small process at the medio-posterior side of the distal end of the femur pointing mesad. Tibiotarsus with a secondary process arising from the lateral side .... *A. bifidus* spec. nov.

— Last two pairs of legs infuscate at least distad of the middle of the tibiae, the others brown only in the distal half of the tarsi. Gonopods without a femoral process, or with a very small knob at the medio-posterior side of the distal end of the femur. Tibiotarsus without a secondary process 2

2. Tibiotarsus of gonopods comparatively small, its greatest length about equal to two thirds of the length of the femur .... *A. edentulus* spec. nov.

— Tibiotarsus of gonopods larger, its greatest length about equal to that of the femur 3

3. Posterior edges of the lateral keels from the 5th segment onwards rounded. Terminal end of tibiotarsus of the gonopods relatively short, acutely angular in profile .... *A. borneonus* (Att.)

— Lateral keels of the segments of the posterior half of the body with minute acuminate posterior edges. Terminal lappet of tibiotarsus of the gonopods longer, rounded in profile .... *A. denticulatus* spec. nov.

Arthrogonopus edentulus spec. nov.

Material. — East Borneo: Blu-u, Mahakkam River, November, 1898 (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 2 ♂ (one of them the holotype), 1 ♀. East Borneo: Upper Mahakkam River, 1899 (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 1 ♂. East Borneo: Upper Mahakkam River (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 2 ♀. East (?) Borneo: S. Bilis, May, 1932 (Coll. H. R. H. PRINCE LEOPOLD OF BELGIUM, Mus. Brussels), 1 ♂. West Borneo: Mt. Tilung, eastern slope, March 1899 (Borneo Exped., Coll. J. BÜTTIKOFER, Mus. Leiden), 1 ♂. West Borneo: Gng. Kenepai, Pondok, January, 1894 (Borneo Exped., Coll. M. MORET, Mus. Leiden), 1 ♂.

Colour. — Difficult to ascertain because of the generally rather poor state of preservation. In the holotype the head is castaneous, with the antennae very dark brown, almost black, only the distal part of the 7th and the 8th joint whitish.

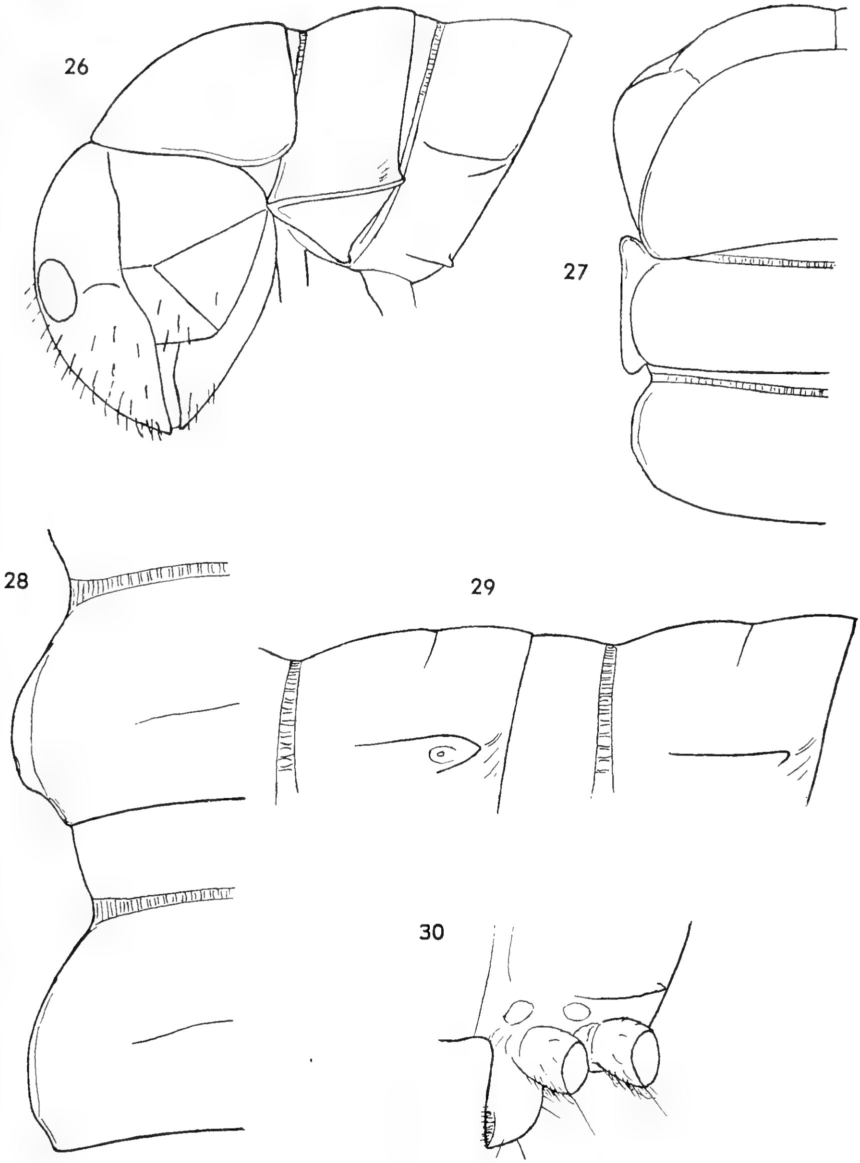


Fig. 26—30. *Arthrogonopus edentulus* spec. nov. — 26: left side of the head and the three anterior segments of the holotype ♂, lateral view. 27: the same, subdorsal view. 28: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 29: the same, lateral view. 30: sternal process of the 5th segment of the holotype ♂, lateral view

Collum of a similar castaneous colour as the head. Subsequent body segments also castaneous, but soon growing darker and from the 5th onwards very dark brown to black, with the keels, in particular those of the poriferous segments yellowish brown to brownish yellow. Venter brown. Sternites yellowish brown to brownish yellow. Legs brownish yellow to yellow, the distal half of the tarsi a little darker brownish. The two last pairs of legs distad of the middle of the femur very dark brown or black. Anal segment brown, the tail entirely brownish yellow. Valves dark brown, scale pale brown. The other ♂ from Blu-u is much paler, being brown all over, but this may be due to preservation. The last two pairs of legs are yellowish, black only distad of the middle of the tibiae. The other specimens studied are mostly discoloured, but as far as could be determined their colour was similar to that of the holotype. The ♂ from S. Bilis is completely pale brownish yellow, and probably freshly moulted. The ♂ from Mt. Tilung seems to be well preserved. It has the head dark castaneous, darkest in the frontal area. The colour of the antennae is as described for the holotype. The collum and the subsequent body segments, including the lateral keels, are black. The venter dark brown to black, with the sternites more or less dark brown. The legs pale brown to yellowish, with the tips of the tarsi not notably darker. The last two pairs black distad of the proximal quarter of the femur. Anal segment black or very dark brown, only the scale paler brown.

Width. — Holotype ♂ 3.1 mm; other ♂ in the order of the above enumeration 3.2 mm, 3.1 mm, 3.0 mm, 3.2 mm, 3.1 mm; ♀: 3.9 mm, 3.9 mm, 4.1 mm.

Head and antennae. — Labrum narrowly and moderately emarginate. Clypeus rather weakly convex, moderately impressed towards the labrum. Lateral sides weakly and widely convex, with a notch above the labrum. Surface of head shining, with some irregular wrinkles. Headplate rather densely to moderately setiferous in the clypeal and frontal regions, four setae on vertex. Antennal sockets separated by slightly more than the diameter of one socket or by about half the length of the 2nd antennal joint. Postantennal groove shallow, the wall in front moderately prominent. Vertex moderately convex, not or only very weakly demarcated from the frontal region. Sulcus rather weakly impressed, running downward to somewhat below the upper level of the sockets. Antennae slender. Length of joints: $3 > 4 = 2 = 5 > 6$, the 6th joint about as long as three quarters to two thirds of the 3rd. The 2nd, 3rd and 6th joints of subequal width, slightly thicker than the 4th and 5th. Antennal joints moderately to rather densely setiferous.

Collum. — (fig. 26—27). Distinctly narrower than the head, subsemicircular in dorsal outline. Anterior border very widely convex in the middle, somewhat more narrowly rounded towards the lateral sides, weakly emarginate or straight above the rounding of the lateral sides. Posterior border very weakly and widely emarginate in the middle, laterally slightly convex and very weakly emarginate or straight immediately above the lateral rounding. Lateral sides widely rounded. Surface smooth and shining, moderately convex, slightly more so towards the sides. A few setae may be present. Lateral and latero-anterior borders with a fine marginal rim, disappearing gradually towards the middle of the anterior border.

Body segments. — Metatergites with some sparse hairs, in particular in the anterior and posterior segments. Transverse furrow present up to the 18th, or, eventually, up to the 17th segment, in the majority of the segments reaching to

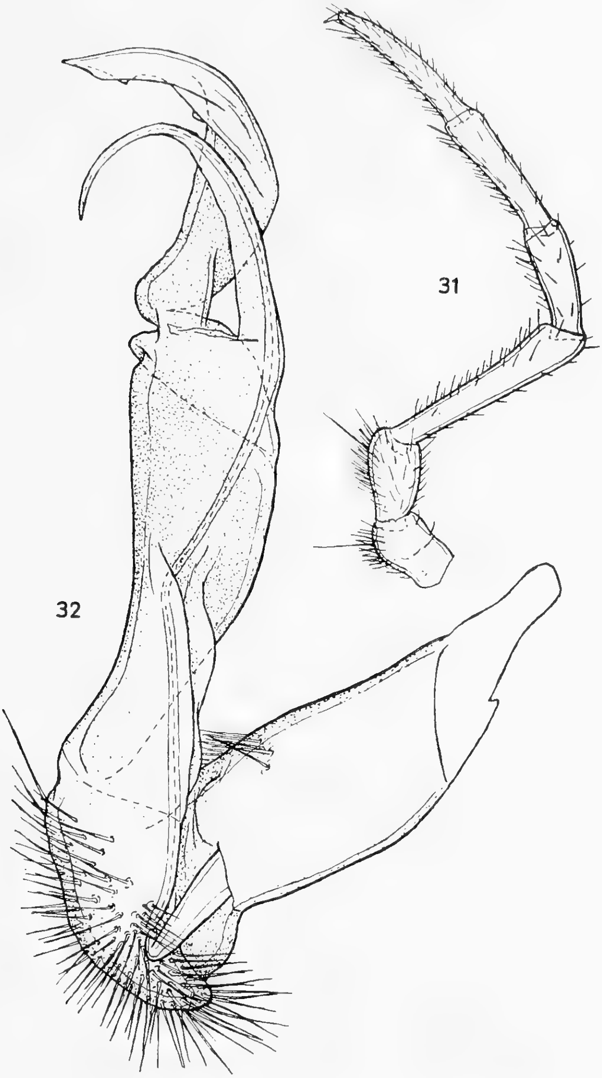


Fig. 31—32. *Arthrogonopus edentulus* spec. nov. — 31: leg of the 7th segment of the holotype ♂. 32: right gonopod of the holotype ♂, medial view. (The solenomerite has moved somewhat out of its natural position)

about halfway the dorsal delimitation of the lateral keels. Sides dispersedly granulate up to the 4th segment, smooth or very weakly wrinkled from the 5th onwards. Pleural keels present up to the 7th segment, obsolete from the 8th onwards. Up to the 4th segment they are represented by complete ridges which are produced posteriorly into a well developed angular lappet projecting behind the posterior margin of the somite. In the 5th, 6th and 7th segments the pleural keels are represented by a small triangular lappet near the posterior margin of the segments, which does not project behind that margin.

Lateral keels. — (fig. 26—29). 2nd segment distinctly wider than the collum. The keels anteriorly somewhat shouldered at the base, the anterior and posterior edges rounded, the posterior edge projecting slightly behind the border of the segment. Marginal rim present only along the anterior margin, laterally obsolete. 3rd and 4th segments of subequal width, somewhat narrower than the 2nd. The keels anteriorly and posteriorly widely rounded, ventrally scarcely demarcated. 5th segment distinctly wider than the 4th. Keels from the 5th segment onwards anteriorly widely rounded, the posterior edges rather narrowly rounded, in particular in the keels of the segments of the posterior half of the body, but in none of these angular. Poriferous keels somewhat more prominent than the poreless. Dorsal furrow of keels narrow, not reaching the waist. Seen from the lateral side the poreless keels have their dorsal margins slightly concave, the poriferous keels are somewhat convex dorsally. Poreless keels ventrally demarcated near the posterior end only, poriferous keels in the posterior half. Pores lateral, in a slight excavation, almost in the middle between the dorsal and ventral demarcations of the keels.

Sternites and legs. — Sternites one and a half times as long as broad, moderately setiferous. Cross impressions rather sharp. Sternite of 5th segment (fig. 30) with a thick process between the anterior legs, directed ventrad and somewhat cephalad and projecting very slightly before the anterior border of the sternite. Lateral sides of the process distinctly diverging in a distal direction. The end widely rounded. Anterior side with a dense brush of short setae at the distal end. The shape of the process appears to be somewhat variable. In some of the specimens it differs from that of the holotype in that, from a lateral view, the distal end may be somewhat more attenuate than illustrated. Sternite of 5th segment with a normal transverse furrow and a normal longitudinal furrow between the posterior legs. Sternite of 6th segment widely concave between the posterior legs, the coxae of which are somewhat more widely separated than those of the anterior pair. Transverse furrow almost obsolete, longitudinal furrow very wide. Legs (fig. 31) moderately setiferous, but the ventral side, especially of the proximal joints, rather densely setiferous. Last two pairs of legs distinctly longer than the preceding. Length of joints: $3>6>5>4>2>1$.

Anal segment. — Tail of moderate length, rather thick at the base, of moderate width, the sides proximally rather strongly, distally more weakly converging. Before the end on each side a well developed setiferous tubercle. The end of the tail truncate and weakly emarginate, the two terminal tubercles weakly developed. Tail without distinct transverse depression at the base. Ventral side weakly concave. Valves with rather narrow and rather low marginal rims. Setiferous tubercles moderately developed. Scale subtrapezoidal or subtriangular, the end slightly convex, the sides almost straight. Setiferous tubercles moderately developed and not projecting.

Gonopods. — (fig. 32). Prefemur moderately developed. Femur without femoral process or knob. Tibiotarsus comparatively small, its greatest length about two thirds of the length of the femur. Tibiotarsus simple, without secondary process, the end acuminate.

Female. — The ♀ from Blu-u, although rather strongly discoloured, appears to agree in colour with the holotype. The two ♀ from Upper Mahakkam River have the collum castaneous, infuscate in the middle and along the margins. The tail here is darker than in the holotype. Morphologically the ♀ differ particularly in being more robust than the ♂. The body segments are somewhat less strongly constricted and the waist is relatively a little narrower. The development of the pleural keels of the 5th, 6th and 7th segments is somewhat weaker, so that a triangular lappet is not distinct in these segments. The sternites of the middle segments are as long as wide to $1^1/_3$ × as long as wide. The legs are slightly more slender; the pubescence, however, is practically similar to that of the legs of the ♂.

Remarks. — Variation of the specimens studied appears to be confined to the coloration and the shape of the sternal process of the 5th segment of the males. The taxonomic value to be attributed to these variations cannot be determined at present in view of the small amount of material studied and because of its rather poor condition. The gonopods of the males from different localities do not present appreciable differences.

Arthrogonopus denticulatus spec. nov.

Material. — East Borneo: Blu-u, 30 September (Mus. Leiden), 1 ♂ (holotype). East Borneo: Blu-u, Mahakkam River, November, 1898 (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 4 ♂, 4 ♀. East Borneo: Long-Blu-u, November, 1898 (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 1 ♂. East Borneo: Upper Mahakkam, 1899 (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 1 ♂. East Borneo: Upper Mahakkam River (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 1 ♂. East (?) Borneo: June to August, 1900 (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 1 ♂. West Borneo: Gng. Kenepai, Pondok, January, 1894 (Borneo Exped., Coll. M. MORET, Mus. Leiden), 1 ♀.

Differing from *edentulus* in the following characters.

Colour. — The holotype has essentially the same colour as the holotype of *edentulus*, but the keels are black and the anal segment is castaneous. The other ♂ have the head castaneous, the collum either completely castaneous or castaneous with the margin and the middle infuscate. The subsequent segments are entirely black, except the brown venter. The sternites and legs are brownish yellow, the legs of the last two pairs black distad of the middle of the femur. Anal segment entirely castaneous.

Width. — Holotype ♂ 3.0 mm; other ♂ in the order of the above enumeration: 3.1 mm, 3.1 mm, 3.0 mm, 3.0 mm, 3.0 mm, 3.2 mm, 3.4 mm, 3.0 mm; ♀ 3.9 mm, 3.9 mm, 3.8 mm, 3.8 mm, 4.0 mm.

Body segments. — The transverse furrow of the metatergites extends slightly further laterad than in *edentulus*. Pleural keels of the 5th to the 7th segments not angular.

Lateral keels. — The posterior edges of the lateral keels are somewhat more narrowly rounded. From about the 12th or 13th segment these edges become angular and on subsequent segments (fig. 33) they are produced posteriorly in a minute, sharp point. The posterior edges of the keels of the posterior segments

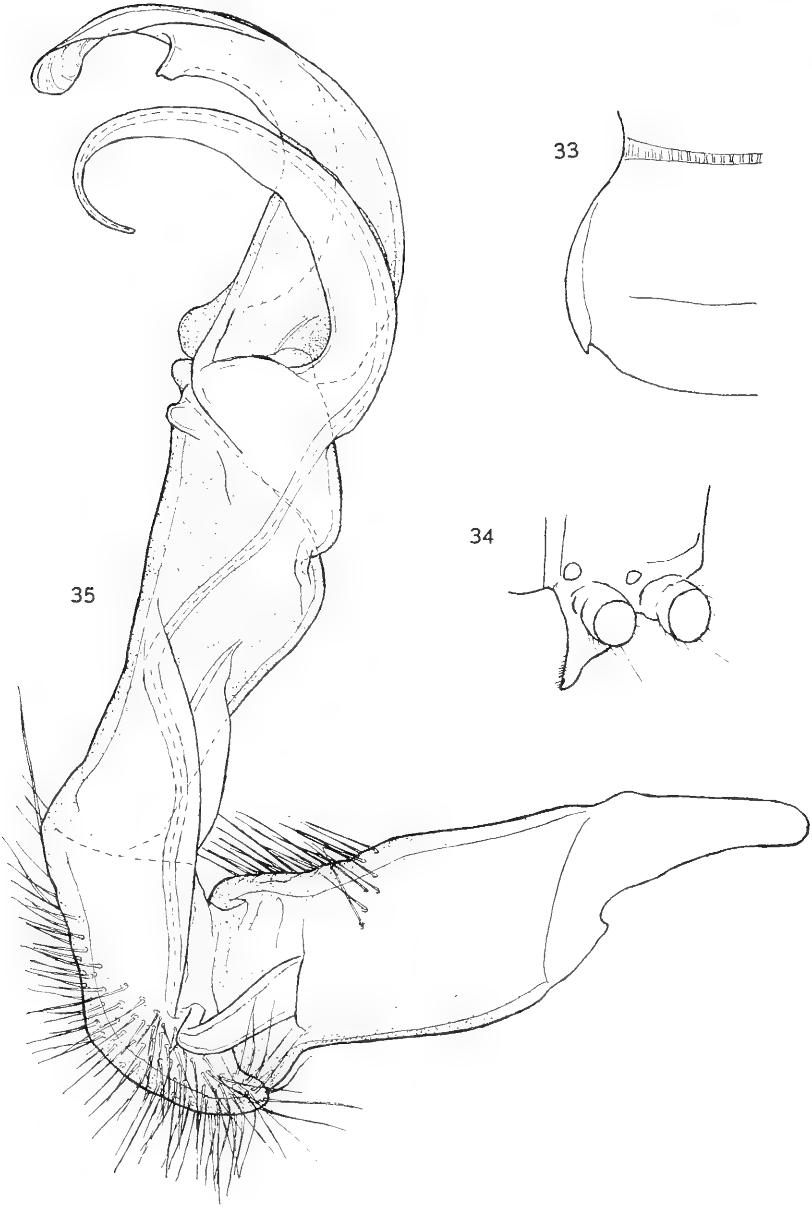


Fig. 33—35. *Arthrogonopus denticulatus* spec. nov. — 33: left side of the 16th segment of the holotype ♂, dorsal view. 34: sternal process of the 5th segment of the holotype ♂, lateral view. 35: right gonopod of the holotype ♂, medial view. (The solonomerite has slightly moved out of its natural position)

are not projecting behind the margins of the metasomites, but in the 19th segment they may attain the margin.

Sternites and legs. — Sternite of 5th segment (fig. 34) with the process distally much more laminate than in *edentulus*. The lateral sides of the process almost parallel or diverging only very slightly in the distal direction. Sternite of 6th segment more concave between the anterior legs than in *edentulus*, scarcely raised above the ventral level of the metasomal ring between the posterior legs; the transverse and longitudinal furrows are almost obsolete. Legs, especially those of the anterior part of the body, somewhat more densely pubescent than in *edentulus*.

Gonopods. — (fig. 35). Prefemur rather strongly developed. At the medio-posterior side of the distal end of the femur a small knob. Tibiotarsus of moderate size, the greatest length about equal to that of the femur.

Female. — The coloration of the females is more variable than that of the males. Of four specimens from Blu-u, one has a colour similar to that of the males, two others have pale spots in the middle of the metatergites, whilst the fourth has the keels and the lateral sides pale, contrasting with the black dorsum. The ♀ from Gng. Kenepai appears to be almost completely discoloured. Morphologically the females differ from the males in a way very similar to that found in *edentulus*. The lateral keels in the posterior segments are not pointed caudally as strongly as in the males: really sharply pointed edges may be present only in a few segments.

Remarks. — The colour variations of this species as represented in the material under report are difficult to interpret. In part they seem to have been caused by the generally rather poor state of preservation. However, the coloration of this species and that of *edentulus* might be somewhat more variable than usually is the case. Without the study of freshly preserved material it is impossible to give an opinion on the systematic value of the variations.

The females of this species are very similar to those of *edentulus*. For the distinction one has to rely in the first instance on the shape of the lateral keels of the posterior segments. It is not possible to estimate the constancy of this character since both species apparently were found to occur in the same localities. It may be that some female specimens of *denticulatus* have been referred here to *edentulus* on account of the absence of distinctly pointed posterior edges in the lateral keels of the posterior segments.

Arthrogonopus borneonus (Att.)

1931 *Orthomorpha* (*O.*) *borneona* Attems, Zoologica, Stuttg., vol. 30, fasc. 3/4, p. 115, fig. 174.

1937 *Orthomorpha* (*O.*) *borneona*, Attems, Tierreich, vol. 68, p. 67, fig. 84.

Distribution. — West Borneo: Mandai River, Mt. Rajah, Sungei Malang

Remarks. — This species, of which I did not see any material, comes very close to *denticulatus*, in particular in the characters of the gonopods. However, the distal end of the tibiotarsus of *denticulatus* appears to be more elongate and is typically rounded, whereas in *borneonus* it is acuminate. The lateral keels in *borneonus* are stated to be rounded posteriorly in all segments, which is certainly not the case in *denticulatus*. The relationship between *borneonus* and *denticulatus* may be of a subspecific nature.

Arthrogonopus bifidus spec. nov.

Material. — West Borneo: Sambas, October, 1893 (Borneo Exped., Coll. Dr. HALLIER, Mus. Leiden), 1 ♂.

Differing from *edentulus* in the following characters.

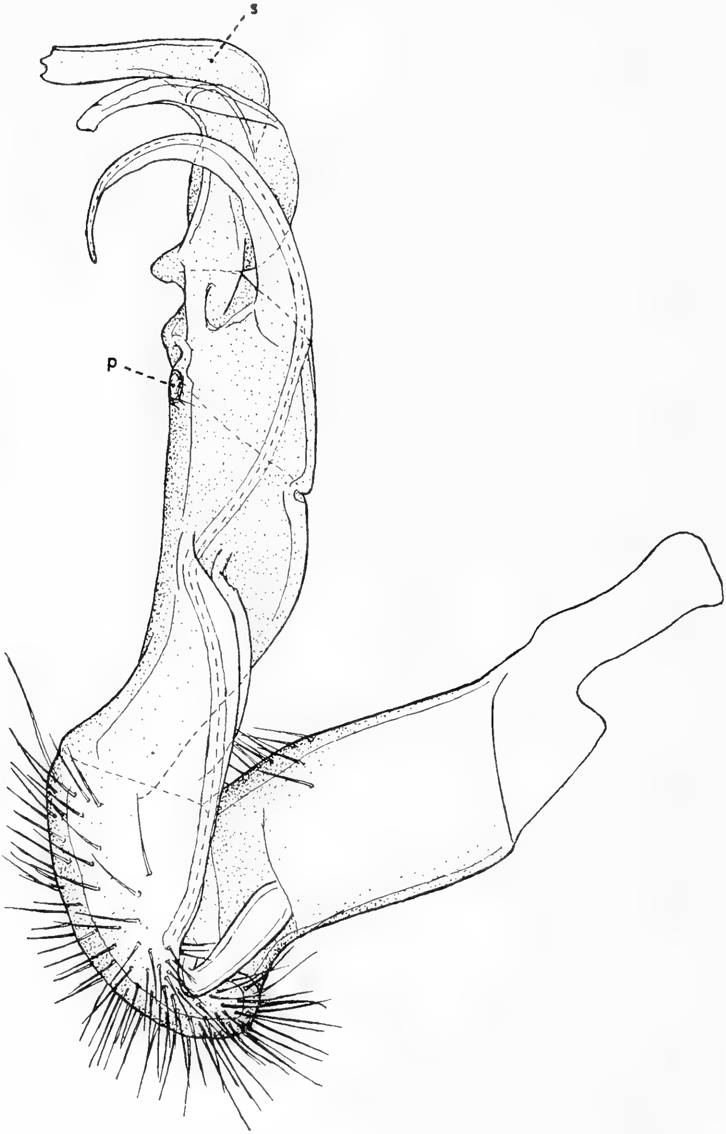


Fig. 36. *Arthrogonopus bifidus* spec. nov. — right gonopod of the holotype ♂, medial view; p: femoral process; s: secondary process of the tibiotarsus

Colour. — Head dark castaneous, darkest in the frontal area. Antennae also dark castaneous, with the tip of the 7th and the 8th joint white. Collum and body segments very dark brown to black, the venter dark brownish grey. Sternites brown to brownish yellow. Legs pale yellow to brownish yellow. Anal segment black, the valves brown, the scale pale brown.

Width. — 2.9 mm.

Body segments. — The transverse furrow of the metatergites extending a little more laterad than in *edentulus.* Pleural keels of the 5th to the 7th segments not angular, similar to those of *denticulatus.*

Sternites and legs. — Sternal process of the 5th segment similar to that of *edentulus*, but much more attenuate distally when seen from the lateral side. The process directed a little more strongly cephalad, the distal end therefore projecting somewhat more distinctly before the anterior border of the sternite. Sternite of the 6th segment as in *denticulatus.*

Gonopods. — (fig. 36). Prefemur rather strongly developed. Femur with a small femoral process at the medio-posterior side near the distal end, pointing mesad. The process is small, elongate triangular, about one and a half times as long as broad at its base. Tibiotarsus comparatively small, its greatest length about equal to two thirds of the length of the femur. From the lateral side of the tibiotarsus arises a laminate secondary process.

Female. — Unknown.

Remarks. — The close relationship between this species and the other species of *Arthrogonopus* is clearly demonstrated by the great similarity in the general morphology and particularly by the gonopod characters. *A. bifidus,* however, seems to be somewhat disjunct by the presence of a small femoral process and a secondary process in the tibiotarsus. The latter, which seems to have the function of keeping in place the distal end of the solenomerite, may be a derivate structure. Probably it is the homologue of the terminal end of the tibiotarsus in species like *denticulatus* and *edentulus,* and the condition might be seen as the result of a cleavage of the end of the tibiotarsus in the course of evolution.

Gigantomorpha gen. nov.

Generic diagnosis. — 20 segments. Poreformula normal. Head without particulars; labrum tridentate. Antennae of moderate length.

Segments moderately (♂) to rather weakly (♀) constricted. Prosomites shagreened or dulled by a very fine cellular structure. Waist narrow, distinctly longitudinally ribbed or "beaded" in the dorsal half, smooth or finely striate in the ventral half dorsad of the sternal level. Metatergites dull or more or less shining, generally hairless, rugulose to subgranulose and with a transverse row of more or less distinctly developed granules along the posterior margin and some dispersed mostly very weakly developed granules in front of the transverse furrow. Transverse furrow distinct but not deeply impressed, finely longitudinally striate, present from the 4th or 5th segment onwards. Pleural keels present at least in the segments of the anterior half of the body, moderately to well developed in the anterior segments.

Lateral keels strongly to rather strongly developed, in all segments from the

2nd to the 19th with an angular, sometimes even spiniform posterior edge, which often projects behind the posterior margin of the segments. Marginal rim of keels narrow, in poriferous segments widening only in the area of the pore. Keels generally on a high level, sometimes, especially in the males, projecting somewhat above the middorsal surface of the metatergites. Keels of the 2nd segment either distinctly below the level of those of the next segment, or on the same level.

Sternites with rather weakly developed cross-impressions, somewhat longer than wide (♂), as long as wide (♂, ♀) or somewhat wider than long (♀), moderately setiferous. Sternite of 5th segment of ♂ with a moderately developed process between the anterior legs. Sternite of 6th segment of ♂ somewhat modified: raised above the ventral surface of the metasomal ring between the anterior legs only. Sternite of 7th segment of ♂ with on each side before the gonopod opening a rounded, somewhat granular process. Sternite of 8th segment of ♂ without modifications. Sternite from the 5th (♀) or from the 8th (♂) to the 17th segment with a more or less developed pointed cone near the base of each leg. Legs of moderate length to rather long. Brushes obsolete to very strongly developed on all joints distad of the coxa, present only in the ♂.

Gonopods with coxa of moderate size, almost straight-cylindrical; distal setiferous area well developed. Prefemur somewhat elongate, slightly oblique on the longitudinal axis of the femur and laterally well demarcated from that joint, the demarcation almost transverse on the femoral axis. Femur well developed, almost straight, somewhat longer than the coxa, narrowing distad. In the basal half the femur on its medial side with two more or less laminate crests. Postfemur laterally sharply demarcated. Spermal channel running along the medial side of the femur. In the proximal half it runs along the posterior laminate crest, or between the two crests, towards the posterior side of the femur, turning in the distal half towards the anterior side. Solenomerite of moderate length, flagelliform, arising from the medio-anterior side of the distal end of the postfemur. Tibiotarsus springing from the posterior side of the distal end of the postfemur, moderately developed, distinctly demarcated from the postfemur. Tibiotarsus consisting of a simple solenophore. Lamina lateralis well developed, lamina medialis developed only in the distal part of the tibiotarsus, where it gives rise to a more or less complicated laminate process. Tibiotarsus sheathing the solenomerite in its distal part only.

Type-species. — *Gigantomorpha immanis* spec. nov.

Range. — Borneo, Celebes.

Number of species. — Eight.

Remarks. — This genus, besides the new species described in the present paper, includes two species previously referred to *Pratinus* Att., viz., *Pratinus fasciatus* (Att.) from Borneo and *Pratinus socialis* (Carl) from Celebes. Like so many of the species brought under the generic heading of *Pratinus* by ATTEMS in his monograph of the "Strongylosomidae" of 1937, these two only have a quite remote relationship with the type of that genus. As a matter of fact, ATTEMS seems to have been ignorant of the true identity of *Pratinus*, for a species closely related to the type of that genus was described by him as *Euphyodesmus greeni* Att. in 1936. In 1941, in following ATTEMS, also CHAMBERLIN referred a typical species of *Pratinus* to the genus *Euphyodesmus* and even went as far as creating a new subgenus for this species and *greeni*. In short the synonymy of *Pratinus* is as follows:

Pratinus Att.
1895 *Prionopeltis* Pocock, Ann. Mus. Genova, vol. 34, p. 828 (nom. praeocc.). Type-species: *P. cervinus* Poc., by original designation.
1937 *Pratinus* Attems, Tierreich, vol. 68, p. 113. Type-species: *P. planatus* (Poc.), by original designation.
1941 *Euphyodesmus* (*Ceylonesmus*) Chamberlin, Proc. Ent. Soc. Wash., vol. 43, p. 33. Type-species: *E.* (*C.*) *vector* Chamb., by original designation.

Type-species. — *P. cervinus* (Poc.). There may be some controversy as to what species should be regarded as the type of *Pratinus*. The name quite obviously has been proposed as a substitute for *Prionopeltis*, judging from the indication "nom. nov.". However, ATTEMS apparently overlooked the type designation by POCOCK, which, as a matter of fact, is somewhat concealed in the text of POCOCK's paper, and selected *planatus* as the type species of *Pratinus*, thus taking the first of the three original species of *Prionopeltis*. In view of the doubtless intention of ATTEMS to substitute the name *Prionopeltis* rather than to erect a new genus, it seems best to revert to *cervinus* as the type of *Pratinus*.

Range. — Ceylon, Burma, Tenasserim, Andaman Is.

Species. — Five: *cervinus* (Poc., 1895), *greeni* (Att., 1936), *planatus* (Poc., 1895), *taurinus* (Poc., 1895), *vector* (Chamb., 1941).

Thus *Pratinus* is restricted to the original concept of *Prionopeltis* with the addition of two misplaced species of *Euphyodesmus*. Its generic characters are to be determined yet, although it seems clear that the genus may be regarded as intermediate between *Centrodesmus* Poc. and *Orthomorpha* Bollm. From the latter genus *Pratinus* is distinguished by the strongly developed, horn-like lateral keels, the thin marginal rims of the keels and the remarkably condensed type of tibiotarsus of the gonopods. A sharply demarcated postfemur seems to be absent. The differences between *Pratinus* and *Centrodesmus*, especially the Indochinese species referred to that genus, are less obvious. The lateral keels in *Centrodesmus* are even more strongly developed than in *Pratinus*, but it remains to be seen whether or not this evolutional tendency is of sufficient importance to justify a generic separation. Since, however, the Sumatran type-species of *Centrodesmus* was based upon a female specimen and its more important characters are unknown, a discussion on the status of the genus and its boundaries becomes rather useless.

Aside from the true species of *Pratinus* enumerated above, the following have been referred to the same genus in the "Tierreich": *P. fasciatus* (Att.), *P. socialis* (Carl), *P. flaviventer* (Att.), *P. tenuipes* (Att.), *P. levigatus* Att., *P. rotundicollis* Att., *P. tuberculatus* Att., *P. glandulosus* Att., *P. arboricola* Att. and *P. butteli* (Carl). Besides, the following species were enlisted as "unsichere Arten": *P. montanus* (Chamb.), *P. bicolor* (Carl), *P. haasti* (Humb. & Sauss.), *P. paviei* (Brol.), *P. beaumontii* (Att.)?, *P. clarus* (Chamb.) and *P. dasys* (Chamb.). All of these species, except the six mentioned hereafter, will be discussed under *Orthomorpha*.

As has been stated already, *P. fasciatus* (Att.) and *P. socialis* (Carl), for reasons to be given below, are referable to the new genus *Gigantomorpha*. *P. bicolor*

(Carl) and *P. haasti* (Humb. & Sauss.), both from New Zealand and both based upon female specimens, are certainly not referable to any of the genera treated in this paper. In fact, one may wonder whether their location in the family Paradoxosomatidae was correct. The presence of polygonal areas on the metatergites in the two species points in the direction of the Sphaerotrichopodidae, a family, in contradistinction to the Paradoxosomatidae, rather well represented in the New Zealand fauna. My attempt to verify this question failed, inasmuch as the type specimens of the two species could not be found in the museums of Bern and Geneva (respectively Dr. W. KÜENZI, 12.IV.1955, and Dr. H. GISIN, 27.V.1955, in litt.). *P. clarus* (Chamb.) from the Fiji Is. and Samoa is doubtless to be regarded as a synonym of *Chondromorpha xanthotricha* (Att.), a species now known to have an almost world-wide range. *P. dasys* (Chamb.) from the Fiji Is. may be either a species of *Chondromorpha* or *Anoplodesmus,* possibly introduced from elsewhere.

Rather than to *Pratinus, Gigantomorpha* appears to be related to the group of species assigned in the present paper to *Orthomorpha.* The general gonopod-structure in *Gigantomorpha* is in close agreement with that of the typical species of *Orthomorpha,* such as *O. weberi* (Poc.), *O. hydrobiologica* Att., etc. Differences, however, are found in the presence of two laminate femoral crests, the somewhat different course of the spermal channel and the presence of a laminate or spiniform process at the distal end of the lamina medialis of the tibiotarsus in *Gigantomorpha.* Other characters for distinguishing this genus from *Orthomorpha* probably will be found in the shape of the marginal thickenings of the lateral keels of the metasomites, in the development of the pleural keels, in the sternites, legs, etc., but unfortunately many species of *Orthomorpha* are not sufficiently well described as regards these characters.

Attention may be drawn to the similarity in the structure of the femoral crests of the gonopods in *Gigantomorpha* and *Arthrogonopus.* This resemblance seems to indicate a certain degree of relationship between the two genera, but other characters, either of the gonopods or of the external morphology, show this relationship to be quite remote and fully justify a generic separation.

Among the species of *Gigantomorpha* are to be found the largest Paradoxosomatidae yet described. The fact that these giants remained undiscovered for such a long time, reveals once again the enormous amount of taxonomic work to be done on tropical millipedes.

Key to the species. — As in related genera, the gonopod characters in the genus *Gigantomorpha* offer few possibilities for the distinction of species. Characters of diagnostic value are found mainly in the shape of the lateral keels, the development of the pleural keels, the coloration, and various secondary sexual features of the males.

The present key pertains only to the species from Borneo. The single species known from Celebes needs a re-examination as regards several important characters.

1. Colour of body segments in both pro- and metasomites brown, without yellowish mid-dorsal spots or band. Lateral keels entirely yellow. Lateral sides of collum rounded, without an acute latero-posterior angle. Lateral keels of 2nd segment turned somewhat downwards, distinctly below the level of those of the 3rd segment. Proximal joints of the legs of the male normally setiferous,

the femora straight. Basal and distal lateral setiferous tubercles of the tail weakly developed, terminal tubercles well developed. Anal scale with the setiferous tubercles equalling or surpassing the middle of the posterior margin 2

— Colour different. Sides of collum with an angular latero-posterior edge. Lateral keels of the 2nd segment turned somewhat upwards, nearly at the same level as those of the 3rd segment. Proximal joints of the legs of the male, especially in the anterior half of the body, ventrally more or less densely setiferous, the femora distinctly arched. Either the basal or the distal lateral tubercles of the tail, or both, well developed; terminal tubercles more or less well developed. Anal scale with vestigial or weakly developed setiferous tubercles, which do not surpass the middle of the posterior margin 3

2. Along the posterior margin of nearly all segments laterally and ventrally an irregular row of setae. Metatergites with rather small tubercles, of which there are eight to ten behind the transverse furrow. Pleural keels strongly developed, present up to the 17th segment. Lateral keels in none of the segments projecting dorsad of the middle of the metatergites. Width (♂, ♀) 5.0 to 5.4 mm .... *G. trichopleura* spec. nov.

— Posterior margin of segments without setae. Tubercles on metatergites larger, generally six behind the transverse furrow. Pleural keels somewhat less strongly developed, present up to the 14th or 15th segment. Lateral keels somewhat more strongly developed, slightly raised above the level of the middle of the metatergites in a few posterior segments of the male. Width (♂, ♀) 6.3 to 8.0 mm .... *G. spinescens* spec. nov.

3. Colour of body segments very dark brown to blackish, with the lateral keels and a rather narrow continuous middorsal band pale brownish. Femur of gonopods rather strongly constricted about halfway. Process of lamina medialis of the tibiotarsus rather weakly developed, acuminate. Terminal end of tibiotarsus finely bifid .... *G. fasciata* (Att.)

— Body segments without a continuous middorsal pale band. Femur of gonopods without a distinct constriction. Process of lamina medialis rather strongly developed, the end truncate. Terminal end of tibiotarsus a rounded or somewhat triangular lobe 4

4. Colour of body segments uniformly black, with only the marginal rim of the lateral keels near the posterior edges somewhat paler brown. Legs of the male with the proximal joints set with short curved setae, the femora somewhat arched .... *G. aterrima* spec. nov.

— Colour of body segments dorsally either pale brownish gray, or dark purplish brown with a large yellowish spot in the middle of the prosomites and yellow posterior edges in the lateral keels. Legs of the male with long erect setae, the femora more strongly arched 5

5. Lateral keels of male raised above the middorsal surface of the metasomites in the 3rd to the 19th segments. Legs of male slender, the proximal joints not strongly incrassate and their ventral pubescence not brush-like .... *G. cornalata* spec. nov.

— Lateral keels of male raised above the middorsal surface of the metasomites in the 17th to the 19th segments only. Legs of male rather strongly incrassate, especially the proximal joints. The ventral side of all joints distad of the coxa with a dense brush-like pubescence 6

6. Colour of body segments dorsally dark purplish brown, a broad median spot on the prosomites and the latero-posterior edges of the lateral keels yellow. Pleural keels disappearing in the 10th or 11th segment ... *G. immanis* spec. nov.

— Colour of body segments dorsally entirely pale brownish gray. Pleural keels disappearing in the 16th or 17th segment .... *G. pallida* spec. nov.

Gigantomorpha immanis spec. nov.

Material. — East Borneo: Mt. Tibang, 1400 m (Coll. Dr. E. Mjöberg, Mus. Stockholm), 2 ♂ (one of them the holotype). East Borneo: Pajan River (Coll. Dr. E. Mjöberg, Mus. Stockholm), 1 ♂, 1 ♀. East Borneo: Blu-u, Mahakkam River, November, 1898 (Borneo Exped., Coll. Dr. A. W. Nieuwenhuis, Mus. Leiden), 1 ♂, 2 ♀, 1 juv. ♀. East Borneo: Blu-u, 25 September (Mus. Leiden), 1 ♂. East Borneo: Upper Mahakkam River, 1899 (Borneo Exped., Coll. Dr. A. W. Nieuwenhuis, Mus. Leiden), 2 ♀. East Borneo: Upper Mahakkam River (Borneo Exped., Coll. Dr. A. W. Nieuwenhuis, Mus. Leiden), 1 ♂, 1 fragm. of ♂, 3 ♀. East Borneo: Mahakkam (Borneo Exped., Coll. Dr. A. W. Nieuwenhuis, Mus. Leiden), 1 ♂.

Colour. — Head dark purplish brown, the clypeal area and a spot at the posterior border of each of the antennal sockets pale yellow. Antennae pale yellow to brownish yellow, the 6th joint infuscate towards the end, the 7th joint dark brown, its distal end and the 8th joint whitish. Collum dark purplish brown, the lateral keels and sometimes a weakly defined narrow band along the posterior margin pale yellow. Body segments of same dark groundcolour as the collum. A large middorsal spot on the prosomites, the latero-posterior edges of the lateral keels and sometimes a weakly defined narrow band along the posterior margin of the metatergites pale yellow. Venter pale brownish, sternites and legs pale yellow. Anal segment dark purplish brown, the tail yellow, the margins of the valves and the scale pale brownish.

Width. — Holotype ♂ 7.2 mm; other ♂ in the order of the above enumeration 7.0 mm; 7.2 mm; 6.0 mm; 6.5 mm; 6.6 mm; 6.6 mm; 6.6 mm; ♀ 7.3 mm; 7.0 mm; 7.2 mm; 6.8 mm; 7.3 mm; 6.7 mm; 6.9 mm; 7.2 mm; juv. ♀ with 19 segments 4.6 mm.

Head and antennae. — Labrum moderately emarginate. Clypeus rather weakly convex, moderately impressed towards the labrum. Lateral sides widely and weakly convex, somewhat emarginate or straight near the labrum. Surface of headplate shining, slightly rugulose. Head moderately to rather dispersedly setiferous in the clypeal and frontal region, vertex with four, two, or without setae. Antennal

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Fig. 37—43. *Gigantomorpha immanis* spec. nov. — 37: left side of the head and the four anterior segments of the holotype ♂, lateral view. 38: left side of the head and the three anterior segments of the holotype ♂, dorsal view. 39: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 40: the same, lateral view. 41: left side of the 17th, 18th and 19th segments of the holotype ♂, dorsal view. 42: leg of the 7th segment of the holotype ♂. 43: anal segment of the holotype ♂, ventral view

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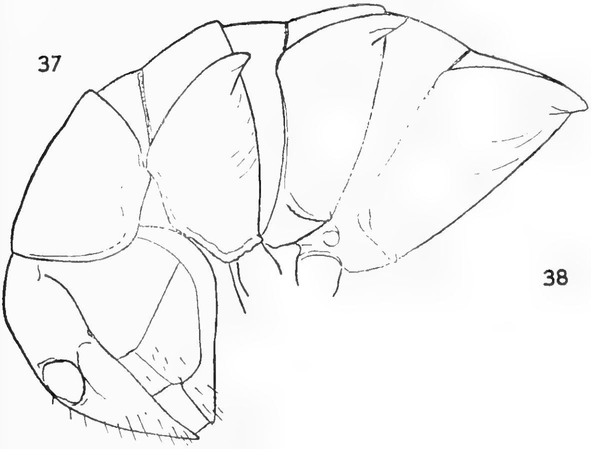

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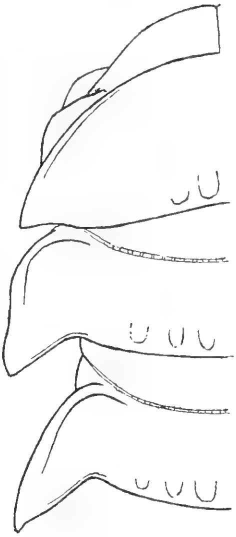

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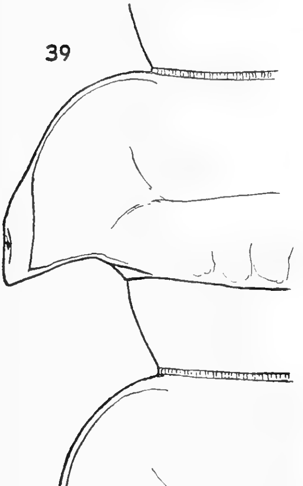

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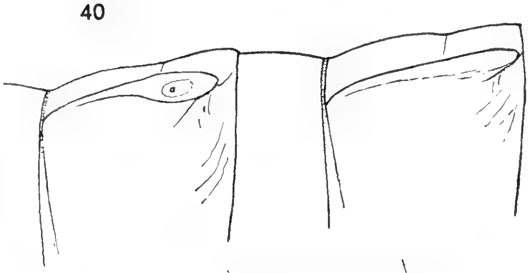

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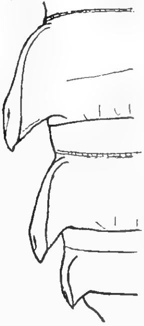

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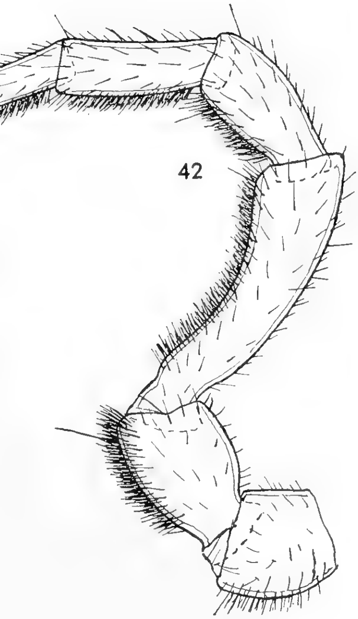

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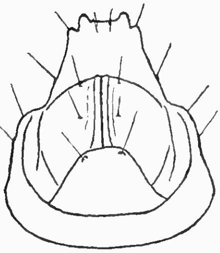


sockets separated by $1^1/_3 \times$ the diameter of one of the sockets, or by about three quarters of the length of the 2nd antennal joint. Postantennal groove shallow, the wall in front moderately prominent. Vertex moderately convex, not or weakly demarcated from the frontal area. Sulcus moderately impressed, running downward to the upper level of the antennal sockets or just below that level. Sulcus with some fine transverse wrinkles. Antennae not particularly slender. Length of joints: $3 > 2 = 4 = 5 = 6$, or the 6th sligthly shorter and about three quarters of the length of the 2nd. Joints of subequal width, only the 6th slightly thicker than the others. Pubescence of antennae moderate to, distally, rather dense.

Collum. — (fig. 37—38). Somewhat wider than the head, subtrapezoidal in dorsal outline. Anterior border very widely convex in the middle, somewhat more narrowly rounded towards the sides, lateral border almost straight. Posterior border scarcely emarginate in the middle, weakly convex more laterally; posterior border of lateral keels somewhat emarginate. Latero-posterior edge acuminate, almost rectangular. Surface shining, leathery rugulose, hairless, rather weakly convex. In the middle at about one third from the anterior border a weak transverse depression. Along the posterior margin some low, flat, large tubercles are indicated, generally represented by some rather coarse wrinkles. Lateral keels somewhat raised to a horizontal level. Latero-anterior border with a marginal rim ending posteriorly at some distance from the posterior border, gradually disappearing anteriorly towards the middle of the anterior border.

Body segments. — Metatergites leathery rugulose, shining, hairless. Along the posterior margin a row of generally six flat larger tubercles, which generally are weakly developed and often resemble coarse wrinkles. Tubercles in the anterior part of the metatergites vestigial. Transverse furrow present from the 5th to the 17th segments, generally reaching laterad to the base of the lateral keels and bifurcating there into two furrows or depressions, curving cephalad and caudad respectively. Sides rugulose, rather densely and minutely granular up to the 4th segment, more dispersedly granular from the 5th segment onwards. Pleural keels present up to the 9th or 10th segment, obsolete from the 10th or 11th. Up to the 4th segment they are represented by well developed, complete, granulate ridges which are posteriorly produced into a conical process projecting a little behind the posterior margin of the somites. From the 5th segment onwards the pleural keels are represented by a well developed swelling which is rather densely granulate above the anterior legs and a well developed pointed cone near the posterior margin of the segment, directed caudo-laterad and not projecting behind the margin. Both, swellings and cones, gradually diminish in size in subsequent segments.

Lateral keels. — (fig. 37—41). 2nd segment somewhat wider than the collum. The keels anteriorly somewhat shouldered at the base, the anterior margin rounded, the lateral margin a little emarginate in the middle, the posterior edge acutely angular and projecting rather strongly behind the posterior margin of the segment, the posterior margin straight. Keels of 2nd segment directed somewhat upwards, their level scarcely below that of the keels of the 3rd segment. Marginal rim well developed along the anterior and latero-anterior borders; a very fine rim along the posterior border. 3rd and 4th segments of subequal width, somewhat narrower than the 2nd. The keels anteriorly very weakly shouldered at the base, rather widely rounded. The posterior edges projecting rather strongly behind the margins of the segments. Keels directed upwards a little, those of the 4th segment less than those of the 3rd. Premarginal furrow not reaching the posterior margin. Posterior margin with a fine rim. Marginal rim ventrally not marked off by a furrow. 5th segment distinctly wider than the 4th. Keels from the 5th segment onwards anteriorly and laterally widely rounded, scarcely or not shouldered at the base. Posterior edges acutely angular, especially in the posterior segments projecting well behind the margins of the segments. In the segments of the middle part of the body, however, they hardly project behind the posterior margins. Keels horizontal in most of the segments, only in the 17th or 18th to 19th segments they are raised a little above the middorsal surface of the metasomites. Poriferous keels extending very slightly more laterad than the poreless. Dorsal premarginal furrow reaching from the waist to near the posterior border; a fine marginal rim along the posterior border. Marginal rim ventrally generally demarcated only in the posterior half of the poriferous keels. The rim generally not ventrally demarcated in the poreless keels. Pores dorso-lateral in a slight excavation of the marginal rim. In most segments the pores are visible from the dorsal side.

Sternites and legs. — Sternites about as long as wide in middle segments. Cross impressions represented by a rather sharp transverse furrow and a very weak and wide longitudinal impression. Sternal process of 5th segment somewhat broader than long, the sides almost parallel, the end truncate and scarcely incised in the middle. In lateral view the process is thick, a little acuminate towards the rounded end. Process directed ventrad, not projecting before the anterior border of the sternite. Anterior side of process near the end densely set with short setae. Sternite of 5th segment with a normal transverse furrow behind the process and a normal longitudinal impression between the posterior legs; sternal cones at the bases of the posterior legs vestigial. Sternite of 6th segment somewhat longitudinally convex and transversely concave between the anterior legs, without transverse furrow and sternal cones. Granular protuberances of the sternite of the 7th segment well developed. Sternites from the 8th to the 17th segments with rather well developed pointed cones near the bases of the legs. The cones are pointing ventrad and a little caudad. Legs (fig. 42) moderately setiferous, the ventral side of the joints distad of the coxa with dense brushes up to the legs of the 17th segment. The last two pairs without brushes, more normally setiferous. Legs rather strongly incrassate, in particular the three proximal joints. From the 3rd or 4th pair onwards the legs have the femora rather strongly arched. Legs of moderate length. Length of joints: $3>6>5>4=2>1$.

Anal segment. — (fig. 43). Tail of moderate length, rather broad and thick at the base. Sides rather strongly converging. Basal lateral setiferous tubercles rather weakly developed, distal lateral setiferous tubercles and terminal tubercles moderately developed. Near the base of the tail a more or less developed dorsal transverse depression. Ventral side of tail somewhat concave. Valves with rather narrow rims, the setiferous tubercles weakly developed. Scale parabolically rounded, the sides a little concave, the setiferous tubercles rather weakly developed and not projecting behind the margin.

Gonopods. — (fig. 44—45). Coxal setiferous area extending from the lateral, over the anterior towards the medial side. Anterior crest of the femur gradually

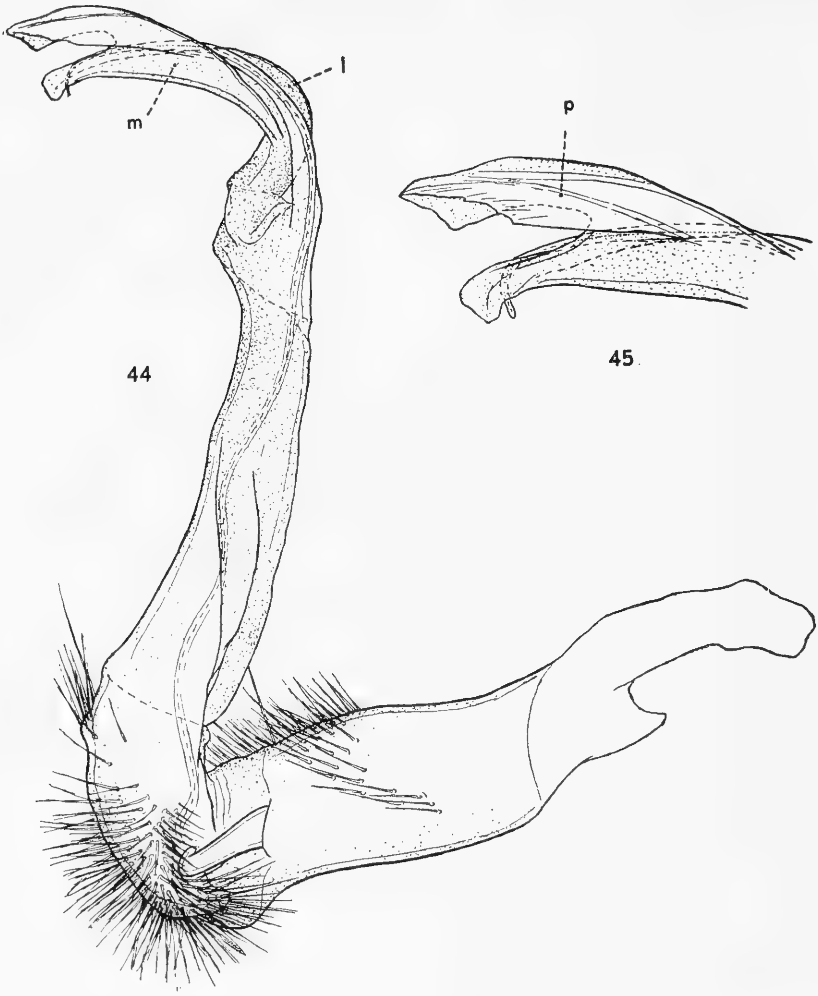


Fig. 44—45. *Gigantomorpha immanis* spec. nov. — 44: right gonopod of the holotype ♂, medial view; l: lamina lateralis; m: lamina medialis. 45: distal portion of the tibiotarsus of the same; p: laminate process of the lamina medialis

fading away towards the distal end. Femur not constricted halfway. End of tibiotarsus with a small simply rounded lobe. Lamina medialis with a well developed laminate process (*p*), which is T-shaped in cross section.

Female. — Aside from the usual secondary sexual characters the females differ from males by the somewhat more robust build, caused by the weaker constriction of the somites. Collum with a rectangular latero-posterior edge; the posterior margins of the lateral keels of the collum scarcely emarginate. Dorsal surface of metasomites a little more convex transversely, so that in none of the segments the lateral keels project dorsad of the middle of the tergites. Lateral keels comparatively a little less prominent, the posterior angles of the corresponding keels less acute than in the males. Sternites somewhat longer than broad; sternal cones present from the 5th to the 17th segments, somewhat more weakly developed than in the males. Legs not notably shorter, but disinctly more slender, in particular in the three proximal joints. Pubescence moderate, the ventral side of the joints without dense brushes, but only slightly more densely setiferous than the dorsal side. Femora straight. Length of joints: 3>6>5>2>4>1. The 6th joint somewhat more distinctly longer than the 5th than in the males.

Juvenile. — The juvenile ♀ with 19 segments is essentially similar to the adult females, although most of the characters are less pronounced. In particular the lateral keels are distinctly less prominent and generally do not project behind the margins of the somites.

Remarks. — The specimens of *immanis* collected in the Mahakkam river area differ in some minor details from the typical form from Mt. Tibang and Pajan River. At least the males appear to have a slightly smaller size: 6.0 to 6.6 mm as against 7.0 to 7.2 mm. Moreover the keels are very slightly less prominent because their lateral margins are a little more parallel to the longitudinal axis of the body. In the tail the basal lateral setiferous tubercles are decidedly more strongly developed. The setiferous tubercles of the anal scale are somewhat more strongly developed too, so that they are projecting very slightly behind the posterior margin. However, a much more abundant material is needed to decide whether these characters are of really subspecific value or just represent population varieties.

A form not directly referable to *immanis* although very closely related to that species was represented by a male and a female specimen from East Borneo, without nearer location (Coll. Dr. E. MJÖBERG, Mus. Stockholm). Width of ♂ 7.3 mm, of ♀ 7.6 mm. The male differs from that of *immanis* in the pubescence of the legs. The dense brushes on the ventral side of the joints distad of the coxa are thinning out in the legs of the second half of the body and disappear in those of the 15th to the 18th segments. As regards the characters of the anal segment both specimens agree with the *immanis* specimens from the Mahakkam area. Without more material and an exact locality it seems best not to name this particular form which may represent a subspecies of *immanis*.

Gigantomorpha cornalata spec. nov.

Material. — East Borneo: Birang river (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 2 ♂.

Differing from *immanis* in the following characters.

Colour. — Entirely similar to that of *immanis*.

Width. — 5.8 mm in both ♂.

Head and antennae. — The 6th antennal joint scarcely shorter than the 2nd.

Collum. — (fig. 46—47). Width in relation to the head larger than in *immanis*. Latero-posterior edge of keels somewhat more acute than in *immanis*, the posterior border of the keels almost straight. Surface more finely rugulose to subgranulose. Along the posterior border of the collum a few flat, rather indistinct tubercles resembling coarse wrinkles. The keels slightly turned upwards.

Body segments. — Surface of metatergites more finely rugulose to subgranulose. The tubercles along the posterior margin a little smaller than in *immanis*, but slightly more prominent. Sides somewhat more densely and more coarsely granulate.

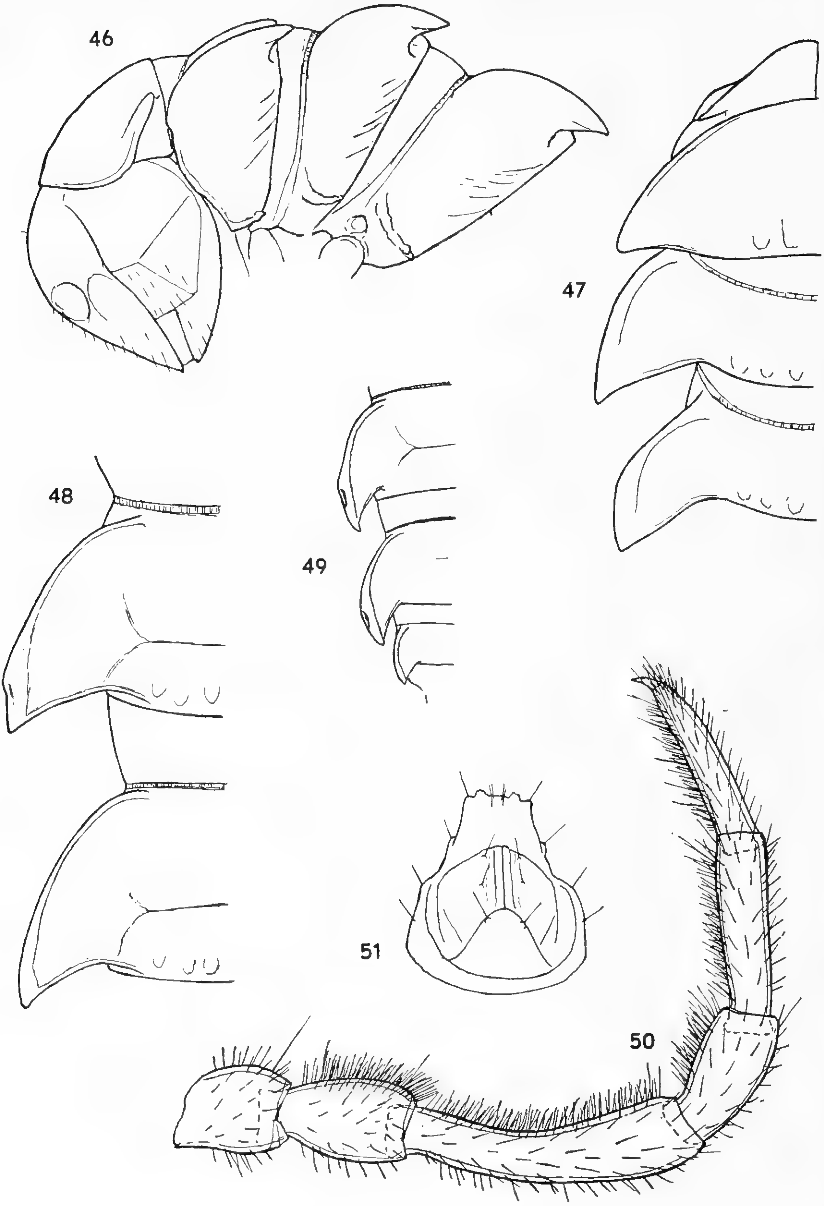


Fig. 46—51. *Gigantomorpha cornalata* spec. nov. — 46: left side of the head and the four anterior segments of the holotype ♂, lateral view. 47: left side of the head and the three anterior segments of the holotype ♂, dorsal view. 48: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 49: left side of the 17th, 18th and 19th segments of the holotype ♂, dorsal view. 50: leg of the 7th segment of the holotype ♂. 51: anal segment of the holotype ♂, ventral view

Pleural keels somewhat more strongly developed than in *immanis.* The anterior swellings more coarsely granular, disappearing earlier than the posterior cones which remain visible up to the 14th or 15th segment.

Lateral keels. — (fig. 47—49). More strongly developed than in *immanis.* The lateral margins more straight, diverging a little more strongly in caudal direction. Posterior edges more acute, curving somewhat inwards in the posterior segments, and projecting distinctly behind the posterior margin of the metasomites in all segments. Keels of all segments slightly turned upwards, projecting dorsad of the middle of the tergites from the 3rd to the 19th segments. Pores situated a little more laterally, the excavation of the marginal rim around the pores more distinct.

Sternites and legs. — Sternal process of 5th segment slightly constricted at the base. The distal end somewhat more rounded, though still weakly incised in the middle. From a lateral view the process is more attenuate and the end more narrowly rounded than in *immanis.* Legs (fig. 50) distinctly longer than in *immanis,* the proximal joints not particularly incrassate. Ventral brushes considerably less dense, the hairs longer. The brushes are gradually thinning out in the postgonopodial legs, but still remain rather dense even in the legs of the 17th segment. Length of joints: $3 > 5 > 6 > 2 = 4 > 1$.

Anal segment. — (fig. 51). The tubercles of the tail are more or less equally developed. Anal scale subtriangular, the posterior end more narrowly rounded.

Gonopods. — Similar to those of *immanis.* The anterior femoral crest more abrubtly ending distally.

Female. — Unknown.

Gigantomorpha aterrima spec. nov.

Material. — East Borneo: Balikpapan, S. Mentawir, 1—11 October, 1950 (Coll. A. M. R. WEGNER, Mus. Bogor), 3 ♂, 1 ♀.

Differing from *immanis* in the following characters.

Colour. — Entirely black, with the clypeal area of the head, the posterior part of the lateral margin of the keels, the venter and the end of the tail dark brown. Antennae, legs and sternite pale yellowish to brownish yellow. The 6th antennal joint infuscate towards the end, the 7th joint dark brown, but its distal part and the 8th joint whitish.

Width. — Holotype ♂ 7.3 mm, other ♂ 7.5 and 7.8 mm; ♀ 7.8 mm.

Head and antennae. — 6th antennal joint of about the same length as the 2nd, the 4th and the 5th; the 3rd somewhat longer.

Collum. — (fig. 52—53). Width in relation to the head larger than in *immanis.* Lateral sides of the keels very weakly emarginate in front of the latero-posterior edge. Latero-posterior angle somewhat more acute than in *immanis.* Posterior border of keels straight. Surface somewhat dull, much more finely rugulose than in *immanis.* Tubercles at the posterior margin weakly indicated.

Body segments. — Metatergites somewhat dull, very finely rugulose. The tubercles at the posterior margin distinct but rather small in most of the segments. Pleural keels as in *immanis,* disappearing in the 10th or 11th segment, those of the 4th segment not projecting behind the margin.

Lateral keels. — (fig. 52—55). Somewhat more strongly developed than in *immanis.* The posterior edges often sharply pointed and bent somewhat inwards, the points especially distinct in the keels of the posterior segments. Posterior edges in all segments projecting more or less behind the margin of the metasomites. Keels either horizontal or turned a little upwards, in the latter case they project dorsad of the middle of the metatergites either in a few anterior and posterior segments or in nearly all segments. Marginal rim of the keels in all segments distinctly narrower dorso-ventrally than in *immanis,* the dilatation around the pores

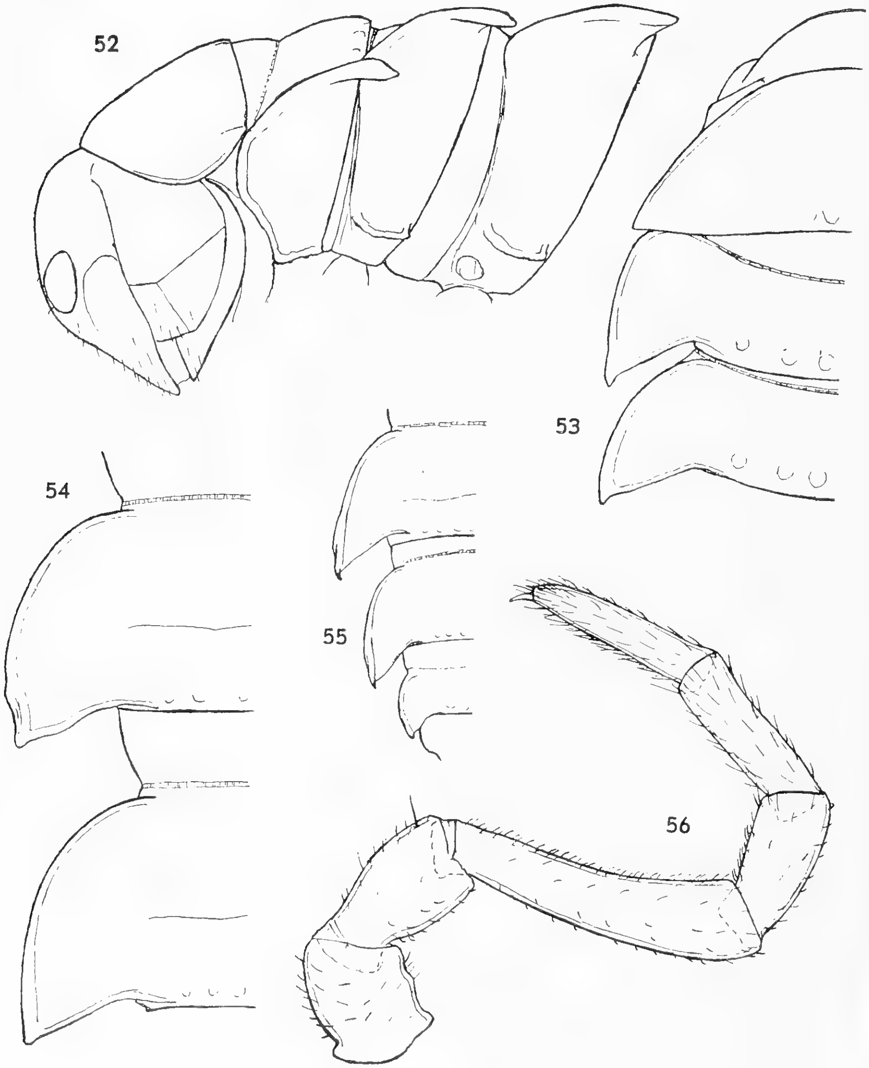


Fig. 52—56. *Gigantomorpha aterrima* spec. nov. — 52: left side of the head and the four anterior segments of the holotype ♂, lateral view. 53: left side of the head and the three anterior segments of the holotype ♂, dorsal view. 54: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 55: left side of the 17th, 18th and 19th segments of the holotype ♂, dorsal view. 56: leg of the 7th segment of the holotype ♂

smaller. Pores somewhat more lateral than in *immanis*, the excavation of the marginal rim in the pore area more distinct.

Sternites and legs. — Sternal process of 5th segment similar to that of *immanis*, but slightly narrower in lateral view. In posterior view the end is very weakly incised, appearing like a wide V. Legs (fig. 56) similar to those of *immanis*, very slightly less incrassate, the femora somewhat less strongly arched, the ventral pubescence of the distal joints less dense. Ventral pubescence of the proximal joints rather dense, at least in the legs of the anterior half of the body; the setae are very short and typically curved distad. In the legs of the second half of the body the pubescence is moderate, but the setae of the proximal joints remain short. Length of joints: 3>6>5>4 >2>1.

Anal segment. — Tail almost as in *cornalata*. Anal scale as in *immanis*, the setiferous tubercles a little more distinct.

Gonopods. — Similar to those of *cornalata*.

Female. — Aside from the usual secondary sexual characters the ♀ differs from the males in having a somewhat more robust appearance. Latero-posterior edge of collum somewhat less acute than in the males. Dorsum of metatergites only very little more convex. Lateral keels on a high level and in some anterior and posterior segments almost projecting dorsad of the middle of the tergites. Keels a little less prominent than in the males, the posterior edges scarcely less acute. Sternites somewhat broader than long, the cones similarly well developed. Legs slightly shorter but much more slender than in the males, moderately setiferous and without a more dense ventral pubescence, the hairs normal. Femora straight. Length of joints: 3>6>5>2 = 4>1.

Gigantomorpha pallida spec. nov.

Material. — East Borneo: S. Mentawir, 13 October, 1950 (Coll. A. M. R. WEGNER, Mus. Bogor), 3 ♂.

Differing from *immanis* in the following characters.

Colour. — Head rather dark brown, paler in the clypeal area. Antennae also rather dark brown, the 6th joint infuscate towards the end, the 7th joint also dark, but the distal end and the 8th joint whitish. Collum and the dorsal part of the pro- and metasomites of the subsequent body segments pale brownish gray. In the middle of the collum on each side straight behind the antennal sockets a rather small rounded brown spot. In the body segments the lateral part of the prosomites near the waist, the lateral part of the waist itself, the area of the metasomites before, immediately below and behind the lateral keels and the lateral part of the posterior border of the metasomites dark brown. The middle portion of the sides pale brownish gray. Venter, sternites and legs very pale brownish gray or pale brownish. Anal segment pale brownish gray, the sides of the anal ring and the valves dark brown.

Width. — Holotype 6.4 mm; other ♂ 6.4 mm and 6.8 mm.

Head and antennae. — Length of antennal joints as in *aterrima*.

Collum. — (fig. 57). Width in relation to the head somewhat larger than in *immanis*. Latero-posterior edges more acute, the posterior border of the keels somewhat more distinctly emarginate. Surface somewhat dull, finely rugulose to

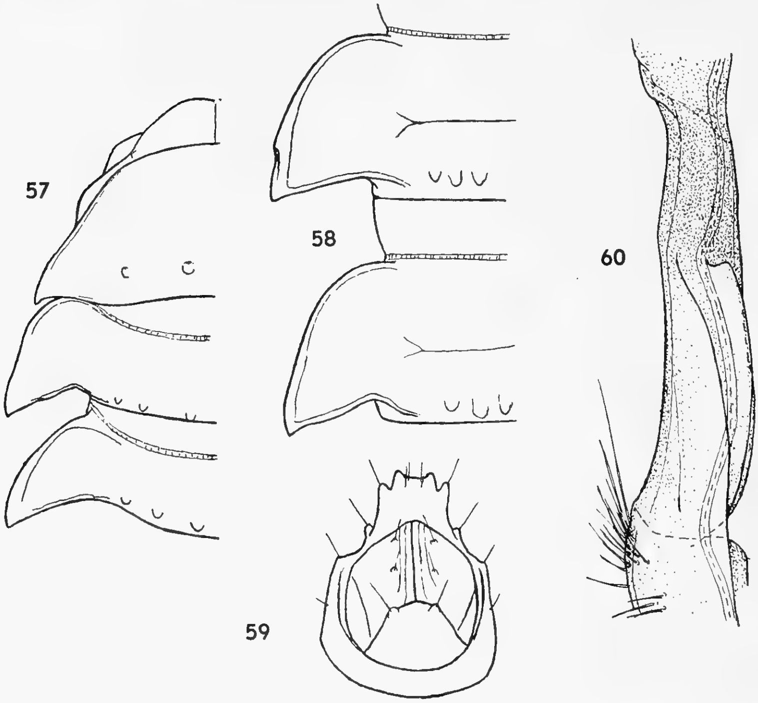


Fig. 57—60. *Gigantomorpha pallida* spec. nov. — 57: left side of the head and the three anterior segments of the holotype ♂, dorsal view. 58: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 59: anal segment of the holotype ♂, ventral view. 60: femur of the right gonopod of the holotype ♂, medial view.

sub-granulose, a few hairs may be present along the anterior border. Tubercles weakly indicated.

Body segments. — Metatergites rugulose to sub-granulose. Tubercles along the posterior margin small, but rather distinct. Tubercles in front of the transverse furrow almost obsolete. Sides somewhat more coarsely and densely granulate. Pleural keels more strongly developed than in *immanis,* the swellings more coarsely granulate, posterior cones well developed, disappearing on the 16th or 17th segment.

Lateral keels. — (fig. 57—58). Somewhat more strongly developed than in *immanis.* The posterior edges often with a small sharp point curving a little inwards, in particular in the posterior segments. The edges slightly more acute, scarcely or not projecting behind the margin of the segments in the middle part of the body, but more strongly than in *immanis* in the posterior segments. Pores more lateral than in *immanis*, the lateral emargination of the rim in the pore area somewhat more distinct.

Sternites and legs. — Sternal process of 5th segment distally acuminate from a lateral view, the distal end sub-laminate. From a posterior view the base is very slightly constricted, and the end is medially incised as in *aterrima.* Legs as in *immanis.*

Anal segment. — (fig. 59). The basal and distal lateral setiferous tubercles of the tail are distinctly more strongly developed. Setiferous tubercles of scale slightly projecting.

Gonopods. — (fig. 60). The anterior femoral crest ends abruptly; the end being even very slightly produced.

Female. — Unknown.

Gigantomorpha fasciata (Att.)

1898 *Prionopeltis fasciatus* Attems, Denks. Ak. Wien, vol. 67, p. 353, pl. 5, fig. 120—121 (1).
1912 *Prionopeltis fasciatus,* Carl, Rev. Suisse Zool., vol. 20, p. 141.
1937 *Pratinus fasciatus,* Attems, Tierreich, vol. 68, p. 115, fig. 150 (2).

Previous records. — Borneo (1); South Borneo: Bandjermasin (1), Pagat, Barabei (2).

Material studied. — East Borneo: S. Mentawir, 1—13 October, 1950 (Coll. A. M. R. WEGNER, Mus. Bogor), 4 ♂.

Differing from *immanis* in the following characters.

Colour. — Head black, brown in the clypeal area. Antennae very dark brown, particularly in the distal joints. The tip of the 7th and the 8th joint whitish. Collum and subsequent body segments black, with a rather narrow continuous pale brown mid-dorsal band running from the anterior border of the collum to the end of the tail. Lateral keels of collum and other segments with pale brown latero-posterior edges. Venter brown. Sternites pale brown to brownish yellow. Legs pale yellow. Anal segment. Sternites pale brown to brownish yellow. Legs pale yellow. Anal segment laterally and dorsally black, aside from the mid-dorsal band. The ventral side and the scale brown, the valves a little darker brown.

Width. — 5.5 mm, 5.5 mm, 5.6 mm and 5.6 mm.

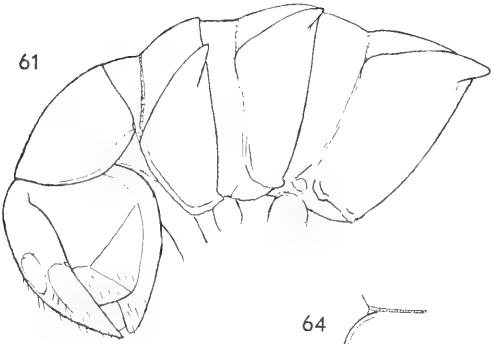
Head and antennae. — Length of antennal joints as in *aterrima.*

Collum. — (fig. 61—62). Width in relation to the head only a little larger than in *immanis.* Latero-posterior edges about rectangular, the posterior border of the keels nearly straight. Surface somewhat dull, sub-granulose, a few hairs along the anterior border. Tubercles obsolete. Lateral keels slightly raised above the horizontal level.

Body segments. — Metatergites somewhat dull, sub-granulose. Tubercles along the posterior margin small but distinct. Sides rather densely and somewhat more coarsely granulate. Pleural keels more strongly developed, similar to those of *cornalata,* disappearing in the 14th or the 15th segment.

Lateral keels. — (fig. 61—64). Very similar to those of *immanis*, but the posterior edges somewhat more acute in the posterior segments. 2nd segment wider than the collum, more distinctly than in *immanis.* All of the keels more or less raised above the horizontal level, projecting above the middle of the metatergites either in all segments from the 4th to the 19th or only in a few anterior and posterior segments. Pores distinctly more lateral, the marginal rim more distinctly emarginate than in *immanis.*

Sternites and legs. — Sternites scarcely longer than wide. Process of the sternite of the 5th segment distally acuminate from a lateral view, though not laminate. From a posterior view the process is slightly constricted at the base, the end



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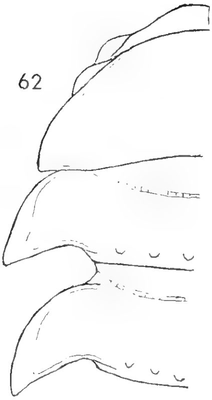

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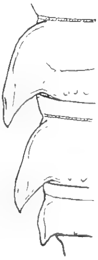

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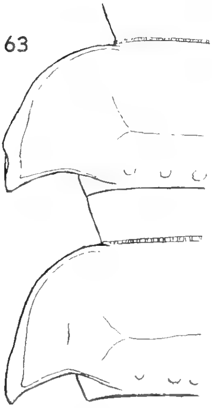

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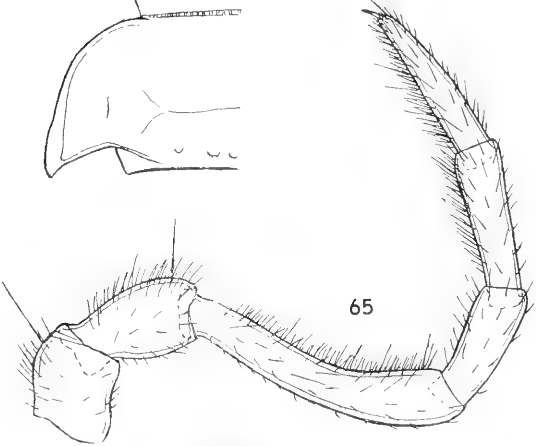

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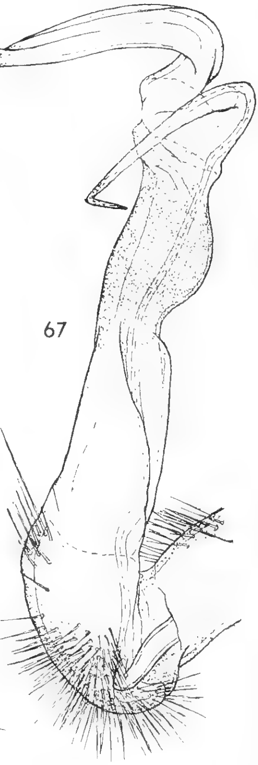

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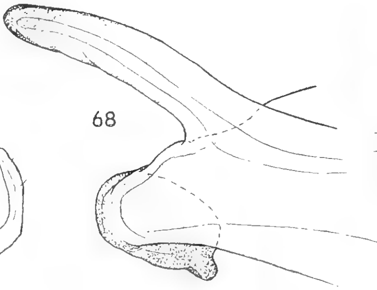

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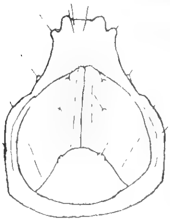

66

scarcely emarginate. Legs (fig. 65) rather long and not particularly incrassate. Ventral pubescence of the joints rather dense in the anterior legs, but gradually thinning out, becoming moderately dense in the legs of the posterior half of the body and normal in the last two pairs. Length of joints: 3 > 6 > 5 > 4 = 2 > 1.

Anal segment. — (fig. 66). Almost similar to that of *immanis*, but especially the distal lateral setiferous tubercles of the tail somewhat more strongly developed.

Gonopods. — (fig. 67—68). The anterior femoral crest rather thick, less laminate than in *immanis*, ending more abruptly distally. Femur distinctly constricted about halfway. Terminal lappet of tibiotarsus small. The end of the tibiotarsus curving laterad. The process of the lamina medialis rather weakly developed, subspiniform.

Remarks. — It is not without some doubt that the presently described material has been referred to *fasciata*, because the characters which actually have proved to be of diagnostic value, such as the shape of the lateral keels, the rate of development of the pleural keels, the shape and pubescence of the legs, etc., have scarcely been mentioned by ATTEMS. Of the lateral keels of the type material of *fasciata* only characters of generic value have been given, of the pleural keels we only know that they are disappearing in the second half of the body, and of the legs it has been said (vide CARL, 1912) that tarsal brushes are found only in the eight anterior pairs of legs.

In the present material typical tarsal brushes are absent, although the tarsi of the anterior legs are more densely setiferous, as usual indeed, than those of the middle and posterior legs.

Still, there appears to be no evidence justifying a specific separation of the present material. Obviously there is no important difference in coloration, the type specimens apparently having been slightly paler. In outline, the gonopods of the present specimens agree largely with the drawings published by ATTEMS, although, there remain some minor discrepancies as a comparison of the figures will show.

Although conforming essentially with the group of very closely related species embracing *immanis, cornalata, aterrima* and *pallida*, *fasciata* is decidedly more disjunct, in particular in the characters of its gonopods such as the femoral constriction, the weaker development of the process of the lamina medialis of the tibiotarsus, etc.

Gigantomorpha trichopleura spec. nov.

Material. — East Borneo: without nearer location (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 3 ♂, 3 ♀, 3 juv. ♂, 2 juv. ♀.

Differing from *immanis* in the following characters.

Fig. 61—68. *Gigantomorpha fasciata* (Att.). — 61: left side of the head and the four anterior segments of a ♂, lateral view. 62: left side of the head and three anterior segments of the same ♂, dorsal view. 63: left side of the 10th and 11th segments of the same ♂, dorsal view. 64: left side of the 17th, 18th and 19th segments of the same ♂, dorsal view. 65: leg of the 7th segment of the same ♂. 66: anal segment of the same ♂, ventral view. 67: telopodite of the right gonopod of the same ♂, medial view. (The solenomerite has moved out of its natural position). 68: distal portion of the tibiotarsus of the same

Colour. — Head more or less dark castaneous, paler in the clypeal area. Antennae brownish yellow, the end of the 6th and particularly the 7th joint dark brown. Tip of 7th and the 8th joint whitish. Collum and body segments more or less dark castaneous, the lateral keels entirely yellow or brownish yellow. Venter pale brown, the sternites and legs brownish yellow. Anal segment dark castaneous, the tail yellowish, the valves and the scales paler castaneous.

Width. — Holotype ♂ 5.0 mm; other ♂ 5.0 mm; ♀ 5.4 mm each juvenile ♂ with 19 segments 3.1 mm, 3.1 mm and 3.2 mm; juvenile ♀ with 19 segments 3.3 mm; juvenile ♀ with 18 segments 2.5 mm.

Head and antennae. — Headplate rather weakly to sparsely setiferous in the clypeal and frontal parts. Length of antennal joints as in *aterrima.*

Collum. — (fig. 69—70). Subsemicircular in dorsal outline. Sides rather widely rounded, without a latero-posterior edge. Latero-anterior border almost straight above the lateral rounding, posterior border with a weak notch above the lateral rounding. Surface shining and rugulose as in *immanis*, a few bristles along the anterior margin, tubercles obsolete. The lateral margins slightly raised, the dorsal surface moderately convex. Marginal rim rather weakly developed but extending to the latero-posterior border.

Body segments. — Metatergites shining, rugulose, tubercles small but distinct, generally 8 to 10 in front of the posterior border and 4 in front of the transverse furrow. Tubercles sometimes setiferous. Transverse furrow indicated in the 3rd segment, generally well developed from the 4th to the 18th segments. Sides rather weakly rugulose but rather coarsely granulate, in particular up to the 4th segment. Along the posterior margin of the metasomites below the level of the keels an irregular row of setae present up to about the 17th or 18th segment. Pleural keels present up to the 17th segment, obsolete from the 18th onwards. They are well developed and represented by complete, granulate to subtuberculate ridges up to the 6th segment. From about the 7th segment the pleural keels consist of a well developed longitudinal swelling which is densely granulate above the anterior legs and granulate to subtuberculate above the posterior legs of each segment. A posterior cone, directed laterad and somewhat caudad is well developed, but it does not project behind the margin of the segments in the posterior half of the body.

Lateral keels. — (fig. 69—72). Anterior border of keels of 2nd segment weakly rounded, latero-anterior edge with a small tooth. Lateral border widely rounded, the margin somewhat irregular. Latero-posterior edge obtusely angular. Marginal rim rather weakly developed, the pre-marginal furrow complete. Keels of 2nd segment directed somewhat ventrad, their level distinctly below that of the keels of the 3rd segment. Keels of the 3rd segment almost horizontal. From the 4th segment onwards the keels are horizontal and do not project dorsad of the metatergites. Pre-marginal furrow of the keels of the 3rd and 4th segments com-

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Fig. 69—76. *Gigantomorpha trichopleura* spec. nov. — 69: left side of the head and the four anterior segments of the holotype ♂, lateral view. 70: left side of the head and the three anterior segments of the holotype ♂, dorsal view. 71: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 72: the same, lateral view. 73: leg of the 7th segment of the holotype ♂. 74: anal segment of the holotype ♂, ventral view. 75: right gonopod of the holotype ♂, medial view. 76: distal portion of the tibiotarsus of the same

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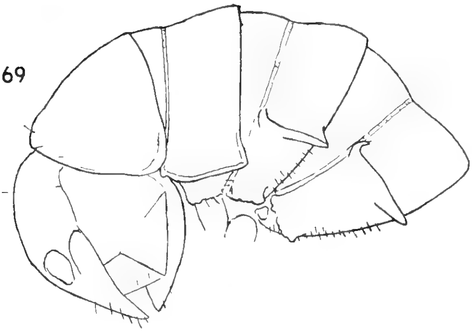

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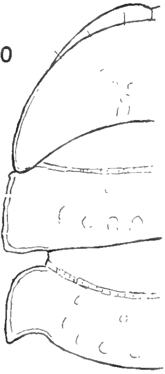

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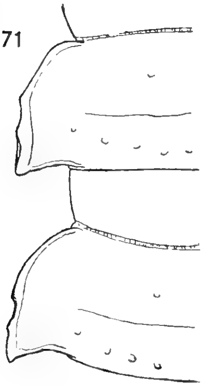

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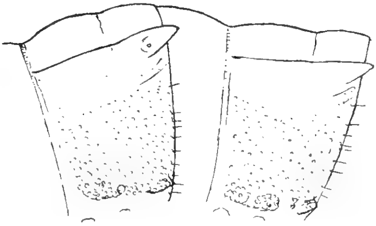

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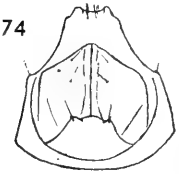

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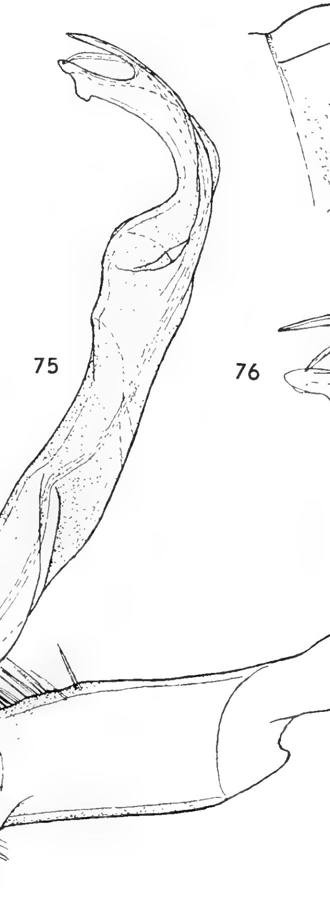

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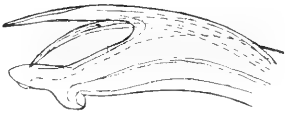

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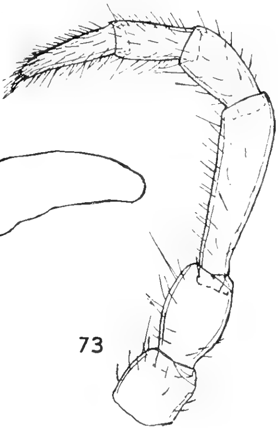

plete. In all segments the lateral keels project behind the posterior margins of the segments, especially in the posterior segments where the posterior edges of the keels are more acute than in *immanis* and have a sharply pointed end curving inwards a little. Marginal rim of keels from the 5th segment onwards with a slight lateral prominence about halfway followed up by an emargination. Pores lateral, in most of the segments not visible from the dorsal side. Pore area rather weakly emarginate.

Sternites and legs. — Sternites of middle segments about one and a quarter longer than wide. Sternal process of the 5th segment distally acuminate when seen from the lateral side, the end even sublaminate. From a posterior view the process is not constricted at the base and the sides are parallel. The end has a very wide V-shaped incision. Legs (fig. 73) moderately setiferous, more densely only in the tarsi. Ventral side of the joints a little more densely setiferous than the dorsal side but without brushes. Legs of moderate length, rather thick, the femora straight. Length of joints: 3>6 = 2>4>5 >1.

Anal segment. — (fig. 74). Tail very broad at the base, the sides strongly converging, a little concave. Basal and distal lateral setiferous tubercles very small, terminal tubercles moderately developed. Dorsal transverse depression weak or obsolete. Scale with well developed setiferous tubercles, projecting behind the margin and equalling the middle of the posterior border.

Gonopods. — (fig. 75—76). The coxal setiferous area does not extend to the medial side. Tibiotarsus comparatively smaller than in *immanis*, the terminal end distinctly bifid. Process of lamina medialis less strongly developed, subspiniform.

Female. — Aside from the usual secondary sexual characters the ♀ differs from the ♂ in having a distinctly more robust appearance. The segments are somewhat less constricted in the waist area and the lateral keels are distinctly less prominent, their posterior edges somewhat less acute. Keels from the 3rd segment to the segments of the middle of the body not projecting behind the posterior margins of the segments. Sternites as long as wide. Legs a little more slender than in the ♂. Pubescence rather weak, that of the ventral side of the joints not different from that of the dorsal side. Length of joints: 6>3>2>4 = 5>1.

Juvenile. — The juvenile specimens agree essentially with the ♀. The sculpture of the collum and the metatergites is rather weakly rugulose, tubercles are missing, but a few more hairs are present. The hairs along the lateral and ventral margins of the somites are absent. The lateral keels are relatively much less developed than in the adults.

Remarks. — Although *trichopleura* and the closely related *spinescens* are rather disjunct from the other species of *Gigantomorpha*, there can be no doubt as to the correctness of the present reference, since the gonopod structure in the two species is basically the same as in *immanis*. In this respect, the genus *Gigantomorpha* is a perfect example to show the dubious value of the level of the lateral keels of the 2nd segment as a taxonomic character. Doubtless previous authors merely on account of this sole character would have referred *immanis* to the genus *Pratinus* and *trichopleura* to *Orthomorpha*.

Gigantomorpha spinescens spec. nov.

Material. — East Borneo: without nearer location (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 2 ♂, 1 ♀.

Differing from *immanis* in the following characters.

Colour. — Exactly similar to that of *trichopleura.*

Width. — Holotype ♂ 6.8 mm; other ♂ 6.3 mm; ♀ 8.0 mm.

Head and antennae. — Pubescence of head as in *trichopleura.* Length of antennal joints as in *aterrima.*

Collum. — (fig. 77—78). Relative width of collum in comparison to the head somewhat larger than in *immanis.* Dorsal outline subtrapezoidal to subsemicircular.

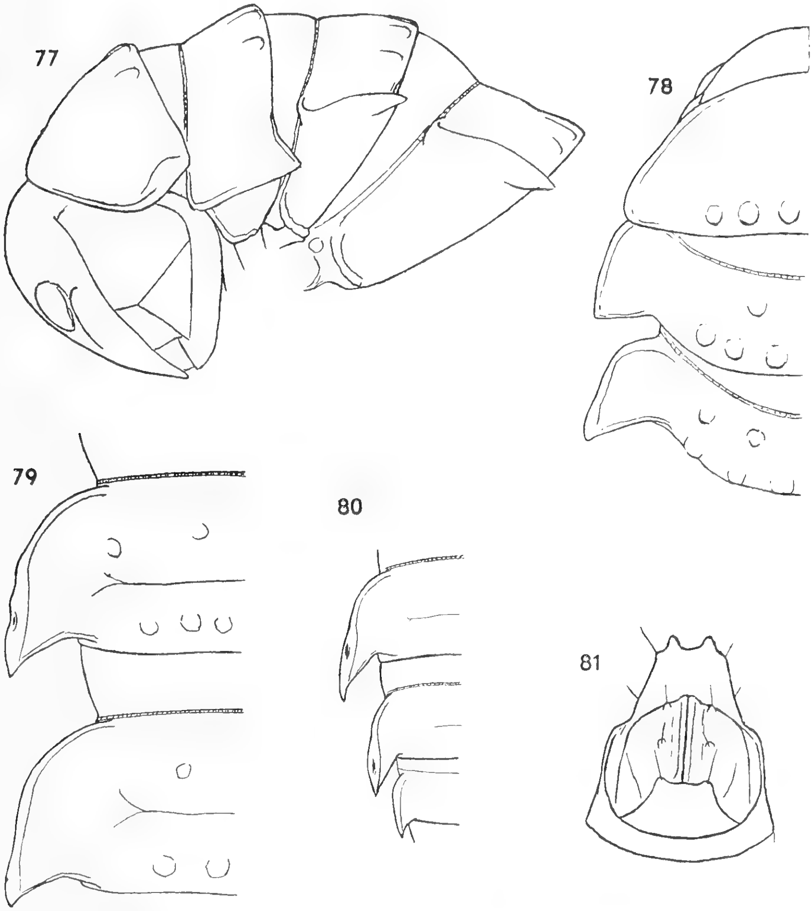

Fig. 77—81. *Gigantomorpha spinescens* spec. nov. — 77: left side of the head and the four anterior segments of the holotype ♂, lateral view. 78: left side of the head and the three anterior segments of the holotype ♂, dorsal view. 79: left side of the 10th and 11th segments of the holotype ♂, dorsal view. 80: left side of the 17th, 18th and 19th segments of the holotype ♂, dorsal view. 81: anal segment of the holotype ♂, ventral view

Anterior border evenly rounded. Sides rather widely rounded, without a distinct latero-posterior edge, although the lateral rounding is somewhat narrower at the posterior side. Posterior border of the lateral sides straight, with a weak notch above the lateral rounding. Surface somewhat dull, rather coarsely rugulose to subgranulose. A few tubercles along the posterior border are either weakly indicated or rather distinct. Lateral keels somewhat raised but not attaining a horizontal level. Marginal rim laterally weakly developed, the furrow almost obsolete laterally.

Body segments. — Metatergites somewhat dull, rather coarsely rugulose to subgranulose. Along the posterior margin six to, sometimes, eight rather large, distinct tubercles. In the anterior segments there are also four large flat tubercles behind the waist, which, however, rapidly grow less distinct on the subsequent segments to become faintly indicated or obsolete in the segments of the middle and posterior parts of the body. Transverse furrow of metatergites present, though weakly developed, also in the 4th and the 18th segments. Sides rather coarsely granular, in particular up to the 4th segment. Pleural keels more or less similarly developed as in *immanis* but the anterior swelling somewhat more densely granulate; the posterior cones disappear in the 14th or 15th segment, the swellings remain up to about the 17th segment.

Lateral keels. — (fig. 77—80). Keels of 2nd segment largely similar to those of *trichopleura*. The latero-anterior edge without a tooth, but obtusely angular. Latero-posterior edge about rectangular. Lateral keels of the other segments also largely similar to those of *trichopleura*, the posterior edges more acute, becoming more or less spiniform in the posterior segments. Keels mostly horizontal, only those of the posterior segments raised slightly above the horizontal level but just not projecting dorsad of the middle of the metatergites. Marginal rim of keels with a similar lateral prominence, though much less distinct, than in *trichopleura.*

Sternites and legs. — Sternal process of the 5th segment differing from that of *trichopleura* only in being somewhat constricted at the base. Legs as in *trichopleura,* the ventral pubescence of the joints somewhat more dense.

Anal segment. — (fig. 81). Tail similar to that of *trichopleura*, the sides, however, converging somewhat less strongly and not concave. Scale with setiferous tubercles strongly developed, projecting well caudad of the middle of the posterior margin.

Gonopods. — Similar to those of *trichopleura.*

Female. — Differing from the ♂ in the same characters as does the ♀ of *trichopleura* from the ♂ of that species. Sternites somewhat broader than long.

Remarks. — A species very closely related to *spinescens* was represented by a single female specimen from West Borneo: Sambas, October, 1893 (Borneo Exped., Coll. Dr. Hallier, Mus. Leiden). It has a width of 7.2 mm and agrees with *spinescens* in colour and general appearance. The main differences are found in the smaller tubercles of the metatergites, the acute posterior edge of the lateral keels of the 2nd segment, the much less elongate lateral keels of the posterior segments and the development of the tubercles of the tail, which resemble those of *pallida.*

In Celebes the genus *Gigantomorpha* is represented by a single species:

Gigantomorpha socialis (Carl)

1912 *Prionopeltis socialis* Carl, Rev. Suisse Zool., vol. 20, p. 139, pl. 5, fig. 13—15.
1937 *Pratinus socialis,* Attems, Tierreich, vol. 68, p. 116, fig. 151.

Distribution. — South Celebes: Bontorio.

In colour this species apparently resembles *immanis* and *cornalata.* In the characters of the legs it seems to agree with *immanis.* The collum, however, has the lateral sides rounded, the pleural keels remain visible up to the 16th or 17th segment, so that *socialis* is clearly distinct from both *immanis* and *cornalata.* The gonopods of *socialis* apparently have the generic characters of *Gigantomorpha,* although the details of the acropodite have not been sufficiently illustrated.

Orthomorpha Bollm.

1859 *Polydesmus* (*Paradesmus*) De Saussure, Linn. Ent., vol. 13, p. 325.
1869 *Polydesmus* (*Paradesmus*), Humbert & De Saussure, Verh. zool. -bot. Ges. Wien, vol. 19, p. 670.
1893 *Orthomorpha* Bollman, Bull. U.S. Nat. Mus., vol. 46, p. 159, 196.
1909 *Orthomorpha,* Pocock, Biol. Centr.-Amer., Diplop., p. 159.
1914 *Orthomorpha* (*Orthomorpha*), Attems, Arch. Naturg., vol. 80A, fasc. 4, p. 190.
1939 *Asiomorpha* Verhoeff, Zool. Anz., vol. 127, p. 117.
1944 *Brasilogonopus* Verhoeff, Arq. Mus. Nac. Rio de Janeiro, vol. 37, p. 274.
1958 *Oxidus* (*Orthomorphina)* Kraus, Senck. Biol., vol. 39, p. 100.

Type-species. — *Polydesmus beaumontii* Le Guillou, by subsequent designation: Pocock, 1909. (Type-species of *Asiomorpha*: *Polydesmus coarctatus* De Saussure, by monotypy; of *Brasilogonopus*: *B. attemsi* Verhoeff, by monotypy; of *Orthomorphina*: *Polydesmus coarctatus* De Saussure, by original designation).

Range. — Burma, Indochina, Siam, Malayan Peninsula, Java, Borneo, Philippines; one species has a circumtropical distribution.

Number of species. — 33 and one variety.

Remarks. — A discussion of the taxonomy of the genus has to be preceded by some remarks relating the correctness of the application of the name *Orthomorpha* and the designation of the type-species.

Orthomorpha was introduced by Bollman in 1893 as a substitute for *Paradesmus* Sauss., a name preoccupied by *Paradesmus* Corda. As such, *Orthomorpha* has been generally accepted and used by all subsequent authors.

It is, therefore, rather surprising to find that the name *Paradesmus* Corda is not included in the well-known Nomenclator Zoologicus by Neave. As a matter of fact, in this Nomenclator we find behind the name *Orthomorpha* the addition: "in err.?", suggesting the probability of Bollman's name being superfluous. Apparently, this condition recently has led to some confusion as regards the correctness of the use of *Orthomorpha* and required some investigation.

Paradesmus has been used as a generic name first by A. J. C. Corda in a paper: "Ueber die Infusorien der Carlsbader Quellen", published in: J. de Carro, Almanach de Carlsbad, 1835. Unfortunately, this paper was not available to me. An abstract, however, was given by A. F. A. Wiegmann in the "Bericht über die Leistungen im Felde der Zoologie während des Jahres 1835" which appeared in Arch. Naturg., vol. 2, fasc. 2, p. 184 (1836).

Besides a discussion of CORDA's paper by WIEGMANN, this article contains also a synonymic list by C. G. EHRENBERG of the genera and species described by CORDA. In this list, *Paradesmus Folium* Corda is referred with some doubt to the genus *Fragilaria* which belongs to the botanical Class Diatomeae. There seems to be little doubt therefore that *Paradesmus* Corda was based on a vegetable organism.

Contrary to this present day opinion, authors around 1835, or at least a number of them, apparently were of the opinion that the Diatomeae (or Bacillaria, as they were called at that time) were part of the animal kingdom. This is proved, for instance, by the admission of *Paradesmus* Corda and other botanical genera, united as a group Polygastrica, in the Nomenclator Zoologicus by AGASSIZ (1842—1846).

Whether or not CORDA actually described *Paradesmus* as a zoological genus I am unable to ascertain since I did not have access to his paper, but from WIEGMANN's discussion it may be inferred that CORDA regarded the organisms described by him as animals. This question, however, becomes irrelevant, since EHRENBERG ended his synonymic list, which included *Paradesmus,* with the significant words: "Alle übrigen Formen kann ich nicht für Thiere anerkennen".

From the available evidence I have concluded that *Paradesmus* Corda at least for some time has figured as a generic name in zoology, so that according to article 2 of the International Code the substitution of *Paradesmus* Sauss. by *Orthomorpha* Bollm. was quite correct.

There has been a considerable diversity of opinion as to the question which species should be regarded as the type of the genus *Orthomorpha.*

In BOLLMAN's paper of 1893 the name has been mentioned two times. The author introduced it first on page 159, where in a footnote is stated: "*Orthomorpha* Bollman for *Paradesmus* Saussure, which is preoccupied". On page 196 of the same paper the name is used again with the addition: "*Orthomorpha,* nom. gen. nov. for *Paradesmus* Saussure, which is preoccupied by *Paradesmus* Corda, Polyg.". From this evidence one can only conclude that the name was proposed as a direct substitute for *Paradesmus* Sauss. The type-species of *Orthomorpha* consequently must be one of the species included in the original concept of *Paradesmus.*

As far as I am aware a type-species of *Paradesmus* has not been designated previous to 1893. Afterwards three opinions on this matter have been brought forward.

The first of these has been the one of COOK and SILVESTRI, who in 1895 and 1896, respectively, without any comment, designated *O. coarctata* (Sauss.) as the type of *Orthomorpha,* in which they were followed subsequently by ATTEMS, for instance in the "Tierreich" in 1937.

The action by SILVESTRI was criticized by POCOCK in 1909, with the following cogent arguments:

"The name *Paradesmus,* Saussure, was originally applied to the following species: — Section I. *P. carolinensis;* Section II. *P. klugi, P. erchsoni, P. picteti;* Section III. *P. beaumonti* (Linn. Ent., xiii, pp. 325, 326, 1859). One of these must be its type, the addition of *P. coarctatus* to the list in 1860 (Mem. Soc. Phys. Genève, xv, p. 297) not in any way affecting the question. As a matter of fact this question was settled by Humbert and Saussure in 1869 (Verh. z.-b. Ges. Wien, xix, p. 670), who eliminated the members of Sections I. and II., respectively under the names *Euryurus* and *Pachyurus*, and restricted *Paradesmus* to Section III., making *P. beaumonti* its type species*). But since *Paradesmus* was preoccupied, Bollman proposed *Orthomorpha* to replace it. Therefore *P. beaumonti* is the type of *Orthomorpha* and not *P. coarctatus* as Silvestri asserts (Ann. Mus. Genova (2) xvi, p. 198, 1896)."

Nothing needs to be added to POCOCK's words, which quite satisfactorily settle the point.

In 1911, however, COOK rejected POCOCK's type designation, maintaining that the Sections I and III of *Paradesmus* were considered by DE SAUSSURE as forming transitions to other genera. According to COOK the name *Orthomorpha* could therefore be applied only to the species of Section II. Fortunately COOK's designation of *P. klugii* Brandt as the type of *Paradesmus* was antedated by that of POCOCK, for the acceptance of his proposal would have caused a lamentable amount of confusion in nomenclature since the species of Section II belong to the family Euryuridae. As a matter of fact his opinion scarcely found any notice in literature.

In the previous pages of this paper I have already emphasized the heterogeneity which exists in the genera *Orthomorpha* and *Pratinus* as conceived by ATTEMS in the Tierreich in 1937. From *Orthomorpha* two species, namely *O. rotundata* Att. and *O. borneona* Att. have already been separated and brought to the new genera *Dajakina* and *Arthrogonopus*, respectively. The genus *Pratinus* was brought back to its original concept, and it was pointed out that most of the species which had been referred to this genus by ATTEMS are true species of *Orthomorpha*. For "*Pratinus*" *fasciatus* (Att.) and "*P.*" *socialis* (Carl) and a number of newly described species the genus *Gigantomorpha* has been erected.

The re-examination of the type-species of *Orthomorpha* gives a good opportunity for a discussion of the taxonomic status of the remaining species of *Orthomorpha* and *Pratinus*.

In 1937, ATTEMS recognized two subgenera of *Orthomorpha*: *Orthomorpha* s. str. and *Kalorthomorpha* Att., 1914. Of course the latter name by isotypy is an objective junior synonym of *Oxidus* Cook, 1911. In 1945, CHAMBERLIN has already proposed to treat *Oxidus* as a separate genus, and in 1953, ATTEMS too, although persistently rejecting COOK's name, appears to have held the same opinion as regards *Kalorthomorpha*. Although this proposal is quite correct inasmuch as the type-species of *Oxidus, O. gracilis* (C. Koch) seems to have no obvious relationship with the type-species of *Orthomorpha,* it does not bring us a step nearer to the solution of the main problem, the unraveling of the systematic confusion existing in both genera.

As I have already stated in connection with the genus *Gigantomorpha*, many of the species previously referred to the genus *Pratinus* are to be reallocated in

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*) Here POCOCK has been obviously mistaken, as HUMBERT and DE SAUSSURE did not actually indicate a type-species; they merely referred *beaumontii,* together with *coarctatus*, to *Paradesmus* in the restricted sense. Of course this does not affect the intention of his argument.

the genus *Orthomorpha.* Up to now the sole character used for the distinction of *Pratinus* and *Orthomorpha* has been the position of the lateral keels of the second segment. Species in which these keels are situated on about the same level as those of the third segment have been referred to *Pratinus*, species in which these keels are situated below the level of those of the third segment have been brought to *Orthomorpha.* That this character is of comparatively little importance was shown already in *Gigantomorpha.* Still, previous authors, namely ATTEMS and VERHOEFF, have attributed to the character a primary systematic value even against the evidence of the gonopods. The latter author even went so far as to base a family, Prionopeltidae (= Pratinidae SCHUBART), on this single character. This family quite correctly was discarded by ATTEMS as an artificial group in 1938 and 1953, but curiously enough the latter author apparently would not risk uniting the generic categories involved.

In 1953, ATTEMS erected the subgenus *Paternostrana* for the species of *Orthomorpha* in which the posterior edges of the lateral keels are rounded instead of angular. The species referred by him to this subgenus were the following: *O. rotundata* Att., *constricta* (Carl), *hirtipes* (Carl), *borneona* Att., *sumbawana* Att., *javanica* (Att.), *thienemanni* Att., and a new species *minuscula* Att. Although ATTEMS was quite correct in separating these species from *Orthomorpha*, the choice of the character upon which he based his subgenus was most unlucky, since by evidence of the gonopod structure of the pertaining species it brings together a number of quite unrelated forms.

As yet a type-species of *Paternostrana* has not been designated. To validate the name, *Orthomorpha sumbawana* Att. is herewith selected as the type-species of *Paternostrana.* Further reference to this genus will be found under category XI of the discussion of the species of *Orthomorpha.*

I arranged the species of *Orthomorpha* s.str., *Pratinus* and *Paternostrana* sensu ATTEMS, as far as they are not referred in the previous pages to other genera, in a number of groups which are based in the first instance on the structure of the gonopods.

Some of these groups may well prove to represent generic categories. For some of them generic names are already available, and these have been used here, although provisionally. For others generic names will have to be proposed; the introduction of new names, however, is deliberately deferred to a later period, pending actual study of the species involved.

The present arrangement is based largely upon literature data. It has been, however, greatly facilitated by an inspection of the POCOCK types in the British Museum during a short visit there.

(I) — In this group are brought the species most closely associated with the type-species of *Orthomorpha, O. beaumontii* (Le Guillou). A comparatively large number of these hitherto have been referred to *Pratinus,* although others already belonged to the genus according to the concept of previous authors. Some species, previously considered of doubtful generic status, also are included, partly as a result of the examination of the type material and partly on the evidence of identified material.

In the species of this group the gonopods are of an extremely uniform type, apparently changing very little during the course of speciation and failing to give us reliable characters for specific distinction generally. The gonopods are characterized by the laterally sharply demarcated postfemur and by a tibiotarsus in which the lamina medialis and the lamina lateralis both are well developed, sheathing the solenomerite for its greater part. The tibiotarsus lacks larger accessory processes and terminates in a number of minute lappets, usually three. The spermal channel runs along the medial side of the femur. However, characteristic for the species of this group seems to be that in the prefemur and at the base of the femur it follows a course along a typical fold in a more or less posterior direction to bend abruptly distad when reaching the posterior side of the femur. All the species of this group seem to have strongly developed lateral keels, with the pores located laterally in a rather strongly thickened marginal rim.

The following species belong here.

Orthomorpha	*acutangulus* (Newport, 1844)	Philippines
—	*arboricola* (Att., 1937)	Indochina
—	*beaumontii* (Le Guillou, 1841)	Borneo
—	*bipunctata* (Sinclair, 1901)	Malacca
—	*cambodjana* (Att., 1953)	Indochina
—	*clivicola* Poc., 1895	Burma
—	*coarctata* (Sauss., 1860)	Circumtropical
—	*coarctata* var. *gigas* Att., 1927	Teun Id., Banda Sea
—	*consocius* Chamb., 1945	Java
—	*conspicua* (Poc., 1894)	Java
—	*flaviventer* (Att., 1898)	Java
—	*francisca* Att., 1930	Lombok
—	*fuscocollaris* Poc., 1895	Tenasserim
—	*gestri* Poc., 1895	Tenasserim
—	*glandulosa* (Att., 1937)	Indochina
—	*granosa* (Att., 1953)	Indochina
—	*hydrobiologica* Att., 1930	Java, Indochina
—	*insularis* Poc., 1895	Tenasserim
—	*intercedens* Att., 1937	Burma, Tenasserim
—	*karschii* (Poc., 1889)	Mergui, Tenasserim
—	*montana* (Chamb., 1921)	Philippines
—	*monticola* Poc., 1895	Burma
—	*oatesii* Poc., 1895	Tenasserim
—	*palonensis* Poc., 1895	Burma
—	*paviei* Brol., 1896	Siam
—	*rotundicollis* (Att., 1937)	Indochina
—	*spinala* Att., 1932	Karimon Djawa
—	*tenuipes* (Att., 1898)	Java
—	*tuberculata* (Att., 1937)	Indochina
—	*unicolor* (Att., 1930)	Java
—	*weberi* (Poc., 1894)	Java
—	*zehntneri* Carl, 1902	Java

The type specimens of *O. acutangulus* (Newp.) in the British Museum, a male and a fragment of a female specimen in the dry collection, have been examined. The species clearly belongs to the present group, although the tibiotarsus in both gonopods is broken off. It is one of the species which previously would have been referred to the genus *Pratinus*, the keels of the 2nd segment being on a high level.

For the reasons why *O. beaumontii* belongs here, the reader is referred to the remarks on page 272 relating to that species.

In the following two categories some species are brought together which although probably rather closely related to those of the first group seem to be somewhat disjunct by evidence of the gonopod structure. Their taxonomic position remains somewhat uncertain.

(II) — The single species of this category differs from the species of group (I) by having a comparatively shorter gonopod femur and by the apparent lack of a sharply demarcated postfemur. The distal end of the tibiotarsus, however, seems to be similar to that in the more typical species of *Orthomorpha*, and the species may prove after re-examination to be only a somewhat aberrant form of the first group.

Orthomorpha butteli (Carl, 1922)	Java

(III) — This group also consists of a single species which, if we may trust CARL's drawing of the gonopod, lacks a sharply defined postfemur. Moreover, the distal end of the tibiotarsus of the gonopods differs from that of the species of the first group by being more deeply split.

Orthomorpha bipulvillata Carl, 1902	Java

The following groups consist of species considered to be either subgenerically or generically distinct from the species of group (I). For some of these categories generic names are already available, for others new names will have to be proposed, an action, however, which better be deferred until actual study of the species involved.

(IV) — The single species of this group was referred to the genus *Pagioprium* by ATTEMS in 1937. In the meantime, however, it was shown (JEEKEL, 1951) that it is not congeneric with the type-species of that genus, a species now belonging to the genus *Tectoporus* Carl. In the gonopods "*O.*" *cornuta* differs from the species of group (I) by the characteristically notched lamina medialis of the tibiotarsus, and apparently also by the absence of a sharply demarcated postfemur. The smooth waist of the body segments, the absence of pleural keels and the typical structure of the margins of the lateral keels also may prove to be characters of subgeneric or generic value.

"*Orthomorpha*" *cornuta* Att., 1930	Sumbawa (and Sabang?)

(V) — This category also consists of one species which apparently has no distinct demarcation between the femur and the postfemur of the gonopods, and has a characteristically reduced tibiotarsus. The lateral keels seem to resemble those of the species in the first group, but the waist of the body segments has no sculpture and pleural keels are missing.

"*Orthomorpha*" *anastasia* Att., 1930	Lombok

(VI) — The two forms referred to this group present another instance of the taxonomic confusion which has resulted from using the position of the lateral keels of the 2nd segment as a discriminating character. The first form was described as a *Pratinus*, the second as an *Orthomorpha*, but if it were not for some small discrepancies in the descriptions, one would be inclined to unite both on account of the practically complete identity of the gonopods.

Both species lack a demarcation between femur and postfemur in the gonopods, and furthermore differ from the species of the first category in the structure of the marginal rim of the lateral keels. The tibiotarsus has not been described clearly, but seems to have a typical structure and way of sheathing the solenomerite.

"*Orthomorpha*" *exarata* (Att., 1953)	Indochina
— *setosa* Att., 1937	Indochina

(VII) — Referable to this category is a single species, which seems to have sufficient characteristic features to justify a generic separation from *Orthomorpha*. As a matter of fact, it was made the type-species of a genus *Leiozonius* by Attems in 1953, after having been referred to *Pratinus* originally. *Leiozonius*, which, as far as I am aware, was in fact a nomen nudum, is characterized in the gonopods by the structure of the tibiotarsus in which the lamina medialis seems to be unusually strongly developed as against the somewhat reduced lamina lateralis, so that the solenomerite appears to be applied to the lateral side of the tibiotarsus, a condition somewhat reminiscent of what is found in the genus *Tectoporus*. Generic characters also may be the absence of a distinct postfemur in the gonopods, the smooth waist of the body segments and the absence of a transverse furrow on the metatergites.

Leiozonius levigatus (Att., 1937)	Indochina

(VIII) — In 1953 Attems described a genus *Piccola* which was based on a single species, *P. odontopyga*. Apparently on account of the position of the lateral keels of the 2nd segment, the genus was compared with *Pratinus* and separated from it by the absence of well developed lateral keels, the absence of a sternal process in the 5th segment of the male, the irregularly wrinkled waist and the long terminal tubercles of the tail. However, a comparison of the gonopod structure of *P. odontopyga* with that of certain species referred to the genus *Orthomorpha* shows once again that too much value has been given to the characters of the lateral keels of the 2nd segment. Indeed, *P. odontopyga* is closely associated with five species previously referred to *Orthomorpha*. The whole group is characterized by the absence of a sharp demarcation between femur and postfemur of the gonopods, by the weak development of the lamina medialis of the tibiotarsus, and, apparently by the presence of a typical laminate crest on the medial side of the basal half of the gonopod femur.

Piccola banana (Att., 1937)	Indochina
— *corrugata* (Att., 1953)	Indochina
— *debilis* (Att., 1953)	Indochina
— *minuscula* (Att., 1953)	Indochina
— *odontopyga* Att., 1953	Indochina
— *spadix* (Att., 1937)	Indochina

(IX) — The three species of this category agree in having the lamina medialis of the tibiotarsus very weakly developed to almost obsolete, whereas the lamina lateralis is well developed. Consequently the solenomerite is more or less freely applied to the medial side of the tibiotarsus, a condition strongly suggesting that of the species of *Arthrogonopus* or the Sumatran species of *Sundanina*. The solenomerite in its natural position has its end near a small more or less triangular lobe of the tibiotarsus, just as for instance in *Arthrogonopus edentulus* or *A. denticulatus.* A postfemur is not indicated. The known species have the lateral keels rather weakly developed.

Verhoeff proposed in 1941 the genus *Opisthodolichopus* for one of the species of this group, viz., *thienemanni,* a generic name which now is adopted for the following species.

Opisthodolichopus javanicus (Att., 1903)	Java
— *nigricornis* (Poc., 1894)	Sumatra
— *thienemanni* (Att., 1930)	Sumatra

(X) — A species, possibly related to the previous group but yet insufficiently known, may be provisionally located here. The tibiotarsus of the gonopods appears to have a somewhat different structure.

"*Orthomorpha*" *semicarnea* (Poc., 1894)	Sumatra

(XI) — This category contains only two species, which are closely related if not identical. The tibiotarsus of the gonopods has a strongly developed lamina medialis, whereas the lamina lateralis appears to be almost completely absent. The distal part of the solenomerite consequently is almost freely applied to the lateral side of the tibiotarsus as in *Leiozonius.* There appears to be, however, no close relationship between this group and *Leiozonius* judging from the differences in the general outline of the gonopods. A postfemur is not demarcated, the lateral keels are rather weakly developed and both forms reportedly lack pleural keels. To this group the genus *Paternostrana* Att., 1953, has been restricted. Possibly it is related to *Tectoporus* Carl.

Paternostrana sumbawana (Att., 1930)	Sumbawa
— *vinosa* (Poc., 1894)	Flores

(XII) — The gonopod structure of the two species enumerated here is not sufficiently known and a positive statement on their status is therefore premature. However, the outline of the tibiotarsus seems to be quite distinct from that met with in any of the other categories.

"*Orthomorpha*" *constricta* (Carl, 1912)	Celebes
— *hirtipes* (Carl, 1912)	Celebes

(XIII) — The species of this group certainly deserves a generic separation from *Orthomorpha.* Actual study of specimens of the original series has shown that it is probably related to species like *Sundanina sigma* Att., 1953, on the one hand and *Anoplodesmus mutilatus* Att., 1953, on the other, although it lacks the processes in the postfemoral region of the gonopods. The postfemur is demarcated from the femur, but not as distinctly as in the more typical species of *Orthomorpha.* The tibiotarsus is more elongate than in any of the species of the previous groups, and has a normally developed lamina medialis and lamina lateralis.

"*Orthomorpha*" *doriae* (Poc., 1895)	Burma

(XIV) — A number of species referred to *Orthomorpha* by previous authors are characterized by the presence of a rather large lanceolate or spine-like process arising from the lamina medialis of the tibiotarsus of the gonopods, more or less similar to what is found in the genus *Gigantomorpha.* These species, enumerated under the present category, may not form an entirely homogeneous group, although at least there appears to be some geographical coherence. Generally a postfemur is rather weakly demarcated. Only in "*O.*" *harpaga* the demarcation appears to be quite distinct, and also by other characters this species may be somewhat disjunct from the others, having some affinities to the species of category (I).

A brief examination of specimens of the typical series of *melanopleuris*, *minlana* and *miranda* has shown a close relationship of these three forms with *festiva*, *orophila* and *uncinata*. However, a thorough study of the species of this group is needed to establish its characters. They certainly seem to be generically distinct from the species of group (I).

For one of the species, *miranda*, a generic name was proposed by Silvestri as far back as 1896. This name, *Brachytropis*, is preoccupied.

"*Orthomorpha*"	*festiva* Brol., 1896	Siam
—	*harpaga* Att., 1937	Indochina
—	*mediovirgata* Carl, 1941	Burma
—	*melanopleuris* Poc., 1895	Burma
—	*minlana* Poc., 1895	Burma
—	*miranda* Poc., 1895	Burma
—	*orophila* Carl, 1941	Burma
—	*uncinata* Att., 1931	Siam

There seems to be good reason to believe that the following species, not represented in the collection of the British Museum, also belong to this group.

"*Orthomorpha*"	*bistriata* Poc., 1895	Burma
—	*bivittata* Poc., 1895	Burma
—	*comotti* Poc., 1895	Burma
—	*pardalis* Poc., 1895	Burma

(XV) — Aside from the process of the lamina medialis also present in the previous group, the three following species have in addition a more basal spiniform process on the medial side of the tibiotarsus. The postfemur appears to be clearly demarcated. Of these species, *coriacea* has been referred to the subgenus *Kalorthomorpha* by Attems.

"*Orthomorpha*"	*armata* Carl, 1902	Java
—	*atrorosea* (Poc., 1894)	Java
—	*coriacea* Carl, 1902	Java

Orthomorpha beaumontii (Le Guillou)

1841 *Polydesmus Beaumontii* Le Guillou, Bull. Soc. Philom. Paris, 1841, p. 85.
1847 *Polydesmus Beaumontii,* Gervais, in: Walckenaer & Gervais, Hist. Nat. Aptères, vol. 4, p. 101.
1859 *Polydesmus* (*Paradesmus*) *Beaumontii,* De Saussure, Linn. Ent., vol. 13, p. 325.
1869 *Polydesmus* (*Paradesmus*) *Beaumontii,* Humbert & De Saussure, Verh. zool. bot. Ges. Wien, vol. 19, p. 670.
1893 *Orthomorpha beaumontii,* Bollman, Bull. U.S. Nat. Mus., vol. 46, p. 196.
Probably misapplied:
1898 *Prionopeltis Beaumontii,* Attems, Denks. Ak. Wien, vol. 67, p. 357.
1937 *Pratinus beaumontii,* Attems, Tierreich, vol. 68, p. 122.

Material. — The label reads: "Polydesmus Beaumontii Gervais/M. Leguillou. Bornéo." (Mus. Paris), 1 ♀ (holotype).

Colour. — The colour has been described originally as being blackish brown, with the lateral keels paler. The specimens now has a dark chocolate brown colour, the prosomites being a little paler. Lateral keels entirely pale dirty brown, tail also pale. Ventral side pale brownish, sternites and legs dirty pale brownish.

Width. — 5.0 mm, the prosomites 3.6 mm.

Body segments. — Rather weakly constricted by a narrow waist, which is distinctly longitudinally ribbed or "beaded" in the dorsal part down to the level of the lateral keels, and smooth below that level. Prosomites somewhat dulled by a fine cellular structure. Metatergites more shining, smooth or with some irregular wrinkles in particular near the bases of the keels, hairless. Transverse furrow well impressed, finely longitudinally striate, extending laterad to the bases of the lateral keels. Transverse furrow present from the 5th segment to the 18th. Sides up to the 4th segment rather densely but minutely granulate; from the 5th

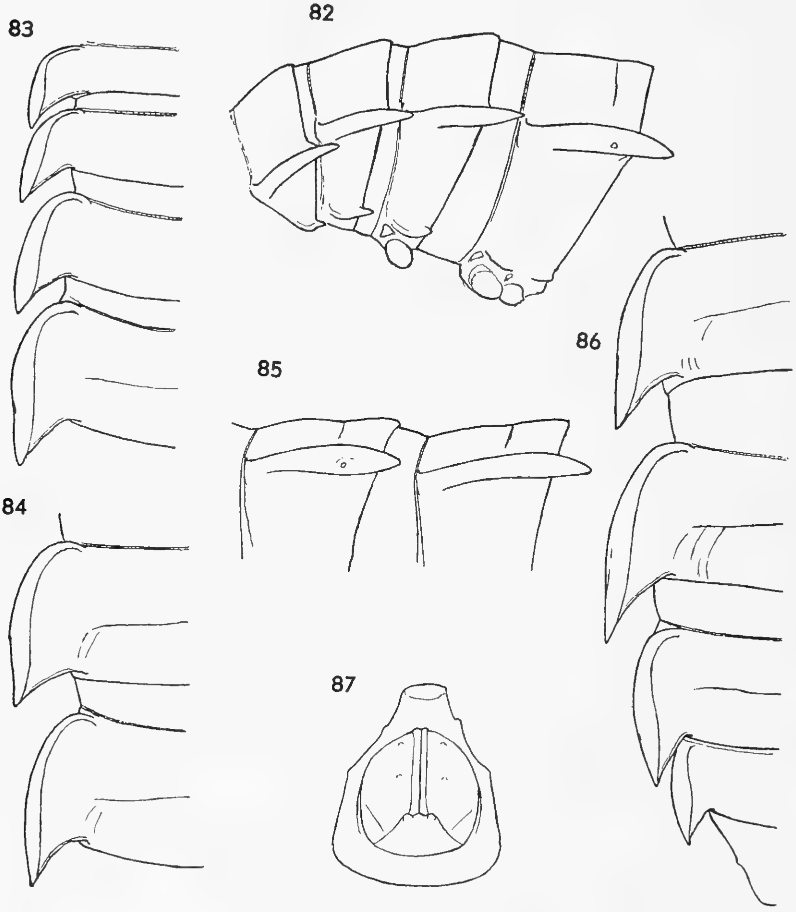


Fig. 82—87. *Orthomorpha beaumontii* (Le Guillou) — 82: left side of the 2nd to the 5th segments of the holotype ♀, lateral view. 83: the same, dorsal view. 84: left side of the 10th and 11th segments of the holotype ♀, dorsal view. 85: the same, lateral view. 86: left side of the 16th to the 20th segments of the holotype ♀, dorsal view. 87: anal segment of the holotype ♀, ventral view

segment onwards the granulation is weak to almost obsolete. Pleural keels well developed, present from the 2nd to about the 15th segments. Up to the 4th segment they are represented by a continuous ridge which is caudally produced into a triangular lappet projecting behind the margin of the segment. From the 5th segment onwards there is in each segment a rather weak swelling above the anterior legs and a triangular lappet near the posterior border of the metasomite. Both, swellings and lappets are diminishing gradually in the subsequent segments and disappear in about the 16th segment. The triangular lappets are projecting very little behind the posterior margin of the segments up to about the middle of the body.

Lateral keels. — (fig. 82—86). Strongly developed. Keels of 2nd segment anteriorly rounded, somewhat shouldered at the base. Lateral border very weakly rounded to almost straight. No tooth at the latero-anterior edge. Posterior edge acutely angular and projecting rather strongly behind the margin of the segment. Keels of 2nd segment scarcely below the level of those of the 3rd, turned slightly ventrad. Marginal rim well developed, demarcated by a sharp premarginal furrow. No ventral premarginal furrow. 3rd and 4th segments of subequal width, somewhat wider than the 2nd. Keels of these segments very similar to those of the 2nd segment, but those of the 3rd somewhat less turned ventrad and those of the 4th almost horizontal. 5th segment somewhat wider than the 4th. Keels from the 5th segment onwards anteriorly distinctly shouldered at the base, anterior and lateral borders widely rounded. Posterior edges acutely angular, projecting rather strongly behind the posterior margin of the segments. Keels on a high level, horizontal. Only in the 18th and 19th segments the keels are raised a little above the horizontal level, but do not project above the mid-dorsal surface of the metatergites. Poriferous keels slightly more prominent than the poreless. Marginal rim rather thick dorso-ventrally, in poriferous keels scarcely thicker than in the poreless, not abruptly widening near the pores. Dorsal premarginal furrow almost reaching the waist. Posterior margin with a very fine rim. Lateral marginal rims ventrally demarcated by a well developed furrow, present in poriferous and poreless keels. Pores lateral in a slight excavation of the rim, the excavation scarcely visible from the dorsal side.

Sternite and legs. — Sternites in middle segments $1^1/_4$—$1^1/_3$ × as broad as long, moderately densely set with rather short setae. Cross-impressions moderately developed, the transverse furrow rather deeply and sharply impressed, the longitudinal furrow less deep and rather wide. Legs of moderate length, rather slender, moderately setiferous. Length of joints: $3>6>5>2>4>1$. The 6th joint about two thirds of the length of the 3rd. The 5th joint about three fifths of the 6th. Tarsal claw of moderate length.

Anal segment. — (fig. 87). Tail rather broad and thick at the base, of moderate length. Sides moderately converging, scarcely concave. Basal lateral setiferous tubercles moderately developed. Distal lateral tubercles and terminal tubercles almost obsolete. Dorsally near the base of the tail a shallow transverse depression, ventral side of tail weakly concave. Valves with rather narrow rims, the setae on weak tubercles. Scale triangular, the sides almost straight, the setiferous tubercles well developed, projecting behind the posterior margin but not surpassing the posterior edge of the scale.

Male. — Unknown.

Remarks. — That the type of *O. beaumontii* has turned out to be a female specimen is certainly a rather unfortunate condition, since as a rule the specific and generic identification of a Paradoxosomatid species is difficult if not impossible with female characters.

Fortunately, however, *O. beaumontii* proves to belong to a group of species in which the structure of the male gonopods is quite uniform and in which specific characters lay mainly in the external structure.

Actual comparison of the type specimen with female co-types of *O. weberi* (Poc.) has convinced me that *weberi* must be regarded as one of the closest relatives of *beaumontii*. The entire morphology of the two species is quite similar, in fact, they seem to differ only in the development of the lateral keels which in *weberi* have the posterior edges a little less acute and distinctly less produced caudad.

We may, therefore, safely assume that the gonopods of *beaumontii* ultimately will prove to be of the type of those of *weberi* and related species like *O. hydrobiologica* Att., *O. francisca* Att., *O. karschii* (Poc.), etc. (see group (I), p. 264).

Orthomorpha coarctata (Sauss.)

1860 *Polydesmus* (*Paradesmus*) *coarctatus* De Saussure, Mém. Soc. Genève, vol. 15, p. 297, pl. 18, fig. 18.
1869 *Polydesmus (Paradesmus) coarctatus,* Humbert & De Saussure, Verh. zool.-bot. Ges. Wien, vol. 19, p. 670 (1).
1937 *Orthomorpha* (*Orthomorpha*) *coarctata,* Attems, Tierreich, vol. 68, p. 62, fig. 75.

Previous records. — Borneo (1). Wide-spread in the tropical parts of all regions.

Material studied. — East Borneo: Long Navang (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 15 ♂, 11 ♀. East Borneo: Songei Boh (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 5 ♂, 1 ♀. East Borneo: without nearer location (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 2 ♂. Maratua Id. off the East coast of Borneo (coll. Dr. E. MJÖBERG, Mus. Stockholm), 5 ♂, 3 ♀.

Remarks. — Not less than three generic names have been based on this species: *Asiomorpha* Verh., 1939, *Brasilogonopus* Verh., 1944, and *Orthomorphina* Kraus, 1958, but at present I am not able to detect any reason for separating *coarctata* either generically or subgenerically from *O. beaumontii.*

Oxidus Cook

1911 *Oxidus* Cook, Proc. U.S. Nat. Mus., vol. 40, p. 628.
1914 *Orthomorpha* (*Kalorthomorpha*) Attems, Arch. Naturg., vol. 80A, fasc. 4, p. 191.
1953 *Kalorthomorpha*, Attems, Mém. Mus. Nat. Hist. Nat. (n.s.), vol. 5, p. 163.

Type-species. — *Fontaria gracilis* C. Koch, by original designation. (Type-species of *Kalorthomorpha*: *Fontaria gracilis* C. Koch, by original designation).

Range and number of species. — To be defined after a revision of the genus.

Remarks. — In its current concept, conforming with the subgenus *Kalorthomorpha* of ATTEMS in the Tierreich, this genus is at least as heterogeneous as the previous one. The only species recorded from Borneo is certainly not congeneric with *Oxidus gracilis* (Koch), but in the absence of material the definition of its true taxonomic position is deferred to a later period.

"Oxidus" kuekenthali (Att.)

1897 *Strongylosoma kükenthali* Attems, Abh. Senckenb. Ges., vol. 23, p. 484, pl. 21, fig. 9.
1937 *Orthomorpha* (*Kalorthomorpha*) *kükenthali,* Attems, Tierreich, vol. 68, p. 86, fig. 107.

Distribution. — Borneo. Celebes: Minahassa.

Remarks. — The occurrence of this species in Borneo as well as in Celebes seems quite dubious. One of the records may be erroneous, and the species, therefore, may not pertain to the fauna of Borneo at all.

Euphyodesmus Att.

1931 *Euphyodesmus* Attems, Zoologica, Stuttg., vol. 30, fasc. 3/4, p. 125.
1937 *Euphyodesmus* (in part), Attems, Tierreich, vol. 68, p. 126.

Generic diagnosis. — 20 segments. Poreformula normal. Head without particulars; labrum tridentate. Antennae very long.

Segments rather strongly constricted. Prosomites with very fine cellular structure, somewhat dull. Waist broad, distinctly and sometimes somewhat irregularly longitudinally ribbed in the dorsal and lateral parts down to the level of the stigmata. Metatergites shining, smooth or with some setiferous tubercles. Transverse furrow well developed, rather deeply impressed, without longitudinal striation, present from the collum onwards. Pleural keels present only in the 2nd, or in the 2nd and 3rd segments.

Lateral keels rather strongly developed, on all segments from the 2nd to the 19th provided with an acutely angular to subspiniform posterior edge surpassing the posterior margin of the metasomites in most segments. Keels on a rather high level, the posterior edges of those of the 5th and the 7th segments are turned slightly upwards and project above the level of the metatergites. Keels of 2nd segment only a little below the level of those of the 3rd segment. Marginal rim of keels narrow, in poriferous segments widening only in the area of the pores.

Sternites much longer than wide, weakly setiferous, with well developed cross impressions. Sternite of 5th segment of ♂ with a strongly developed, distally laminate process between the anterior legs. Sternites of the 6th, 7th and 8th segments of the ♂ without modifications. Legs long to very long. Those of the first pair short and somewhat incrassate. Brushes of tibiae and tarsi present only in a few anterior legs of the ♂, rapidly thinning out and disappearing.

Gonopod coxa of moderate length and rather thick, tapering a little towards the distal end. Latero-distal surface with a setiferous area. Prefemur strongly elongate, in one line with the femur, laterally and in part also medially well demarcated from that joint, the demarcation almost in one line with the longitudinal axis of the femur. Femur rather weakly developed, straight, much shorter than the coxa. Postfemur medially weakly to very sharply demarcated. Spermal channel first running along the medial side of the femur, then curving towards the anterior, lateral and finally posterior sides. Solenomerite of moderate length, rather thick at the base, gradually tapering towards the distal end; the end either simply acuminate or with an accessory lobe. Solenomerite arising from the posterior side of the distal end of the postfemur; it is not sheathed by the tibiotarsus. Tibiotarsus arising from the anterior side of the distal end of the postfemur, not distinctly demarcated from that joint, moderately developed or somewhat reduced, consisting of a more or less compound or of a simple lamella. Lamina medialis or lamina lateralis both not developed.

Type-species. — *Euphyodesmus gracilis* Att., by original designation.

Range. — Borneo.

Number of species. — Three.

Remarks. — After the reallocation in the genus *Pratinus* Att. of *Euphyodesmus greeni* Att. and *E. vector* Chamb. in the preceding pages of this paper, a single species was left in *Euphyodesmus*. From the present collection two new species are added.

The anomalous structure of the gonopods in *Euphyodesmus* makes a homologization of the distal parts of the acropodite rather difficult. Doubtless, the aberrant course of the spermal channel in the femoral division has been caused by a torsion of about 180° of the distal part of the acropodite as against its basal part. The true nature of the parts distad of the femur, however, is less easily determined and, in fact, could be ascertained only after the examination of the gonopods of the newly described *E. postfemoralis.*

As will be seen in the gonopod drawings for *E. gracilis* (fig. 94—95), the acropodite has a distinct constriction somewhat proximad of its branching into solenomerite and tibiotarsus, a constriction which laterally is accompanied by a very thin laminate transverse crest and which is the only indication of an articulation in the acropodite.

Comparison of this with the usual type of gonopods in the Oriental Paradoxosomatidae might lead to the conjecture that the constriction represents the boundaries beween the tibiotarsus on the one hand and the femur and postfemur combined on the other. However, this would imply that the solenomerite in *Euphyodesmus* arises from the base of the tibiotarsus, a quite unusual condition since it is generally admitted that the solenomerite in the Paradoxosomatidae is a process arising from the postfemur, or, if this joint is not demarcated, from the distal end of the femur.

Indeed, a comparison of the gonopod drawings of *E. postfemoralis* with those of *gracilis* shows that the constriction in the acropodite of the latter species marks the end of the femur proper. The undivided part of the acropodite distad of the constriction therefore must be regarded as a postfemur. In *postfemoralis* there is a sharp demarcation between femur and postfemur on the medial side, homologous to a similar demarcation visible on the lateral side of the acropodite of the gonopods of, e.g., *Arthrogonopus* and *Gigantomorpha.* In *postfemoralis* the postfemur is furthermore also more clearly demarcated from the tibiotarsus, at least laterally, and, medially from the solenomerite.

Thus, it is interesting to note that in *Euphyodesmus*, where the demarcation between postfemur and tibiotarsus tends to disappear, the demarcation between femur and postfemur, which otherwise has disappeared in so many of the Paradoxosomatidae, remains distinct.

It is necessary to emphasize here, that I have considered the possibility that what is regarded here as a solenomerite could have been a solenomerite concealed in a closely applied solenophorous part of the tibiotarsus. Such a condition, of course, would involve a quite different homologization of the distal part of the acropodite. However, by studying a preparation of a gonopod crushed somewhat by the cover glass I could ascertain that the solenomerite is a simple, undivided process.

The fact that both ATTEMS and CHAMBERLIN have referred species of the genus *Pratinus* to *Euphyodesmus* might suggest a close relationship between the two genera. In reality, however, there exists only a superficial resemblance. In particular the gonopods of *Pratinus* are fundamentally different from those of *Euphyodesmus*. In *Pratinus* the spermal channel follows a straight course along the medio-anterior side of the femur, the solenomerite arising, consequently, from the anterior side of the distal end of the femur. Moreover, the tibiotarsus in *Pratinus* seems to be distinctly demarcated from the femur, and a postfemur is apparently not marked.

In the morphology of the body segments, in particular in the shape of the lateral keels *Euphyodesmus* is also quite distinct from *Pratinus*. The subdorsal location of the pores and the more or less rhomboid dilatation of the marginal rim of the poriferous keels are strongly reminiscent of similar structures found in some species of *Tectoporus*, e.g., *T. hispidus* Jeek., 1951.

Key to the species. — The species of *Euphyodesmus* are very similar in their external morphology. Important specific differences are to be found mainly in the male gonopods.

1. Metatergites with two transverse rows of four granules each; in the anterior rows the granules are setiferous. Tibiotarsus of the gonopods simply laminate. End of solenomerite bifurcate .... *E. granulifer* spec. nov.
— Metatergites without granules, hairless. Tibiotarsus of the gonopods more complicated. End of solenomerite not bifurcate 2
2. Postfemur of gonopods medially sharply demarcated from the femur by a furrow. Solenomerite distinctly longer than tibiotarsus, the end with a triangular lamellar lobe. Head much wider than collum ...... *E. postfemoralis* spec. nov.
— Postfemur of gonopods medially not sharply demarcated from the femur. Solenomerite about as long as tibiotarsus, simply acuminate at the end. Head not much wider than collum .... *E. gracilis* Att.

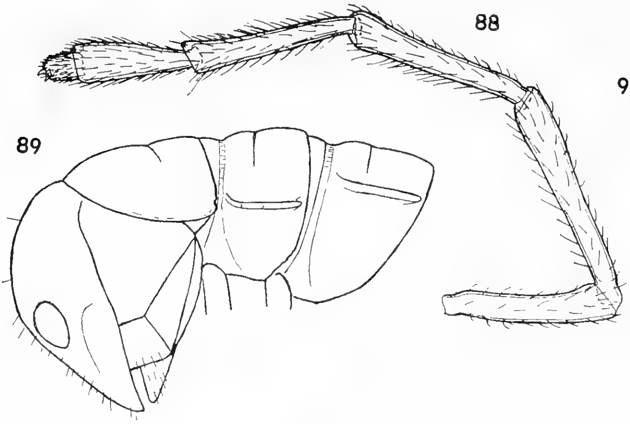
Euphyodesmus gracilis Att.

1931 *Euphyodesmus gracilis* Attems, Zoologica, Stuttg., vol. 30, fasc. 3/4, p. 126, fig. 195—199.
1937 *Euphyodesmus gracilis,* Attems, Tierreich, vol. 68, p. 127, fig. 163—164.

Previous record. — West Borneo: Sungei Malang.

Material studied. — West Borneo: Bungan River, July, 1894 (Borneo Exped., Coll. Dr. A. W. NIEUWENHUIS, Mus. Leiden), 1 ♂, 1 ♀.

Colour. — Head brownish yellow to yellowish brown. Antennae pale brown,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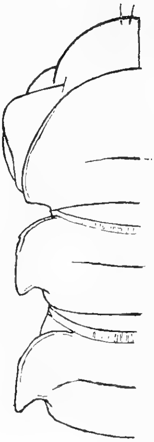
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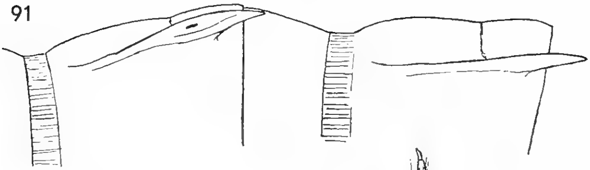
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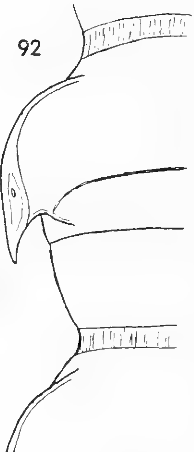
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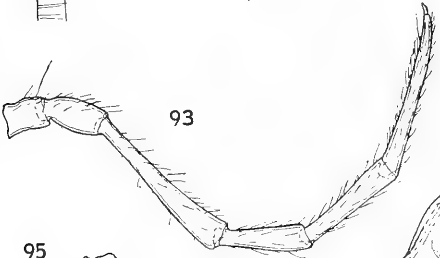
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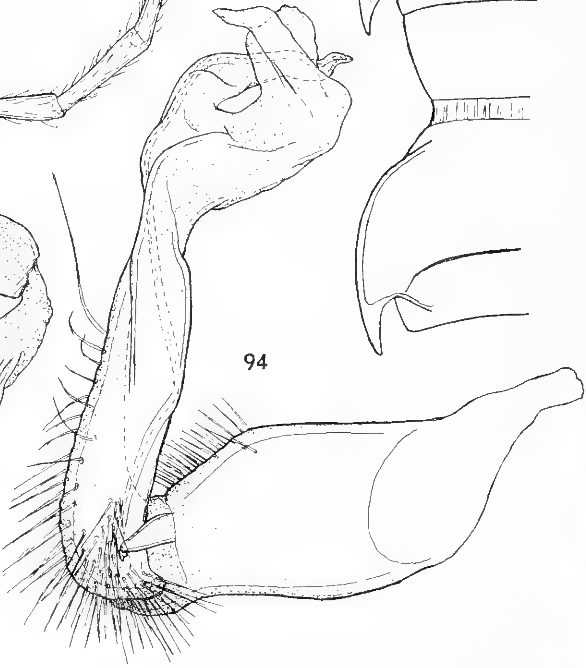
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darker in the distal half of the 6th joint and in the 7th joint. Distal end of the 7th and the 8th joint whitish. Collum and subsequent segments castaneous, the latero-posterior edges of the collum and of the lateral keels of the body segments paler, yellowish. Venter pale brownish, the sternites yellowish. Legs proximally and distally yellowish, the middle part from the distal end of the femur to about the middle of the tarsi dark castaneous. In the two last pairs the dark colour extends to the base of the femur. Anal segment castaneous, its ventral side paler.

Width. — ♂ 1.6 mm; ♀ 1.9 mm.

Head and antennae. — Labrum rather widely but weakly emarginate. Clypeus weakly convex, weakly impressed towards the labrum; the lateral margins widely and rather weakly emarginate. Surface of head smooth and shining, densely to rather densely setiferous in the clypeal and frontal parts. Vertex with four setae. Antennal sockets separated by little more than the diameter of a socket or by about one third of the length of the 2nd antennal joint. Postantennal groove well developed, the wall in front of it rather prominent. Vertex strongly convex, not demarcated from the frontal area. Sulcus weakly impressed, not reaching the upper level of the antennal sockets. Antennae (fig. 88) slender. Length of joints: $3>4>5=2>6$. The 6th joint about half as long as the 3rd. Joints of subequal width, only the 6th somewhat thicker than the others. Pubescence of antennae moderate to, distally, rather dense.

Collum. — (fig. 89—90). Distinctly narrower than the head, subsemicircular in dorsal outline. Anterior border evenly rounded. Posterior border widely and weakly emarginate in the middle, almost straight laterally. Latero-posterior edge narrowly rounded, obtusely angular. Surface rather shining, somewhat irregularly uneven, apparently hairless. At about one third from the posterior margin a well developed transverse furrow. Surface of collum transversely almost flat in the middle, much more convex towards the lateral sides; the lateral sides slightly raised but not attaining a horizontal level. Marginal rim narrow and rather weakly demarcated, present only along the latero-anterior border.

Body segments. — Metatergites somewhat uneven in a few anterior segments, but in most segments smooth with a few weak wrinkles. Transverse furrow present up to the 18th segment, from the 5th to the 17th segments running laterad to the base of the keels and curving caudad there to end at the posterior margin of the keels. Metatergites hairless, only the 19th segment with a transverse row of four hairs. Sides up to the 4th segment rather densely granulate, smooth or weakly granulose from the 5th segment onwards. Pleural keels very weakly present in the 2nd segment only.

Lateral keels. — (fig. 89—92). 2nd segment a little wider than the collum. The border of the keels anteriorly rounded, laterally straight with two very weak

Fig. 88—95. *Euphyodesmus gracilis* Att. — 88: antenna, without the basal joint, of the ♂. 89: left side of the head and the three anterior segments of the ♂, lateral view. 90: the same, dorsal view. 91: left side of the 10th and 11th segments of the ♂, lateral view. 92: the same, dorsal view. 93: leg of the 7th segment of the ♂. 94: right gonopod of the ♂, medial view. 95: distal portion of the telopodite of the left gonopod of the ♂, lateral view notches. Posterior edge acutely angular, but not sharply pointed; not projecting behind the margin of the segment. Posterior border emarginate. Marginal rim weakly developed, obsolete in the posterior half of the keels. 3rd and 4th segments of subequal width, scarcely narrower than the 2nd. Keels subsimilar to those of the 2nd segment; the notches of the lateral border vestigial or absent. The posterior edges are more acute, and project a little behind the margin of the metasomite in the 4th segment. Up to the 4th segment the lateral keels are horizontal. 5th segment a little wider than the 4th. Lateral border of the keels from the 5th segment onwards with widely to very widely rounded latero-anterior borders which laterally are straight or even a little concave in poriferous segments. Latero-posterior edges very acute and sharply pointed, in all segments projecting behind the posterior margin of the metasomites. Posterior borders of keels emarginate. Lateral margins often with a weak notch. Keels raised a little above the horizontal level. The posterior edges of those of the 5th and 7th segments bent upwards and projecting dorsad of the level of the metatergites. Posterior edges of the keels of the 13th, 15th, and 17th segments curving a little ventrad. Poriferous keels extending slightly more laterad than the poreless. Marginal rim of poreless keels narrow but distinct. The premarginal furrow running from near the waist to near the posterior margin. In poriferous keels the premarginal furrow reaches the posterior border, and the rim widens considerably in the area of the pores. Pores latero-dorsad, situated in a wide and shallow excavation of the rim. Posterior margin of all keels with a fine marginal rim. On the ventral side of the keels from the 5th segment onwards the marginal rim is demarcated by a premarginal furrow in the middle part of each keel.

Sternites and legs. — Sternites of middle segments somewhat more than two times longer than broad, sparsely setiferous. Cross impressions represented by a deep transverse depression and a moderately deep longitudinal impression. Sternal process of the 5th segment narrow, subrectangular, about two times longer than broad; the distal end widely and weakly rounded. The process is directed ventrad and does not project before the anterior margin of the sternite. Anterior side distally with a small brush of moderately short setae, normally setiferous. Posterior portion of the sternite of the 5th segment normal. Legs (fig. 93) long; the last two pairs distinctly longer than the preceding pairs. First pair of legs rather short, distinctly incrassate; the joints of subequal length, but the tarsus much longer. The first pair has well developed tibial and tarsal brushes, which in a few of the following pairs are rapidly thinning out and disappear. Legs of middle segments rather weakly to, distally, moderately setiferous, especially on the ventral side of the joints. Length of joints: $3 = 6 > 5 > 4 > 2 > 1$. The 5th joint about two thirds of the 6th.

Anal segment. — Tail of moderate length. Sides rather strongly converging, straight. The end narrowly truncate, rounded, with weak lateral and terminal tubercles. Valves with rather narrow and rather low marginal rims. Scale triangular; the sides rounded. Setiferous tubercles small, not projecting.

Gonopods. — (fig. 94—95). Postfemur indicated by a constriction and by a thin transverse lateral crest. Solenomerite simply acuminate, without secondary processes. Tibiotarsus moderately developed, rather complicated by several lobes, apparently supporting though not actually sheathing the solenomerite.

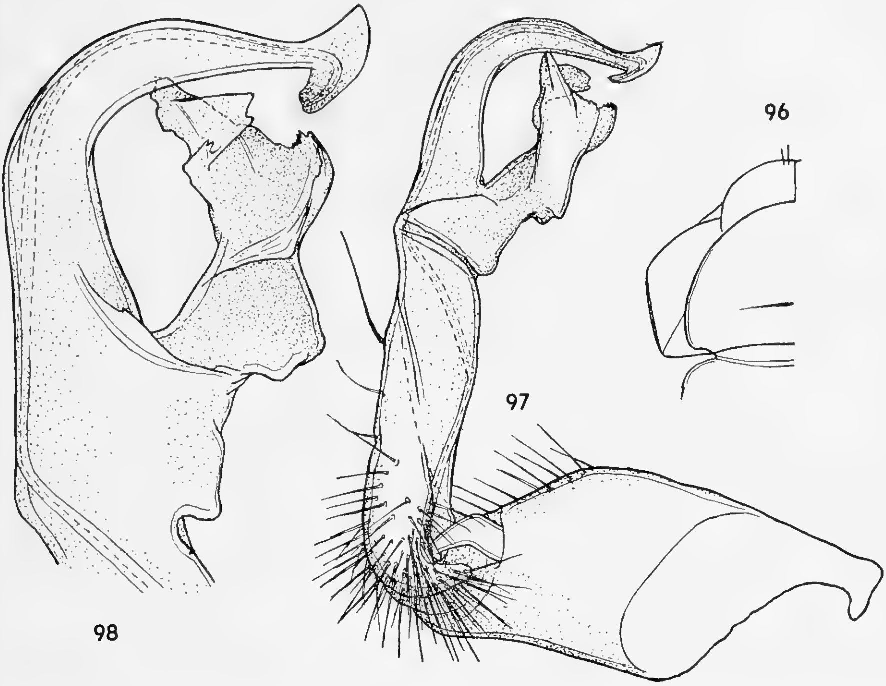

Fig. 96—98. *Euphyodesmus postfemoralis* spec. nov. — 96: left side of the head and the collum of the holotype ♂, dorsal view. 97: right gonopod of the holotype ♂, medial view. 98: distal end of the left gonopod of the holotype ♂, lateral view

Female. — Distinctly more robust than the male. Aside from the usual secondary sexual characters also differing in that the somites are somewhat less strongly constricted in the waist area. The waist a little narrower. Sternites of middle segments about $1^3/_4$ × longer than broad. First pair of legs incrassate as in the male, but without dense brushes. The other legs comparatively a little shorter than in the male.

Remarks. — Although there can be little doubt as to the correctness of the identification of the present material with *gracilis* Att., there are some minor differences between the gonopods of the male at hand and the type specimen described by Attems. The various lamellae of the tibiotarsus differ slightly in their outline, whereas the solenomerite is curved a little in the end instead of being almost straight. No doubt these variations are at most of a subspecific nature, but of not sufficient significance to justify a denomination.

Euphyodesmus postfemoralis spec. nov.

Material. — East Borneo: Mt. Tibang, 1700 m (Coll. Dr. E. Mjöberg, Mus. Stockholm), 5 ♂ (one of which the holotype), 4 ♀, 2 juv. ♀. East Borneo: Mt. Tibang, 1400 m (Coll. Dr. E. Mjöberg, Mus. Stockholm), 6 ♂, 3 ♀, 2 juv. ♂, 6 juv. ♀. East Borneo: Mt. Tibang, 1300 m (Coll. E. Mjöberg, Mus. Stockholm), 2 ♀, 3 juv. ♂, 2 juv. ♀. East Borneo: without nearer location (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 2 ♂, 1 ♀.

Differing from *gracilis* in the following characters.

Colour. — Most of the material of this species apparently was not in full colour when it was collected. The colour of the darkest specimens, however, agrees with that of *gracilis,* but the legs almost wholly lack the dark colouring.

Width. — Holotype ♂ 1.6 mm. The other ♂ in the order of the above enumeration: 1.6 mm, 1.5 mm, 1.5 mm, 1.4 mm; 1.5 mm, 1.5 mm, 1.5 mm, 1.4 mm, 1.4 mm, 1.3 mm; 1.5 mm, 1.5 mm; ♀: 2.2 mm, 2.2 mm, 2.1 mm, 2.0 mm; 2.0 mm, 2.0 mm, 1.8 mm; 2.0 mm, 2.0 mm; 2.1 mm. Juvenile ♂ with 19 segments: 1.0 to 1.1 mm. Juvenile ♀ with 19 segments: 1.0 tot 1.4 mm.

Collum. — Much narrower than the head, as a consequence of the strongly inflated lateral sides of the latter (fig. 96).

Gonopods. — (fig. 97—98). Femur sharply demarcated from the postfemur by a furrow on the median side. Solenomerite more strongly developed, the end with a triangular lamellate lappet. Tibiotarsus shorter than the solenomerite, apparently free from the solenomerite.

Female. — Differing from the ♂ in the same way as in *gracilis.*

Juvenile. — Although in general features agreeing with the adult ♀ specimens, the juvenile specimens have much more "normal" aspect because of the weaker constriction of the waist area of the body segments. The antennae and legs are comparatively much shorter than in the adults. The posterior edges of the lateral keels are less produced caudad.

Euphyodesmus granulifer spec. nov.

Material. — East Borneo: Pajan River (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 4 ♂ (one of which the holotype), 2 ♀, 3 juv. ♂, 1 juv. ♀. East Borneo: Mt. Tibang, 1400 m (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 1 ♀. East Borneo: without nearer location (Coll. Dr. E. MJÖBERG, Mus. Stockholm), 1 ♂.

Differing from *gracilis* in the following characters.

Colour. — The best preserved specimens of this species are darker than *gracilis*. Head dark castaneous, the clypeal area lighter, yellowish towards the labrum. Antennae also dark castaneous, only the tip of the 7th and the 8th joints whitish. Collum and subsequent body segments dark castaneous, but the collum with a dirty whitish zone along the anterior margin and similarly coloured lateral edges. Lateral keels of the 2nd to the 4th segments entirely, of subsequent segments only in the latero-posterior portion pale yellowish. Dark portion of the legs also deeper brown than in *gracilis*, the brown colour extending to the end of the tarsi.

Width. — Holotype ♂ 1.6 mm. The other ♂ in the order of the above enumeration: 1.6 mm, 1.5 mm, 1.5 mm; 1.4 mm. ♀: 2.0 mm, 1.9 mm; 1.9 mm. Juvenile ♂ with 19 segments: 1.4 mm, 1.3 mm, 1.2 mm. Juvenile ♀ with 19 segments: 1.3 mm.

Head and antennae. — Antennal sockets separated by about 4/5 of the diameter of a socket, or by a quarter of the length of the 2nd antennal joint.

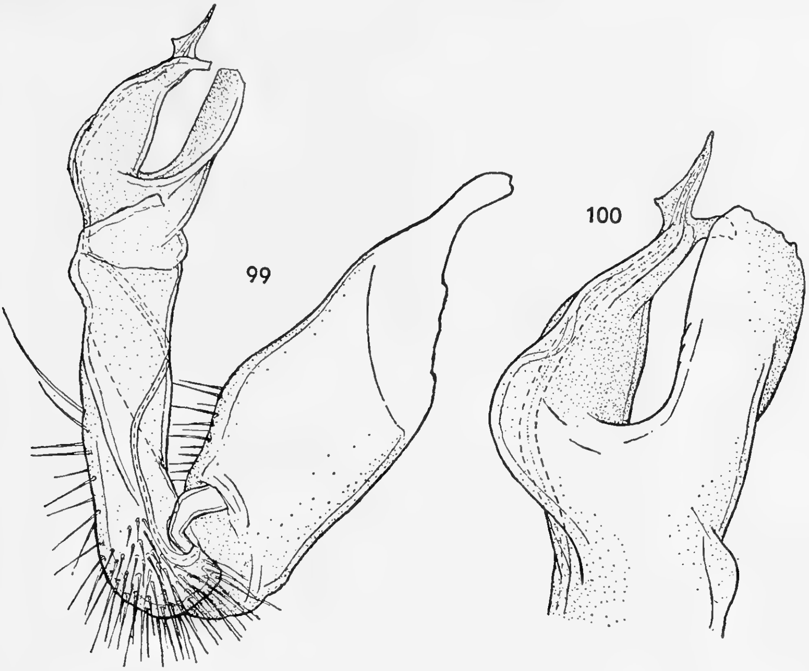

Fig. 99—100. *Euphyodesmus granulifer* spec. nov. — 99: right gonopod of the holotype ♂, medial view. 100: distal end of the left gonopod of the holotype ♂, lateral view

Vertigial sulcus running downward to just below the upper level of the antennal sockets.

Collum. — 4 + 4 minute but distinct setiferous granules along the anterior margin. The hairs of moderate length, rather stiff.

Body segments. — Metatergites with a row of 4 setiferous granules behind the waist, and 4 somewhat less distinct hairless granules behind the transverse sulcus. Waist with weakly developed, somewhat irregular ridges. Pleural keels on the 2nd segment represented by a triangular lappet projecting downward. In the 3rd segment weakly developed, in subsequent segments absent.

Lateral keels. — 2nd segment slightly narrower than the collum, the keels pointed. In general the lateral keels are slightly more strongly developed than in the two preceding species, the posterior points being a little longer.

Gonopods. — (fig. 99—100). Postfemur demarcated from the femur by a thin transverse crest on the medial side. Solenomerite bifurcate in the end. Tibiotarsus a simple subrectangular lamina, entirely free from the solenomerite.

Female. — Differing from the ♂ in the same way as in *gracilis.*

Juvenile. — See the remarks made for the juvenile of *postfemoralis.*

"Strongylosoma" nodulosum Att.

1897 *Strongylosoma nodulosum* Attems, Abh. Senckenb. Ges., vol. 23, p. 486.

Distribution. — Borneo.

Remarks. — The male characters of this species are unknown, reason why its generic position has remained a mystery. Even in the light of the present additions to the Borneo Paradoxosomatid fauna little can be said of its relationship. The weak development of the lateral keels at least seems to exclude the possibility that it might belong to *Gigantomorpha, Orthomorpha* or *Euphyodesmus.* The colour pattern as described by ATTEMS suggests a similarity with the colour of *Borneonina retrorsa.* To say more would be mere speculation, so *nodulosum* is condemned to remain an enigma probably for a long time to come.

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DEEL 106 AFLEVERING 7 1963

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UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

INHOUD:

Tijdschrift voor Entomologie, deel 106, afl. 7. Gepubliceerd 16-IX-1963

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AFRICAN SPECIES OF THE GENUS BACTRA STEPHENS (LEPIDOPTERA, TORTRICIDAE)

BY

A. DIAKONOFF

Rijksmuseum van Natuurlijke Historie, Leiden

After having published surveys of the species of the genus *Bactra* Stephens from tropical Asia (1950, 1956), and from the Palaearctic and Mediterranean Regions (1956, 1959 and 1962), I now present a preliminary survey of the species from the Aethiopian Region, chiefly South Africa.

Does the genus show a rich speciation in tropical Asia, in South Africa this abundance is almost exceeded. At first I had the impression that India might represent the country of origin, a zoocentre, of *Bactra* species. The present results, however, suggest that we may be dealing with a very old group which may have originated in some ancient central region of the Old World Tropics, somewhere between the Asiatic and African continents, to spread east and west. This might explain the partly very puzzling distribution of certain species groups, e.g., the *boschmai* group: in New Guinea, Africa and the West Indies (!), the *coronata* group: in Australia, South Asia, and South Africa, etc.

The species of *Bactra* can easily be grouped in five natural subgenera, four of which have been defined by me previously (1956), while the fifth is described below. The general character of these subgenera, their taxonomic "behaviour", is not at all similar. So the species of the most extensive subgenus, *Chiloides* Butler, possess strongly specialized genitalia in the two sexes and show marked differences from one another. The group offers the greatest diversity of genital structure which makes its study very fascinating. *Chiloides* contains many species occurring throughout the tropical and subtropical regions of the Old and the New World. These features suggest a great antiquity of the group.

On the other hand, the two following subgenera, *Bactra* and *Nannobactra,* are different from *Chiloides,* but are rather similar to each other with regard to this taxonomic behaviour, viz., within each subgenus the species show but minor differences of genitalia; especially the females are rather uniform in each of these two subgenera. While those of *Bactra* Stephens may mostly be discriminated without difficulty, the females of *Nannobactra* Diakonoff often are so similar that their separation becomes a hazardous or even an impossible task. These two subgenera must be much younger than *Chiloides,* although of unequal origin: while *Bactra* must have developed from some simplified *Chiloides*-like ancestors through the loss of the valvula, *Nannobactra* may be regarded as a quite different off-shoot of the *Chiloides* stock, having originated through the speciation of the cucullus portion of the valva and of its armatures, but with the retention of the valvula.

Finally *Spinobactra* subgen. nov. and *Noteraula* (New Zealand) are endemic developments of *Bactra*-like ancestors.

The rather numerous species are very similar in appearance and facies. Most are subject to considerable variation along parallel lines, so giving rise to a series of infraspecific forms which in diverse species look very much alike. Therefore, the student is almost entirely thrown on the study of the genital characters — and there he finds a remarkable richness of structure, in males as well as in females. These structures are of a great specific rigidity and have a pronounced specific, as well as subgeneric, taxonomic value.

EDWARD MEYRICK, who described most African *Bactra* species (1909, 1911), and a few other Lepidopterists of his time (ZELLER, 1852, WALKER, 1866, WALSINGHAM, 1881, MABILLE, 1900), were not aware of this internal diversity and used exclusively external characters. The result was rather chaotic.

So the extensive collection of *Bactra* species in the Transvaal Museum, forming the backbone of this survey, has been named by MEYRICK for more than three quarters. The results bear evidence of the impossibility to discriminate these species without dissecting and mounting the genitalia of every available specimen. Therefore, the older identifications be better entirely disregarded, except, of course, the types. That is the reason why I am not citing any of MEYRICK's determination labels in most cases.

In order to facilitate the use of some terms in the male genitalia in the subgenus *Bactra,* the reader is referred to fig. 1. The new concept, defined below and depicted in that figure is the "antebasal hairs". For explanations of a few more new terms I may refer to the descriptions of the subgenera.

The present survey is preliminary, for I expect to find more interesting material of African *Bactra* in other museums on that continent and elsewhere, for which I did not apply as yet. Not to delay the present results I am publishing them now, although several problems had to remain unsolved, chiefly by lack of sufficient material.

Two subgenera and 17 species are described as new and 9 earlier described species are recorded.

For material and information I am greatly indebted to the following persons and institutions. In the first place, to Dr. L. VÁRI, Transvaal Museum, Pretoria, South Africa; furthermore to Mr. J. D. BRADLEY, British Museum (Natural History), London, England; Dr. F. KASY, Naturhistorisches Museum, Vienna, Austria; Dr. J. F. GATES CLARKE, U.S. National Museum, Washington, D.C., U.S.A.; Dr. P. E. L. VIETTE, Muséum National d'Histoire Naturelle, Paris, France; Mr. E. TAYLOR, Hope Department, University Museum, Oxford, England, and finally, to the Information Attaché, South African Embassy, The Hague, Netherlands, for information on localities.

Figures 7 and 8 were made by W. BERGMANS, 38 and 73 by Miss R. VAN CREVEL, 64 and 72 by A. VAN DIJK, the rest by myself.

KEY TO THE AFRICAN SPECIES OF *Bactra* BASED ON GENITAL CHARACTERS

Males

1. A separate valvula absent 2

— A well-developed, clavate and coronate valvula present between cucullus and sacculus 10

2. Entire cucullus beset with numerous rigid spines; sacculus not bulbous, with an edge of very dense spines, punctulate area extending over the rest of sacculus . . . . *Spinobactra spinosa*

— Cucullus bristles and spines slender, only along its ventral portion; sacculus bulbous, without a dense fringe of spines, with Spc_1 only. Subgenus *Bactra* 3

3. Bases of socii with a rigid, sclerotized edge, making the socius to stand upright . . . . *lanceolana*

— Bases of socii never with a rigid edge, socius limply pending or recumbent 4

4. Punctulate area of sacculus extended, usually its distal half with numerous spines . . . . *pythonia*

— Punctulate area limited, mostly suboval, spines less numerous 5

5. Ms series formed of strong spines . . . . *crithopa*

— Ms series formed of small bristles or hairs 6

6. Uncus long and slender, pointed and curved, thus corona of spines long. Sacculus small, rigid, triangular or quadrate in profile, Spc_1 dense *graminivora*

— Uncus of normal length. Sacculus usually spherical, not rigid, nor sclerotized; Spc_1 normal 7

7. Terminal patch of cucullus bristles not developed, these bristles do not extend basad byond the edge of sacculus . . . . *furfurana*

— Terminal patch of cucullus bristles well-developed, extending basad beyond the edge of sacculus 8

8. There is a well-defined, isolated, elevated wart halfway between edge of sacculus and punctulate area, beset with spines and hairs . . . *scrupulosa*

— No such isolated, elevated wart on sacculus 9

9. Punctulate area semioval, well-defined, longer; Spc_1 spines slender, straight and longer; basal hairs normal, not extended; terminal patch extended basad; its anterior edge forming a well-defined elevated ridge, beset with spines. Species with broader, less pointed wings and a straight termen . . *confusa*

— Punctulate area shorter, narrowed against top, at base not limited but extended transversely and merging into patch of basal hairs; Spc_1 spines less numerous (3—4), shorter, flattened and curved; terminal patch less extended basad, its anterior edge not elevated. Species with dilated, pointed fore wings and a sinuate termen . . . . *tradens*

10. Cucullus diversely shaped, usually elongate, not sclerotized, always with normal spines and bristles. Subgenus *Chiloides* 11

— Cucullus short and broad, rounded and sclerotized, with one to three series of very large spines, increasing in size downward. Subgenus *Nannobactra* . 23

11. Vinculum triangularly thickened in middle, dentate . . . . . *venosana*

— Vinculum smooth, never dentate 12

12. Base of sacculus outwardly and inwardly with extremely dense long spines . . . . *punctistrigana*

— If sacculus spined then not only at base and not so densely 13

13. Sacculus with a marginal corona of long spines of equal length . . . 14

— Sacculus without a marginal corona of equal spines (seldom a few spines of

diverse length at the bottom only, or spines short) 16
14. Top of sacculus strongly extended laterad, so as to form a triangular process crowned with long spines (cf. *tornastis*, p. 71) . . . . *triceps*
— Sacculus broadly rounded, circular or semicircular in circumference . . 15
15. Juxta very long, almost twice as long as sacculus is broad . . . *sinassula*
— Juxta of normal length, not longer than sacculus is broad . . . . *fasciata*
16. Top of very concave sacculus with an inside-turned process 17
— Top of sacculus sometimes with a low and obtuse ridge but without a process 18
17. Apical process of sacculus long, conspicuous, obtuse . . . . . . *tylophora*
— Apical process of sacculus aculety-triangular, more or less concealed . *aletha*
18. Aedeagus short, straight, tubular, not exceeding width of juxta. Sacculus with not numerous stout or thin spines 19
— Aedeagus long, mostly curved, by far exceeding width of juxta, if moderate then flattened laterally 20
19. Sacculus with 5—10 stout spines . . . . *jansei*
— Sacculus with a few (4—5) thin spines . . . . *adelpha*
20. Aedeagus moderate, strongly flattened laterally, appearing very broad, with denticulations before middle of upper edge . . . . *stagnicolana*
— Aedeagus long, never flattened laterally 21
21. Sacculus not spined . . . . *sordidata*
Sacculus distinctly spined 22
22. Sacculus spines long and slender, of diverse length, arranged in patches . . . . *trimera*
— Sacculus spines short, numerous along lower half of outer edge, and few on top of sacculus . . . . *rhabdonoma*
23. Valvula extremely large, corona forming a long sinuate band . . *sardonia*
— Valvula of normal size 24
24. Tegumen with rounded-triangular shoulder lobes (bases of gnathos) distinctly aciculate . . . . *dasioma*
— Tegumen either with entirely smooth shoulder lobes, or these lobes obliterate 25
25. Shape of sacculus vertically oblong, its upper half formed by a small and globular punctulate area, lower half appearing empty; spines of punctulate area numerous, long . . . . *legitima*
— Sacculus not thus vertically extended; punctulate area occupying its larger part, its lower portion not thus extended; spines shorter 26
26. Spines of punctulate area numerous, dark, moderate, pointed; corona spines inequal: ultimate spine spindle-shaped, thick, point slightly bent . . *minima*
— Sacculus spines few, short, less pointed, not conspicuously dark; corona spines subequal: two or three ultimate spines approximately similar in size and shape . . . . *aciculata*

Females

1. No or very faint sclerotizations of the seventh segment; eighth + ninth segment not sclerotized; if posterior edge of tergite and bases of anapophyses

slightly sclerotized, and there are small angulate sclerites on both sides of the ostium, then signum is absent. Subgenus *Bactra* (part.) 2

— Eighth + ninth segment more or less distinctly sclerotized, sometimes strongly sclerotized and modified. Signum usually larger, basket-shaped, always present 7

— Ostium moderate, pear-shaped, lamella postvaginalis vertical, narrow and wrinkled, posterior edges of genital sternite also finely wrinkled. Ostium flanked by two weak oval plates, their median edges thickened, so as to form a small refracting crescentic structure (figs. 6—7). Colliculum tubular, short. Signum absent. Subgenus *Bactra* (part.) . . . . *pythonia*

— Eighth ± ninth segment diversely sclerotized, usually only along its edge, or only sterigma moderately sclerotized, or there is a pair of rounded sclerites at the sides of sterigma; the latter always weakly modified, ostium usually being surrounded by aciculate or minutely haired simple folds or rounded prominences; genitalia rather uniform , species difficult to separate. Subgenus *Nannobactra* 21

2\. Lamella postvaginalis with a transverse horizontal band of fine punctulations, or with a series of horizontal fine folds, or almost simple, never cap-shaped 3

— Lamella postvaginalis with a more or less developed cap-shaped structure, concave below. (Ostium usually on top of a prominence, visible only in profile) 4

3\. Lamella postvaginalis with a series of fine horizontal almost straight folds, not concave below, sometimes hardly traceable. Ostium, shallow, of a crescentic aspect, its outer edge concave. Lobus analis elongate-semioval, with a gradually rounded top, outer edge convex . . . . *graminivora*

— Lamella postvaginalis with a well-defined transverse band of fine punctulations, edged above and beneath by a smooth fold, dilated and truncate at extremities. Lobus analis not distinctly semioval, its outer edge not so convex, top subobtuse but not gradually rounded . . . . *lanceolana*

4\. Lamella postvaginalis with a simple cap, being a slender curved fold over ostium; rarely minute punctulations present above this. Signum always present, although small . . . . *furfurana*

— Cap of lamella postvaginalis more developed, or there are additional folds at the sides of the sterigma, or some sclerotizations, or there is more punctulation above the cap 5

5\. Apophyses very long, free part of postapophyse distinctly longer than lobus analis. Lamella postvaginalis with punctulations and also several bristles on basal warts. Signum absent . . . . *dolia*

— Apophyses normal, free part of postapophyse about as long as lobus analis. No bristles on lamella postvaginalis 6

6\. Cap of lamella postvaginalis broad, formed of one or two horizontal median folds and a small additional cap on each side. Ostium wider. A more or less sclerotized curved plate on each side supporting ostium. Signum absent . . . . *confusa*

— Cap of lamella postvaginalis less broad, without additional lateral caps;

punctulation above this cap distinct, forming a well-defined elongate field; no plates at the sides of sterigma, instead a pair of darkly coloured small rods. Rostral margin of genital tergite often sclerotized and appearing as a semi-annular structure joining the bases of anapophyses. Signum absent . *tradens*

— Cap of lamella postvaginalis small, very narrow in middle, with slight lateral caps, the lateral edges traceable downwards and forming some additional folds on each side of sterigma; there is always some punctulation above cap. Signum absent . . . . *scrupulosa*

7. Sterigma strongly sclerotized, forming a complicated rigid and wide tubular structure rising collar-like around the ostium. Colliculum absent. Signum small. Subgenus *Spinobactra* . . . . *spinosa*

— Sterigma, when sclerotized, not forming a collar-like structure around the ostium. The ventral rim of ostium usually small or there is a colliculum. Signum larger, basket-shaped 8

8. Sterigma strongly sclerotized, sclerotization extending over the whole genital segment. Large species 9

— Sclerotizations not so extensive 11

9. Sterigma with a rounded median lobe connected with an asymmetrical colliculum . . . . *trimera*

— Sterigma mesially not lobate. Colliculum symmetrical 10

10. Colliculum shorter, gradually narrowed downward, its upper edge not extended laterally; anapophyses longer . . . . *triceps*

— Colliculum longer, constricted below upper edge which is strongly extended laterally and narrowed again from above middle to above end; anapophyses shorter . . . . *sinassula*

11. Sterigma, a moderate, subpentagonal or transversely oblong plate. Colliculum, a long, strongly sclerotized tube 12

— Sterigma and colliculum not thus 13

12. Sterigma pentagonal, colliculum appearing to originate from its centre, not distinctly dilated downward . . . . *tylophora*

— Sterigma transversely oblong, colliculum originating from its lower edge, dilated downwards . . . . *nesiotis*

13. Colliculum well-developed, more or less sclerotized, adjacent to ostium . 14

— Colliculum either small, not distincly adjacent to the ostium but beginning below it, or colliculum ill-defined; if well-defined, then calyciform and little sclerotized 19

14. Ostium, a large pear-shaped simple opening. Colliculum, a large and thick tube . . . . *salpictris*

— Ostium not so large, less simple 15

15. Colliculum a completely sclerotized diversely shaped tube 16

— Colliculum more sclerotized laterally than in the middle 18

16. Colliculum spindle-shaped, very large . . . . *stagnicolana*

— Colliculum tubular 17

17. Colliculum rather long, dilated above middle; a sclerotized curved transverse fold along edge of genital segment . . . . *fasciata*

— Colliculum shorter, gradually narrowed. No transverse fold . . *rhabdonoma*

18. Folds and structures of lamella antevaginalis less extended, outer as well as inner usually less than semicircular, the circle being widely open above . . . . *venosana*

— These folds more extended, inner folds closed, forming several concentric circles; outer structure extended, strongly corrugated, forming more than a semicircle . . . . *punctistrigana*

19. Ostium and colliculum little sclerotized, calyciform, upper (anterior) edge strongly convex, with a median excision; this structure flanked by semicircular folds and two oval plates of the 7th segment . . . . *endea*

— Ostium and colliculum not thus 20

20. Colliculum moderately sclerotized, subconical, formed by two sclerites; ostium flanked by an oval structure with double rim and partly sclerotized inner portion. Lobus analis normal . . . . *adelpha*

— Colliculum weak, tubular, little sclerotized. Sterigma strongly projecting forwards (ventrad) which is visible only in profile. Ostium flanked by moderate, strongly sclerotized folds with a hyaline rim. Lobus analis very slender and elongate . . . . *jansei*

21. A sclerotized sinuate transverse band below ostium bursae . . . *sardonia*

— No such band . . . . other species of African *Nannobactra*

Subgenus **Spinobactra** nov.

Figs. 2—4

With the superficial characters of *Bactra* Stephens, but with the valva shaped differently. Sacculus little indicated, only moderately broader than the base of cucullus, not swollen, from beyond base with an extremely dense row of long spines along outer edge; surface of sacculus entirely occupied by punctulations with fine hairs, although less dense than in other subgenera. Cucullus gradually narrowed, entirely beset with long spines, especially dense along the base. Aedeagus broad, curved, moderately long. Cornuti, a small group of spines.

Female genitalia with sterigma strongly sclerotized and forming a complicated rigid collar-like structure around ostium. Colliculum proper, absent. Signum, a small denticulate sclerite (similar to that in the subgenus *Bactra*).

Type-species, *Bactra (Spinobactra) spinosa* spec. nov.

An interesting novelty of the *Bactra* group. Apparently a specialized endemic form. *Bactra (B.) pythonia* is a transitional form, uniting *Spinobactra* with *Bactra.* The slender insect shows distinct markings that are of a for *Bactra* unusual pattern and intensity. It is rather similar to that in *pythonia* which also suggests the proximity of these two species.

Bactra (Spinobactra) spinosa spec. nov.

Figs. 2—4

♂ 10.5—15 mm (holotype 12 mm). Head, antenna, and palpus white, tuft on vertex tinged creamy, palpus very slightly dusted with greyish laterally. Thorax white, shoulder mixed with grey. Abdomen whitish-ochreous.

Fore wing oblong-oval, costa rather curved at extremities, less curved in middle, apex moderately rounded, termen hardly convex, almost straight, oblique. White, partly suffused with pale fuscous-grey with a leaden gloss; markings darker fuscous, partially suffused with tawny. Basal patch to 1/3, indicated by its dark fuscous edge, ill-defined above, rather obtusely prominent in middle, narrow, slightly sinuate and vertical below; this patch moderately strigulated with grey-fuscous, hardly darker than the rest of wing; the prominence of edge of patch forming the first discal spot, dark fuscous; less than anterior half of costa with very short transverse strigulae, also obscured by fuscous-grey suffusion; posterior half of costa with 5 rather thick wedge-shaped oblique transverse streaks, separated by the usual pairs of whitish strigulae; these streaks short, except the fourth which is straight and traversing wing to before termen below apex; transverse fascia reduced to following dark fuscous suffused markings, mixed with tawny: a longitudinal moderate streak along posterior third of upper edge of cell and base of vein 9; an oblong conspicuous second discal spot, rounded-prominent below posteriorly and with a slender upcurved tooth-like appendix, continued across wing obliquely upwards and branching into fine dark lines along veins; above mentioned longitudinal streak and second discal spot interconnected by tawny suffusion along closing vein; ultimate costal streak followed by a slender short line, inwards-oblique and converging with streak below costa; an irregular zigzag blackish line from costa before apex, to middle of termen, followed by a semicircular outwards-convex line before lower half of termen; apex beyond black line grey; a conspicuous white area beyond cell, limited by the described remains of transverse fascia, so as to form an oblique, suboval well-defined spot with an extension towards costa before apex; spot in centre of ocellar area present but divided in blackish longitudinal strigulae. Cilia pale fuscous, dusted with dark fuscous.

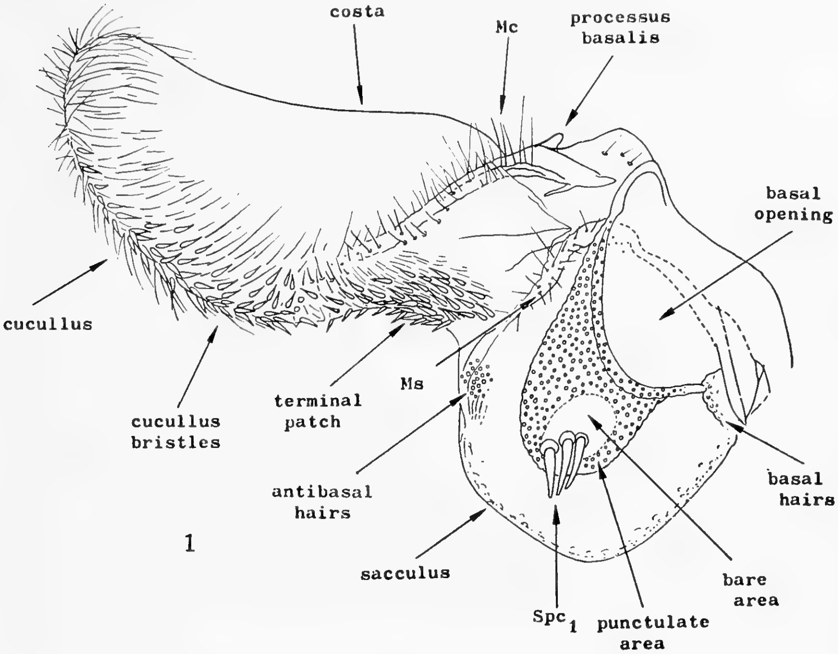
Hind wing greyish-fuscous, with a slight bronze gloss, paler towards base, darker towards apex. Cilia pale fuscous with a grey-fuscous subbasal band.

The long series of males available is variable to some extent, but the species is characteristically marked and may be confounded only with *pythonia.* The markings usually are contrasting, dark on a white ground. Most characteristic is the large second discal spot, either not incorporated in a transverse fascia, deeply concave posteriorly and so embracing the white spot beyond cell. Often the edge of the basal patch is complete, oblique above middle, once more angulate but concave above dorsum; also the transverse fascia may be complete, its upper portion moderate, oblique, to middle of longitudinal fasciate portion (as described in the holotype), second discal spot strongly extended so as to fill posterior part of cell, its posterior edge concave, containing the white area; usually also the ocellar dot is dark, conspicuous, and oval. Seldom the wing is infuscated and the markings obscured.

♀ 12—16 mm (allotype 15 mm). Fore wing slightly broader and more pointed than in the male. Much paler, the markings being light to pale ochreous-tawny, otherwise similar to male, but with the pale area beyond cell smaller, more longitudinally extended, fasciate and less clearly defined, the entire wing dusted with pale purple; streaks along veins posteriorly dark and distinct.

Hind wing light greyish-fuscous, slightly tinged brownish.

Other females rather variable (most rather worn); they all are considerably



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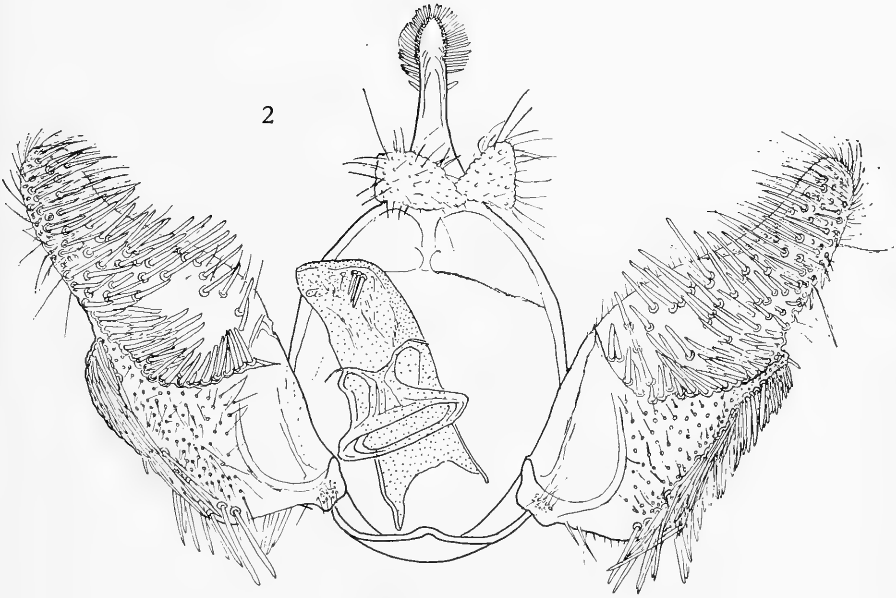

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Fig. 1. Valva of *Bactra (Bactra)* species *(lacteana)*, explaining the used terminology of the parts. Fig. 2. *Bactra (Spinobactra) spinosa* subgen. et sp. n., holotype, ♂, genitalia

paler, with markings delicate and rather fainter than in the males. Characteristic is the small and slender semicircular strigula before lower part of termen, concave posteriorly (as described in male); the ocellar dot is mostly distinct. One specimen has the second discal spot suffused with orange-ochreous.

Male genitalia. Tegumen and vinculum rounded, together forming an oval, vinculum rather broad, band-like. Uncus slender and rather long, corona long. Socius large. Valva rather broad, cucullus moderate and narrowed, entirely beset with long spines. Sacculus as described above, entirely covered with sparse punctulations, its outer edge heavily spinose. Aedeagus as described above.

Female genitalia as described above. Lamella antevaginalis strongly corrugated and of a peculiar shape. Colliculum not sclerotized. Signum very small.

Material examined. Males. South Africa, Transvaal, Pretoria North, 14.II.17 (C. J. SWIERSTRA), 1 ♂, holotype, gen. no. 4420. Paratypes: Transvaal, Pretoria, 2.III.1911 (D. BURGER), 2 ♂, gen. 4298, 4412; 31.XII.1909 (4446), 18.III.1910 (4445) (A. J. T. JANSE); Pretoria North, 5.II.1918 (4419), 13.III.1917 (4426), 4.II.1918 (4433), 17.III.1917 (4434) (C. J. SWIERSTRA). Nelspruit, XII.1917 (4421), II.1918, 2 ♂, 4422, 4424, 4428 (H. G. BREIJER), Nylstroom, 20.XII.-1925 (4455, 4468) (A. J. T. JANSE). Three Sisters (near Barberton), 2.III.1911 (4440) (A. J. T. JANSE). Natal: Nkwaleni, 10.I.1916 (4460—62) (A. J. T. JANSE).

Females. Transvaal, Pretoria. 4.I.1910 (A. J. T. JANSE), allotype, gen. 4318. Paratypes: the same locality, 23.II.1909 (2873), 5.II.1913 (4435), 1.III.1910 (4431). Pretoria North, 27.I.1917 (4425), 10.II.1918 (4427) (C. J. SWIERSTRA). Barberton, 20.XII.1910 (4442). Nelspruit, XI.1917 (no abdomen), II.1918 (4439). Natal, Nkwaleni, 10.I.1916, 3 ♀ (3784, 4310, 4314), 12.I.1916 (4225) (A. J. T. JANSE).

Subgenus **Bactra** Stephens, 1834

Bactra Stephens, 1834, Ill. Brit. Ent. Haust., vol. 4, p. 124. — Diakonoff, 1956, Zool. Verh., no. 29, p. 5 (subgenus).

Aphelia Stephens, 1829 nec Hübner, 1826 (preocc.), Syst. Cat. Brit. Ins., vol. 2, p. 180. Type-species, *Tortrix lanceolana* (Hübner, 1796).

This group, presenting so many difficulties with discrimination of its species in the Palaearctic region (cf. DIAKONOFF, 1962), appears to give even more trouble in Africa. The northern African representatives of the subgenus are Palaearctic; they introduce their own, already familiar, problems. The veritable Aethiopian element, the three species *scrupulosa, tradens,* and *confusa,* discussed below, present difficulties very similar to those of the Palaearctic species, although to a lesser degree. Also their females are not all too clearly defined. As an exception to the rule in *Bactra,* size, shape of the fore wing, colouring and markings of these species help identification considerably.

Still it may be pointed out that I separated *scrupulosa* and *confusa* with the help of the genitalia first, and was surprised to notice the above mentioned superficial differences afterwards, now that they were more evident after this sorting out. A second step was in the opposite direction: I found two different types of males under *confusa* first, and after rechecking the slides, discovered the specific differences of the genitalia afterwards. So three groups of males were separated; subsequent

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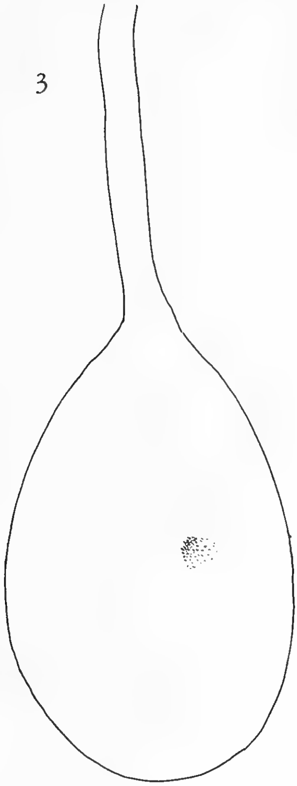

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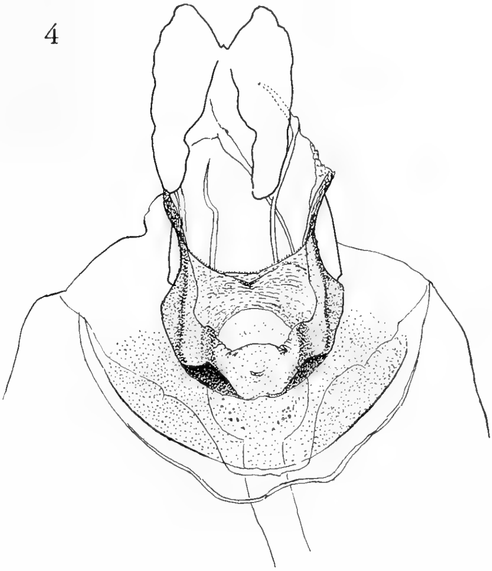

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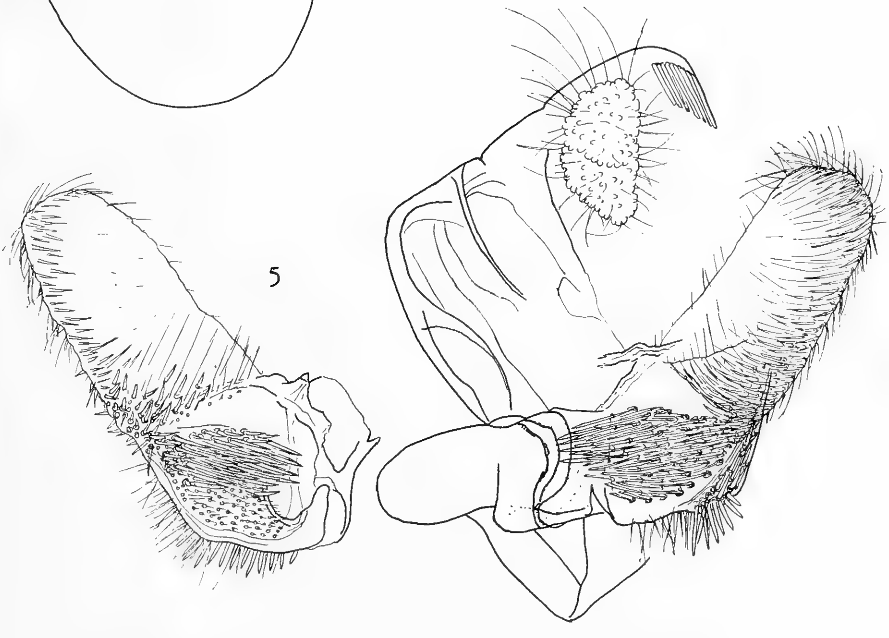

Fig. 3. *Bactra* (*Spinobactra*) *spinosa* subgen. et sp.n., ♀ allotype, bursa. Fig. 4. The same, sterigma. Fig. 5. *Bactra* (*B.*) *hebetata* Meyr. (= *pythonia* Meyr.), ♂ holotype, genitalia

selection of sex partners for *scrupulosa* and *confusa* presented now no excessive difficulties, for these females superficially are similar to the males. Much more difficult were females of *tradens,* being intermediate in character. Rearing experiments in some remote future might prove the correctness of my choice.

For the present I prefer to regard the three groups as good species, this in harmony with my experiences with the Palaearctic species of the subgenus *Bactra,* already mentioned in the introduction to the present paper, when referring to differences in the taxonomic "behaviour" of the three subgenera of the genus *Bactra.*

The groups in question — *scrupulosa, tradens,* and *confusa* — cannot be subspecies, because they occur together. I am greatly reluctant to regard them as "forms" or "varieties", because, as far as I am familiar with the Tortricidae, the differences of the male genitalia in these three species, though not striking, certainly exceed the limits of differences between infra-subspecific categories.

Bactra (Bactra) pythonia Meyrick, 1909
Figs. 5—8

Bactra pythonia Meyrick, 1909, Ann. Transv. Mus., vol. 2, p. 9, t. 3 fig. 7 (♀). — Clarke, 1953, Meyrick's Types, vol. 1, p. 267. — Anonymous, 1958, List Types S. & E. Afr. Museums, vol. 1, p. 57 ("holotype" indicated).

Bactra hebetata Meyrick, 1911, Ann. Trans. Mus., vol. 2, p. 227 (♂). — Clarke, 1953, Meyrick's Types, vol. 1, p. 154. Syn. nov.

Distribution. South Africa: Pretoria; Woodbush Village.

The original description of *pythonia* is based upon two female syntypes; no original designation of a holotype had taken place. Where in the "List of Types in the South and East African Museums" a "holotype" (abbreviated as "H.T.") is indicated, actually a lectotype is selected.

This is the first syntype; it was returned to the Transvaal Museum. The second syntype (a female without the abdomen, but conspecific beyond doubt) was retained by MEYRICK and is now in the British Museum.

After a critical comparison of a nice series of specimens of the two sexes I am satisfied that *pythonia* is the female and *hebetata* the male of the same species. The markings, facies and also many localities and dates (cf. below) correspond closely. The slight superficial differences of the two types fall within the individual variability, as well as within the sexual dimorphism.

This is a remarkable member of the subgenus *Bactra,* with markings rather differing from the patterns which are usual in the Palaearctic species, as summed up by me lately (1962, p. 5). JANSE's figure (*in* MEYRICK, 1909) is accurate but the colour is slightly too green. The genitalia are considerably different from those in the familiar Palaearctic species.

The types may be redescribed as follows.

Bactra pythonia Meyrick (Figs. 6—8).

♀ lectotype, 13 mm. Head whitish, edges of vertex suffused with pale tawny-fuscous. Palpus expanded anteriorly, edge roughish, terminal segment small, slender, almost concealed; sordid pale ochreous-tawny. Thorax ochreous-fuscous, tegulae scattered with fine tawny specks. Abdomen fuscous, venter pale fuscous.

Fore wing sublanceolate, rather narrow, costa gently curved, apex moderately pointed, termen gently concave above, oblique. Ground colour of anterior half of wing pale grey, of posterior, white. Markings brownish and olive-tawny. Anterior 2/5 of wing whitish-grey slightly dusted with olive and tawny, with about seven curved and interrupted, rather incomplete transverse brownish lines; every other line originating from a dark brown triangular dot; this area containing basal patch which is indicated by deeper and denser olive-tawny suffusion; edge of patch well-defined, before $^1/_3$, angulate in middle, convex above, concave below angulation; extreme edge of basal patch suffused with dark fuscous; posterior half of costa with five dark brown oblique wedge-shaped marks, alternating with minute, less oblique strigulae: first of these marks on transverse fascia, more distant from other, fourth continued across wing by a very oblique olive-tawny line; transverse fascia median, little oblique, formed by a rather irregular broad suffusion, dilated downward, with moderately suffused edges; fascia narrow and brown on costa, abruptly dilated and becoming olive-tawny below costa, with a pointed projection on each side above cell; anterior edge of fascia with a crescentic dark brown projection on a lower angle of cell, edging white discal dot from below; fascia below limited by fold; clear white ground colour of posterior half of wing forming the discal white dot and filling out disc beyond closing vein, thence extended apicad as a suffused streak directed towards costa before apex; apex with a tawny spot, centred with black; termen suffused with tawny and dusted with purplish; purple lines running between and parallel to veins, slightly thickened posteriorly; ocellus (distinct in left wing) centred with a subquadrate brown mark, indicated by an irregularly oval brown line along termen and between veins 4 and 5 above mark, anteriorly curved downwards and running in transverse fascia well below cell; dorsal margin with a series of dark brown strigulae and dots. Cilia pale grey, dusted with purple, with a white basal line and purple tips.

Hind wing pale grey, strewn with light tawny-fuscous except towards base, darker towards apex. Cilia concolorous, infuscated opposite apex.

Female genitalia. Eighth segment not sclerotized, ventral posterior edge with numerous light wrinkles. Lamella postvaginalis shaped as a slender longitudinal sclerite, narrowed downward, surface with many small folds; lower extremity of this sclerite deeply excised. Ostium bursae transversely oval or almost circular, simple, flanked by two oval refracting and transparent plates, each with a characteristic bent, also refracting and transparent small thickening of the edge directed towards ostium. Colliculum present, tubular, rather short, little sclerotized. Signum absent.

The lectotype is labelled thus: a printed label "Pretoria, A. J. T. JANSE", in the middle written "26.12.07. 11". Second label in red ink: "*Bactra pythonia* M., Type No. 1001".

The females are subject to some variation, the basal patch and the transverse fascia sometimes being obliterate; sometimes there is a black irregular spot in disc at the place of the obliterated basal patch. In some specimens there is a line along termen edging ocellus posteriorly, and originating out of a small black streak along posterior part of vein 5. The ocellus may be dissolved in two horizontal strigulae. The hind wing sometimes is considerably infuscated.

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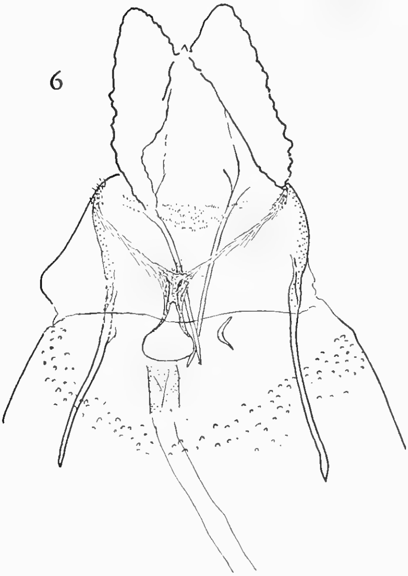

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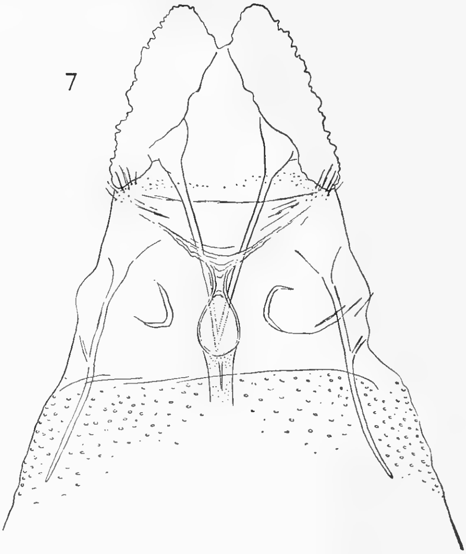

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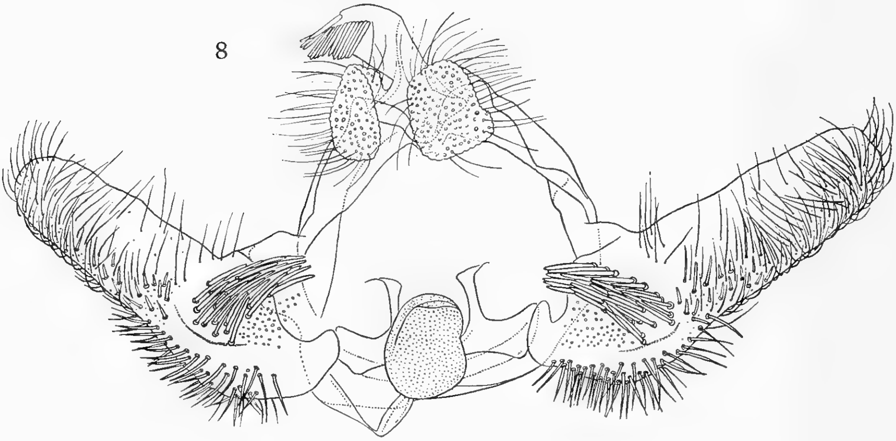

Fig. 6. *Bactra* (*B.*) *pythonia* Meyr., ♀ holotype, sterigma. Fig. 7. The same, ♀, gen. no. 3557. Fig. 8. The same, ♂, gen. no. 4415

Finally two specimens are melanistic, with the fore wing entirely and evenly dark fuscous (gen. nos. 4353, 4359).

Bactra hebetata Meyrick (Fig. 5).

♂ lectotype, hereby selected, 13 mm. Head sordid ochreous-white, sides of vertex infuscated. Palpus rather slender and smooth, subobtuse, pale grey-fuscous. Thorax dark fuscous with three pairs of large oval ochreous-whitish spots, more or less confluent.

Fore wing oblong, gently dilated, slightly broader than in female, costa gently curved, apex subobtuse, termen faintly convex. Whitish, partly suffused with grey (tips of scales grey). Markings dark fuscous, slightly suffused with tawny. Basal patch shaped as in female, but darker fuscous; transverse fascia also fuscous and darker than in female, shape similar, but tooth of posterior edge above cell absent (possibly rubbed) and transverse fascia reaching dorsum; costal markings similar but more extended, also lines originating from them; a round dot in apex, larger, black; posterior portion of wing more suffused with dark fuscous, thus rather limiting the white spots described in female, but not quite obscuring them; distinct are: the white transverse patch beyond closing vein and a stripe from there towards costa before apex; veins beyond cell, however, suffused with dark grey, interneural lines extended and black; terminal line distinct throughout; ocellus as in female but anterior part of bordering line obscured, dark central dot smaller, confluent with posterior edge of transverse fascia. Cilia light grey with a white basal line and black submedian and apical lines.

Hind wing rather dark fuscous with a brown gloss. Cilia dark fuscous with a pale basal line.

Male genitalia. Tegumen rather high, comparable with that of *graminivora.* Uncus moderately long. Socius rather large. Valva elongate-oval, with almost parallel edges, top gradually rounded; hairy and bristly; sacculus swollen, along the outer edge with rather numerous strong spines, less distinct anteriorly and posteriorly, punctulate area large, extending over almost the whole surface of the saccular dilatation, anterior half (left valva) or the whole area (right valva) beset with strong and long, very dense and numerous spines, directed mesiad and partly projecting over the cavity of sacculus. The Mc series not distinct, obscured by numerous long bristles and short spines, densely scattered in this region. The same concerns Ms series. (The mount no. 4542 is overstained, the dark colouring obscuring the structure).

The lectotype, present in the Transvaal Museum Collection, has a damaged right wing and is rather darkly suffused. It is labelled thus. Printed label with green edge: "Woodb. Vill., C. J. Swierstra", in the middle written: "15.12.1909". A written label "G(enitalia) 4542".

Usually a clearly marked species, with distinct white spot beyond cell and white streak towards end of costa, contrasting with deep tawny or brown of the transverse fascia and its crescentic projection; the ocellus is also characteristic.

Material studied. South Africa, Transvaal: Pretoria, Pretoria North, N.E. Pretoria, Heidelberg, Naboomspruit, Woodbush Village, Zoutpansberg, Waterval-Onder, Nelspruit, Kranspoort. Natal: New Hanover, Karkloof. Cape Province: Durban, Congella near Durban. Southern Rhodesia: Bulawayo. (A. J. T. Janse, C. J. Swierstra, H. G. Breijer, Leigh). 25 ♂, 13 ♀ (Genital nos. except types: ♂ 3521, 4411, 4413—4418, 4423, 4430—32, 4438—39, 4444, 4449, 4451—54, 4458, 4469. ♀ 2881, 3558, 3649, 4347, 4353, 4359, 4376, 4429, 4435—36, 4441, 4443, 4447—48, 4464, 4467, 4470, 4545).

A widely distributed species. Its position is very interesting for it is intermediate between the subgenera *Spinobactra* and *Bactra*, but closer to the latter and therefore incorporated in *Bactra.* Still it does not fit in the older conception of the subgenus, for the female genitalia and also the sacculus of the male are peculiar and very unusual.

Bactra (Bactra) dolia spec. nov.
Figs. 9—11

♀ 20—21 mm (holotype 21 mm). Head, palpus and thorax pale ochreous, palpus strongly dilated, with a roughish edge, slightly mixed with tawny. Abdomen pale ochreous.

Fore wing oblong, rather narrow, costa gently curved towards extremities, apex pointed, termen hardly sinuate, strongly oblique. Pale ochreous, dusted with light ochreous-tawny, markings light and dark fuscous. Costa with numerous light tawny strigulae, oblique and very slender, reaching to cell; dorsum and termen more dusted with light tawny, terminal area denser; a dark fuscous little suffused median stripe along lower half of cell, from base to closing vein; a fuscous-tawny, much lighter suffusion filling out remainder of cell and extending beyond cell so as to reach below apex; an interrupted narrow brownish line; a faint blackish dot in apex; a series of dark fuscous dots along dorsum. Cilia light tawny with a subbasal and a supramedian brownish line.

Hind wing with a strong golden gloss, suffused with light purplish-fuscous, dorsum paler. Cilia pale golden.

All specimens are slightly rubbed and very uniform. Only the Transvaal Museum specimens have paler hind wings and a more contrasting median dark streak; the specimen from St. Lucia Lake has a conspicuous black dot in apex, continued as a narrow bar over cilia.

Female genitalia resembling those of *scrupulosa* but differing as follows. Anapophyses and postapophyses extremely long. Lobi anales longer and more slender along the proximal portion. Ostium bursae very similar to that in *scrupulosa,* but on top of a much larger and considerably sclerotized process or column; these sclerotizations conspicuous, forming an L-shaped sclerite on each side, lower half extended into an oval plate. Lamella postvaginalis forming a strong cap above ostium, above this cap the wall is strongly punctulate and with 1—5 articulating bristles on each side (never present in *scrupulosa).* Signum absent.

Discovery of the corresponding male will be interesting.

Material studied. In the British Museum. South Africa, Natal: Camperdorn, 4.1908 (L.), holotype, ♀, gen. no. 3468, the same III.1908 (L.), paratype ♀, gen. no. 3614 (MEYRICK Collection).

In the Transvaal Museum. Natal, Umkomaas, 1.I.1914 (A. J. T. JANSE), 1 ♀, paratype, gen. no. 4301. St. Lucia Lake, X.1917, 1 ♀, paratype, gen. no. 4409. 4 ♀.

Bactra (Bactra) scrupulosa Meyrick, 1911
Figs. 12—15

Bactra scrupulosa Meyrick, 1911, Ann. Transv. Mus., vol. 2, p. 227. — Clarke, 1955, Meyrick's Types, vol. 1, p. 281. — Anonymous, 1958, List Types S. & E. Afr. Museums, vol. 1, p. 57 ("holotype" and "paratype" indicated).

Distribution. South Africa: Woodbush Village, Albert Mine.

♂ lectotype, 13 mm. Head whitish, vertex pale ochreous with a white median stripe. Palpus pale ochreous, strongly dilated, upper edge and apex roughish; pale

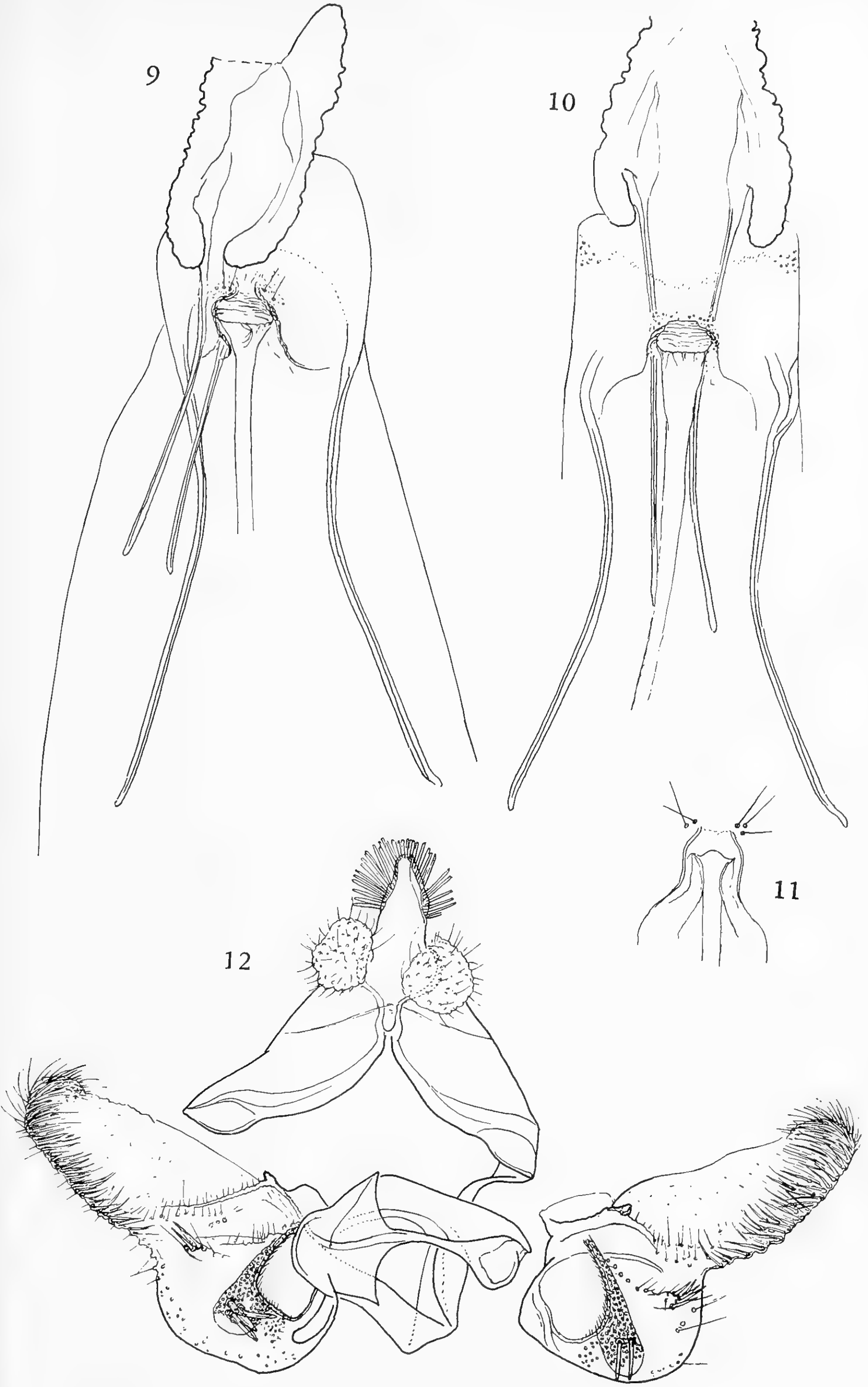

Fig. 9. *Bactra* (*B.*) *dolia* sp.n., ♀ holotype. Fig. 10. The same, ♀ paratype, gen. no. 4409. Fig. 11. The same, sterigma, paratype, gen. no. 4301. Fig. 12. *B.* (*B.*) *scrupulosa* Meyr., ♂ lectotype, gen. no. 4186

ochreous, terminal segment slender, short, blackish. Antenna pale ochreous. Thorax pale ochreous, somewhat streaked longitudinally with white.

Fore wing narrow, sublanceolate, costa gently curved throughout, more curved anteriorly, apex moderately pointed, termen hardly concave, oblique. Ground colour glossy white, marbled, and over terminal third, suffused with pale tawny-ochreous. Costa with a series of large and rather irregular marks, some 12 of them, dark fuscous along anterior half, fuscous mixed with tawny along posterior half; basal patch indicated by an inwards-oblique tooth-shaped mark above fold beyond base of wing and by an irregular obliquely-subquadrate dark fuscous spot just before $^1/_4$, situated in middle of disc, upper edge concave, outer and lower edges rounded; transverse fascia represented by a moderate tawny-fuscous, oblique and zigzag mark from below costa before middle, to below lower angle of cell, rather well-defined, in left wing narrowly connected with costa; this mark followed by a small and short horizontal streak halfway between cell and tornus; wing beyond cell suffused with pale tawny-ochreous, with a faint indication of a regularly oval deeper tawny streak from lower angle of cell to vein 7 beyond its base, along 7 to before termen, thence curved down and running to termen above tornus; blackish dusting forming fine lines above veins 7 and 6; a round tawny spot in apex; dorsal edge with small irregular fuscous blotches. Cilia greyish with a subbasal and a postmedian fuscous lines.

Hind wing pale grey, from middle towards apex becoming rather dark grey. Cilia glossy white, with an interrupted pale fuscous subbasal line.

Lectotype, labelled with a printed, green-edged label: "Woodb. Vill., C. J. SWIERSTRA", in middle written: "11-12.1909". A label in red ink: *"Bactra scrupulosa* Meyr., Type no. 2623." Genitalia no. 4186 ♂. "Cotype" a ♂ with a quadrate label in red ink: *"Bactra scrupulosa* Meyr. Cotype No. 1000" label in black ink: "Alb. mine 9.11.07 11" (gen. no. 4189). This specimen is much darker, strongly marbled and suffused with bright tawny partly dusted with dark fuscous, markings suffused; basal patch complete, edge strongly angulate, to $^1/_3$, upper half more oblique than lower half; transverse fascia shaped as an oblique straight band, from costa before middle to below end of cell, becoming darker brown downwards, merging in an indistinct pale tawny-ochreous marbling along dorsal third of wing; apical streak broad in middle; anterior end connected by a tawny line with $^2/_3$ of costa; two similar costal lines, parallel, between basal patch and transverse fascia; costa slightly sprinkled with black, several vertical series of black strigulae before termen below apex. Cilia pale tawny along termen, towards apex with a distinct white basal streak.

Hind wing similarly obscured but more fuscous-tinged.

The species usually is rather mottly marked and then may be referred to the "maculate" type (DIAKONOFF, 1962, p. 7, t. I, fig. 1); with a well-defined basal patch and a transverse fascia including the second discal spot; this latter, however, is not V-shaped but simply forms a straight and oblique continuation of the transverse fascia. An apical streak is not developed.

The long series available is variable; it is chiefly characterized by the small size and the narrow pointed wings of the two sexes. Furthermore, all males which are not too much rubbed show a transverse fascia originating from middle of costa, usually more distinct and thicker than the parallel costal strigulae; these strigulae are moderate in number, not very slender and rather distant; the fascia runs obliquely across the wing and ends in a rather broad stripe across the lower angle of cell, including the second discal spot. The connection of this spot with the costa may be very narrow, but it is almost always traceable in not rubbed specimens. The basal patch in male is mostly distinct, its edge well-defined, at least along the upper half and is but seldom reduced to a transverse fasciate dark first discal spot.

The hind wing in the males is varying from dark fuscous (seldom) to pale greyish-fuscous, with a whitish base.

Both the fore and the hind wings are narrower and more pointed than in *confusa.*

The females are slightly more variable than the males, but have also narrower and longer wings than in *confusa.* They are usually more differing from this species than the males.

The following is a description of a characteristic female.

18 mm, neallotype. Head pale ochreous suffused with tawny, except on face. Palpus rather long, strongly dilated, edge roughish, pale ochreous, suffused with tawny. Antenna dark brown. Thorax pale ochreous, slightly spotted with pale tawny, tegula light; metathorax white. Abdomen pale ochreous.

Fore wing elongate, narrow, costa considerably sinuate, apex slightly produced, pointed, termen sinuate, oblique. Pale ochreous, along costa strigulated, elsewhere dusted or suffused, with light tawny. Costal strigulae slender, becoming longer along posterior half of costa and deeper tawny towards apex; a median longitudinal streak from base to apex, of bright tawny suffusion, dusted with minute black dots (tips of scales), this streak dilated beyond base, not quite filling cell, beyond cell slightly narrowed; termen suffused with paler tawny; apex with a blackish point, termen with a faint brown line, a series of blackish dots along dorsal edge; apex with a blackish dot. Cilia in tornus pale ochreous; elsewhere cilia tawny dusted with brownish and with white basal line, followed by a postmedian and a subapical narrow whitish lines.

Hind wing whitish golden, posterior half deeper golden tinged and with a faintest fuscous suffusion. Cilia whitish golden, paler towards dorsum, more ochreous-tinged along termen and around apex, a shadow of a subapical fuscous line; opposite apex cilia with brownish subbasal and subapical short lines, apex with a few dark dots.

Female specimen redescribed: Pretoria, 8.I.1910, (A. J. T. JANSE), gen. no. 4373.

Besides the described female which is of the fasciate type, which is the most common, there is also the reduced type present, derivable from the maculate type as described for the male, but with markings for the greater part obliterate; there are also a few pale females, the unicolorous, or almost unicolorous type.

Female genitalia are very close to those of the Palaearctic *Bactra lacteana* Caradja, but differ by the invariable absence of a signum. The ostium bursae is perhaps a trifle wider than in *lacteana*, the colliculum part is very slender, the edge of the ostium usually has several small transverse folds. The lamella postvaginalis sometimes is moderately but distinctly sclerotized around the lateral corners of the

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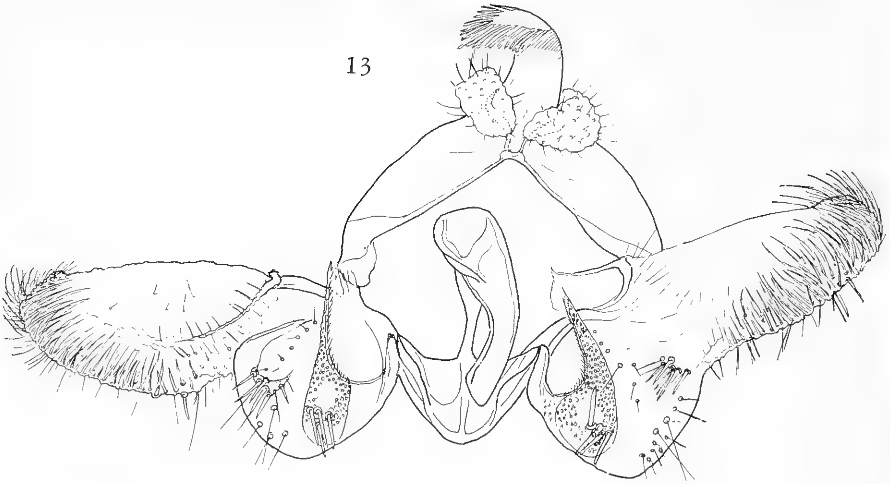

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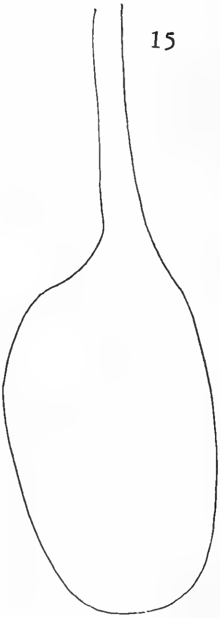

Fig. 13. *Bactra* (*B.*) *scrupulosa* Meyr., ♂ syntype, gen. no. 4189. Fig. 14. The same, ♀ gen. no. 4373. Fig. 15. The same, bursa

ostium; the "cap" above the ostium is as in *lacteana*, convex above, with several longitudinal folds, crowned by some distinct punctulation of the wall, sometimes shaped as small triangles, "ears", at the sides, exactly similar to those in *lacteana*. The lamella antevaginalis may be ill-defined or slightly indicated by a faintest sclerotization and then shaped as a subtriangular small plate with or without a small curved fold on each side of the colliculum part of the ductus bursae; lateral ends of the ostium cap are then continued as the sides of that triangle. The apophyses are moderately long and slender. Actually the ostium is situated on top of a moderate prominence, visible only in profile.

Material studied. Besides the lectotype and the original syntype, mentioned above, the followings males. In the British Museum. South Africa, Transvaal: Pretoria. Natal: Frere, 3600 ft.; Weenen, Kimbolton Estcourt, 13.XI untill 22.II (A. J. T. JANSE, C. J. SWIERSTRA, MARSHALL and HUTCHINSON, in MEYRICK and WALSINGHAM Collections).

In the Transvaal Museum. Transvaal: Pretoria, Fountain Grove, New Smitsdorp, Woodbush Village, Elandshoek, Modderpoort. Natal: Karkloof, Rietvlei, Eshowe, Cathedral Peak. Cape Province: Stellenbosch, Alexandria (Langebos) 27.XI, 3.IV. (Collected by A. J. T. JANSE, C. J. SWIERSTRA, OTTO, S. VILJOEN, Ch. K. BRAIN, A. CAPENER, L. VÁRI). Genit. nos: ♂ 2872, 3461, 3518, 3559, 3637—38, 3642—43, 3647—48, 3777, 3782—83, 4217—18, 4220—22, 4224, 4226, 4229—30, 4256, 4259, 4261, 4265, 4271, 4338, 4340, 4368, 4371, 4408, 4465, and T.M. 4541.

Females. In the British Museum. Transvaal: Pretoria, Barberton. Natal: Weenen, Kimbolton Estcourt. I—II (A. J. T. JANSE, H. THOMASSET, HUTCHINSON, in MEYRICK and WALSINGHAM Collections).

In the Transvaal Museum. Transvaal: Pretoria, Barberton, Pretoria North, Nelspruit, Waterval-Onder, Nylstroom. Natal: Karkloof, Rietvlei. Cape Province: Kleinmond 25.X—23.III (A. J. T. JANSE, C. J. SWIERSTRA, H. G. BREIJER, H. G. DICKSON). Genit. nos.: ♀ 2871, 2905, 3467, 3528, 3553, 3708—9, 3779, 3795—6, 4223, 4227—8, 4245—6, 4248, 4255, 4257—8, 4260, 4262—3, 4266, 4290, 4317, 4324, 4325, 4328, 4332, 4346, 4356, 4360, 4373. In total 33 ♂, 32 ♀.

Bactra (Bactra) tradens spec. nov.

Figs. 17—18

♂ 13.5—17 mm (holotype 16.5 mm). Head pale ochreous, face creamy. Palpus creamy, laterally mixed with grey towards dorsal edge which also bears two well-defined black transverse marks; terminal segment grey. Thorax pale ochreous, tegula mixed with brownish along edge and on apex. Abdomen ochreous-fuscous.

Fore wing oblong-triangular, distinctly dilated, costa curved, apex pointed, termen sinuate, long, oblique. Pale ochreous, evenly suffused with pale leaden, all markings edged with creamy. Markings light tawny and dark brown, of the "tigroid" type. Costa with some 20 dark brown subtriangular transverse marks, each other mark continued as a slender tawny very oblique transverse strigula; along anterior half of costa these strigulae run more or less straight across cell, those along posterior half run parallel to preceding at origin but below costa turn horizontal and run towards termen, thence curve down and become almost vertical; ultimate two or three strigulae run to termen and along this to tornus; posterior extremity of costa with a conspicuous whitish spot; first discal spot somewhat irregular, dark brown with two teeth; second discal spot elongate-semioval, almost black; stigma not defined; space before termen somewhat more suffused with tawny, appearing darker, space above dorsum less so suffused, lighter; a very faint ocellar dark dot; a suffused short blackish streak through apex. Cilia dark grey with a narrow basal, a faint antemedian, and an ill-defined subapical white lines.

Hind wing rather pale fuscous-purplish, becoming paler, almost transparent, on dorsum. Cilia sordid pale fuscous with a paler base and a grey subbasal streak.

Other males all show the same "tigroid" pattern with numerous, well-defined fine strigulae and limited discal spots; one specimen is rather bright tawny tinged, another rather suffused with darker leaden, a third shows a contrasting median blackish streak from base to apex, with an obtuse prominence on end of cell ("tigroid-fasciate", 4362).

♀ 16—19 mm (allotype 17.5 mm). Fore wing narrower, less dilated, but apex more pointed and termen sinuate and more oblique than in male. Colouring more variable. In the allotype fore wing strongly suffused with bright tawny-ochreous, finely reticulate and marbled with dark purplish; cell filled out with purplish; markings reduced to short dark strigulae along costal edge.

Hind wing pale fuscous, becoming paler towards base.

There are four female paratypes with similar genitalia and appearance; they are somewhat brighter tawny suffused and have a more distinct, although strongly suffused, median dark stripe. Three more females have less typical genitalia; these specimens are lighter coloured. It seems advisable to exclude them from the paratype series.

Male genitalia. Perhaps best comparable with the Palaearctic *furfurana,* but distinct. Also close to *confusa.* Tegumen rather low. Uncus moderate, curved, top pointed. Vinculum moderate. Valva broad and short. Cucullus bristles normal or rather weak. Sacculus moderate, somewhat smaller than in *confusa,* spheroidal, outer edge of cucullus is continued over the surface of the sacculus, thus forming a distinct small ridge or fold, the Ms series thus being unusually accentuated; this small ridge continues almost to the punctulate area. Terminal patch present but not dense; Mc series is not clearly defined or separated from the fine setae between this series and the terminal patch, in very much the same way as in *confusa.* The punctulate area is limited, shorter, narrower at the top, with 3—4 short curved spines; the group of basal hairs is clearly extended and entirely united with the punctulate area. The antibasal group of setae large, setae numerous and long (as in *confusa*). Aedeagus and caulis both rather long and sclerotized.

Female genitalia are not easily discriminated from these of *confusa* or *scrupulosa,* this forming the greatest difficulty with the identification of the species of the present paper. Actually intermediate between *confusa* and *scrupulosa.* Ostium wider than in the latter, less wide than in the former species. The rostral edge of the eighth tergite clearly sclerotized, uniting the bases of similarly sclerotized anapophyses as a bow or a semicircle, thus differing from *scrupulosa* where these parts are not sclerotized. The lateral sclerites of the ostium are not defined or indicated by very faint fragments of their caudolateral edges; however, each has a small peculiar dark and tubular appendix caudomesially, not developed in the other two species. Ductus and corpus bursae normal. Signum absent.

Material studied. Males. South Africa, Transvaal: Pretoria, 30.I.1910 (A. J. T. JANSE), holotype, gen. no. 4311. Paratypes: Pretoria, 3 and 29.XI.1909 (4312,

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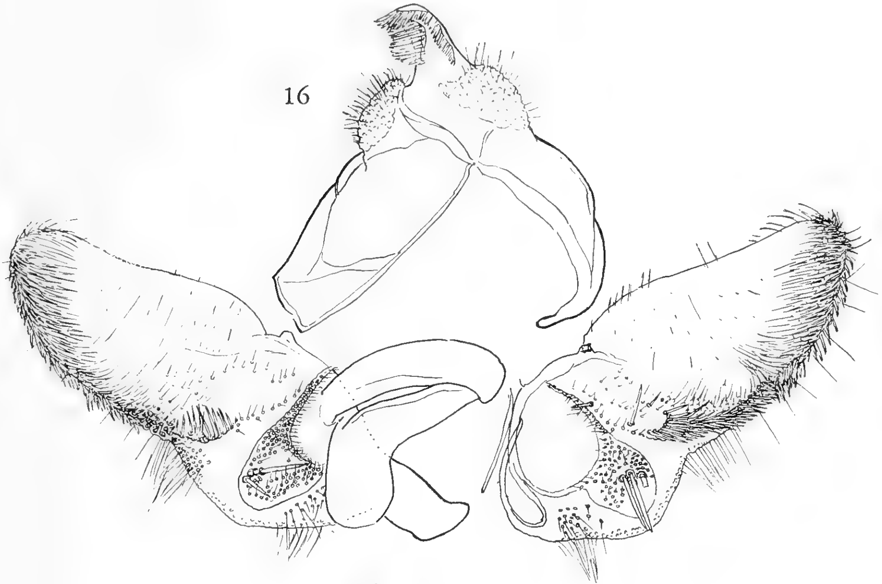

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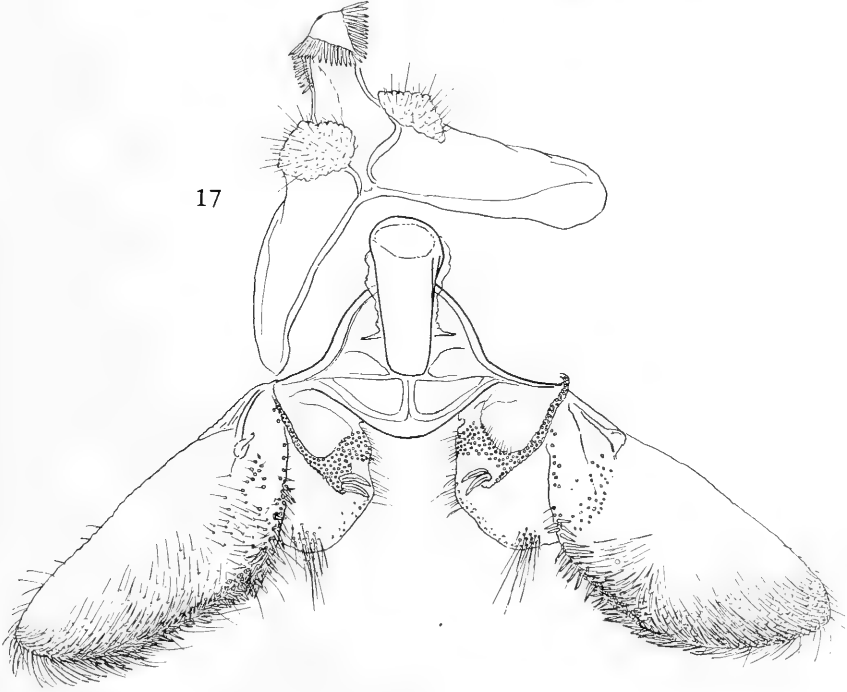

Fig. 16. *Bactra* (*B.*) *confusa* sp.n., ♂, holotype, genitalia. Fig. 17. *B.* (*B.*) *tradens* sp.n., ♂, holotype, genitalia

4326); 17.I.1910 (4313, 4323); 17.XII.1909 (T.M. 4544); 14.X.1917 (4362); Mahuba's Kloof, 1050 m, 18.I.1925 (4357) (All collected by A. J. T. JANSE). Natal, Karkloof, 11.I.1917 (4336) (same collector). Cape Province, Swellendam, IV.1943 (4336) (C. G. DICKSON). (In the Transvaal Museum). Transvaal, Pretoria, 2 and 8.XII.1909 (JANSE), 2 paratypes, gen. 3464 and 3465. (In the British Museum).

Females. Transvaal: Waterval-Onder, 11-13.X.1951 (A. J. T. JANSE), allotype, gen. no. 4404. Paratypes: Transvaal: Nelspruit, XI.1917 and II.1918 (H. G. BREIJER), gen. 4246, 4247 and 4248; Pretoria North, 23.III.1927 (C. J. SWIERSTRA), gen. 4245. Pretoria, 3.II.1910 (A. J. T. JANSE). Besides, the following females: Pretoria, 3.X.1907 (4333), 8.I.1910 (4373); Nylstroom, 4-5.III.1954 (4407). (All collected by A. J. T. JANSE). In total 12 ♂ and 8 ♀.

The species is intermediate between *scrupulosa* and *confusa* and also closely allied with *furfurana*. From the former two species it may be separated by the genitalia, from the latter, by entirely different facies and markings of the two sexes and also by the different sacculus of the male and the absence of a signum in the female.

Bactra (Bactra) confusa spec. nov.

Figs. 16, 19

♂ 12—15 mm (holotype 14 mm). Head, palpus and thorax pale ochreous-fuscous, tinged olive, face whitish, palpus laterally slightly dusted with grey. Abdomen pale fuscous.

Fore wing oblong, subovate, broad, costa rather curved throughout, less curved in median portion, apex pointed, termen long, straight, oblique. Whitish-ochreous, generally with olive tinge, markings being formed by fine olive reticulation, only partly mixed with fuscous. Costal markings not numerous, about 7—8 strigulae, dark fuscous on costal margin, pale olive thence, moderately oblique, faint along anterior half of costa, well-defined along posterior, throughout alternating with minute dark lines; basal patch not reaching to $^1/_3$, indicated by a narrow dark fuscous edge only, which is angulate slightly above middle, rather obtusely, and gently sinuate above dorsum; transverse fascia well-traceable, from middle of costa to just above end of fold, strongly suffused, olive-tinged, mixed with fuscous; this fascia moderate on costa, including a very irregular and strongly suffused second discal spot which is obliquely transverse; stigma hardly perceptible and ill-defined; lower third of posterior edge of fascia abruptly well-defined, serrate and little oblique; a fuscous suffused streak from apex to end of termen, gradually attenuated downwards, marked with a few blackish vertical strigulae. Cilia fuscous, a basal line and some tips of scales whitish.

Hind wing unicolorous dark grey-fuscous, with a very faint golden gloss. Cilia grey-fuscous with a whitish basal line.

The most conspicuous features of the species are broad and pointed wings with not sinuate termen, the fuscous-olive marbled markings and the unicolorous dark hind wings. The series of males is uniform, one specimen is rather suffused with brighter ochreous-olive and has a pronounced row of dark brown costal dots.

♀ 16—18 mm (allotype 17.5). Head and palpus paler, whitish-creamy, woolly by rather loose scales, palpus finely dusted with grey, terminal segment grey. Fore wing slightly broader, costa a trifle more curved. Very similar to male but paler, less suffused, markings therefore more pronounced, thicker, unicolourous pale tawny-olive, without dark marks along costal margin; strigulae along posterior part of costa more complete, reaching to termen, one from beyond $^1/_3$ of costa even traceable to tornus, forming a loop in centre of disc; transverse fascia including a second discal spot of more usual shape; semicircular, with a traceable stigma; first discal patch is dissolved so as to form fuscous marbling.

Cilia and hind wing exactly as in male.

Another female (4385) is coloured thus. Rather densely suffused with tawny-olive, almost entirely obscuring the strigulae, except along costal edge where they are distinctly dark brown and short; transverse fascia similarly obscured by olive suffusion, only the second discal spot is distinct, being dusted with dark brown, as also is the terminal streak in apex and along its lower half; some dark dots along dorsum.

Other females similar, two are somewhat brighter coloured and with dark fuscous first discal spot rather extended along fold.

Male genitalia. Rather similar to those of the Palaearctic *B.* (*B.*) *lacteana* Car., but distinctly different. Tegumen and socius normal. Uncus rather long (longer than in *lacteana*), top distinctly more pointed. Valva similar, rather broad and short, with a rounded top. Cucullus bristles in a broad row which becomes less and less dense towards sacculus; terminal patch is present, broad but not dense and somewhat irregular, continued far up the surface of sacculus; anterior edge of this patch beset with long and straight spines, then abruptly changing into Ms series which is seemingly double but sparse, then becoming single; the Mc series is rather ill-defined, occupying a broad area on and between the ridge of the processus basalis and extending halfway towards the Ms. The punctulate area similar to that of *lacteana,* large, semioval, top gradually rounded. Spc_1 spines rather long, slender and straight. The group of basal hairs is moderate but larger than in *lacteana*. There is another characteristic feature: a group of hairs on the opposite side of the sacculus just below the terminal patch, which I indicate with the name of antibasal hairs. This group consists of rather numerous long and thin setae. (In *lacteana* there are only a few very small setae there). The outer surface of sacculus is strongly wrinkled because of numerous scars of scales. Aedeagus and caulis rather long.

Female genitalia. Of a type similar to that of *scrupulosa,* but clearly distinct. Sterigma forming a prominence, much broader than in that species; this structure is flanked by two subcrescentic plates, clearly sclerotized, gradually dilated upwards, lower portions forming a semioval horizontal plate on each side. Cap of the ostium (lamella postvaginalis) wide, with several longitudinal folds, forming a smaller cap on each side, moderately sclerotized. Wall above cap only with a few wrinkles laterally. Ostium wide, single, calyciform. Ductus bursae narrow. Signum absent.

Material studied. South Africa, Transvaal: Wylie's Poort, 6.XI.1920 (C. J. SWIERSTRA), 1 ♂, holotype, gen. no. 4386. The same locality and collector, 6.XI.1920, 1 ♀, allotype, gen. no. 4387. All other paratypes: the same locality and collector, 3-10.XI.1920, 1 ♂, 4 ♀, nos. 4383 ♂, 4380—1, 4384—5. Natal: Sarnia (Mrs. GURRY), XI.1913, 1 ♂, 1 ♀ (4383 ♂, 3786); the same locality. 10.II.1912 (WILLIAMSON), 1 ♀ (4278) (Coll. JANSE). Umkomaas, 4.XI.1920 (C. J. SWIERSTRA), 1 ♂ (4382); the same, 23.I.1914 (A. J. T. JANSE) 1 ♂ T.M. 4642). Karkloof: 12-20.I.1917 (A. J. T. JANSE), 2 ♀ (3797, 4475). Natal, Pinetown (L.), I.1909 (MEYRICK Coll., British Museum), 1, ♀, gen. no. 3460. 5 ♂, 10 ♀.

The present species could be separated without much difficulty. After having sorted out the specimens with the aid of the genital characters I was struck by the uniformity of the so selected series of the rather large, broad-winged insects.

Intermediate between *tradens* and *scrupulosa*.

Bactra (Bactra) furfurana (Haworth, 1811)

Tortrix furfurana Haworth, 1811, Lep. Brit., p. 466.

Bactra furfurana: Wilkinson, 1859, Brit. Tortr., p. 147. — Zeller, 1875, Verh. zool.-bot. Ges. Wien, vol. 25, p. 41. — Fernald, 1882, Trans. Am. Ent. Soc., vol. 10, p. 29.

Grapholitha (Aphelia) furfurana: Heinemann, 1863, Schmett. Deutschl., Kleinschm., vol. 1, p. 135.

——— *acutana* Eversmann, 1844, Faun. Lep. Volgo-Ural, p. 529 (non binom.).

Phoxopteris lamana Zeller, 1846, Isis, vol. 30, p. 257.

Tortrix (Aphelia) scirpana Herrich-Schäffer, 1849, Syst. Bearb. Schmett. Eur., vol. 4, p. 243.

Tortrix (Aphelia) pauperana Herrich-Schäffer, 1849 (nec Haworth, 1811), Suppl. p. 302.

Sciaphila canuisana Millière, 1847, Rev. & Magas. Zool., ser. 3, vol. 2, p. 247. — 1875, Ann. Soc. ent. Cannes, t. 1, f. 6.

Distribution. Northern Africa, Morocco: Buhasen. Palaearctic and Nearctic regions. Must have been introduced from Europe.

Bactra (Bactra) lanceolana (Hübner, 1796)

Tortrix lancealana Hübner, 1796, Samml. europ. Schmett., vol. 7, Tortr., t. 13, f. 80.

Ancylis lanceolana: Hübner, 1825, Verz. bek. Schmett., p. 376.

Phoxopteris lanceolana: Treitschke, 1830, Schmett. Eur., vol. 8, p. 232, no. 1.

Phoxopterix lanceolana: Duponchel, 1834, Hist. nat. Lép., p. 339, t. 253, fig. 1.

Tortrix (Aphelia) lanceolana: Herrich-Schäffer, 1849, Syst. Bearb. Schmett. Eur., vol. 4, p. 243. — Suppl. 1849, p. 317.

Bactra lanceolana: Wilkinson, 1859, Brit. Tortr., p. 115. — Stainton, 1859, Manual, vol. 2, p. 226. — Fernald, 1882, Trans. Amer. Ent. Soc., vol. 10, p. 28.

Grapholitha (Aphelia) lanceolana: Heinemann, 1863, Schmett. Deutschl., Kleinschm., vol. 1, p. 134.

Tortrix dibeliana Hübner, 1800, Samml. europ. Schmett., vol. 7, Tort, p. 272.

Tortrix pauperana Haworth, 1811, Lep. Brit., p. 469.

Tortrix expallidana Haworth, 1811. Lep. Brit., p. 469.

Tortrix egenana Haworth, 1811, Lep. Brit., p. 469.

Tortrix egestana Haworth, 1811, Lep. Brit., p. 470.

Tortrix lanceana Frölich, 1828, Ent. Tortr. Würt., p. 98.

Bactra nigrovittana Stephens, 1852, List Brit. Anim., vol. 10, p. 99.

Fig. 18. *Bactra* (*B.*) *tradens* sp.n., ♀ allotype, sterigma and ovipositor. Fig. 19. *B.* (*B.*) *confusa* sp.n., ♀ allotype, sterigma and ovipositor. Fig. 20. *B. (B.) crithopa* Diak., ♂ holotype, genitalia (fig. 20 after Diakonoff, 1960)

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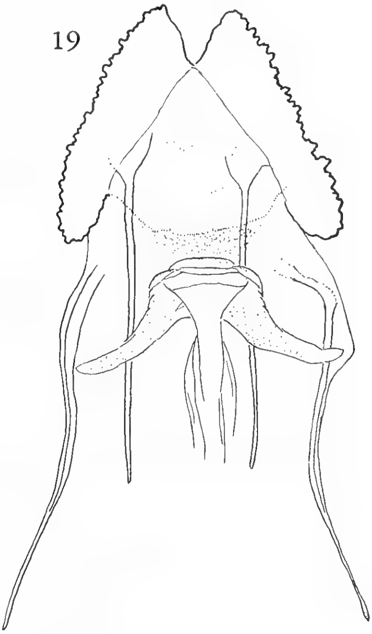

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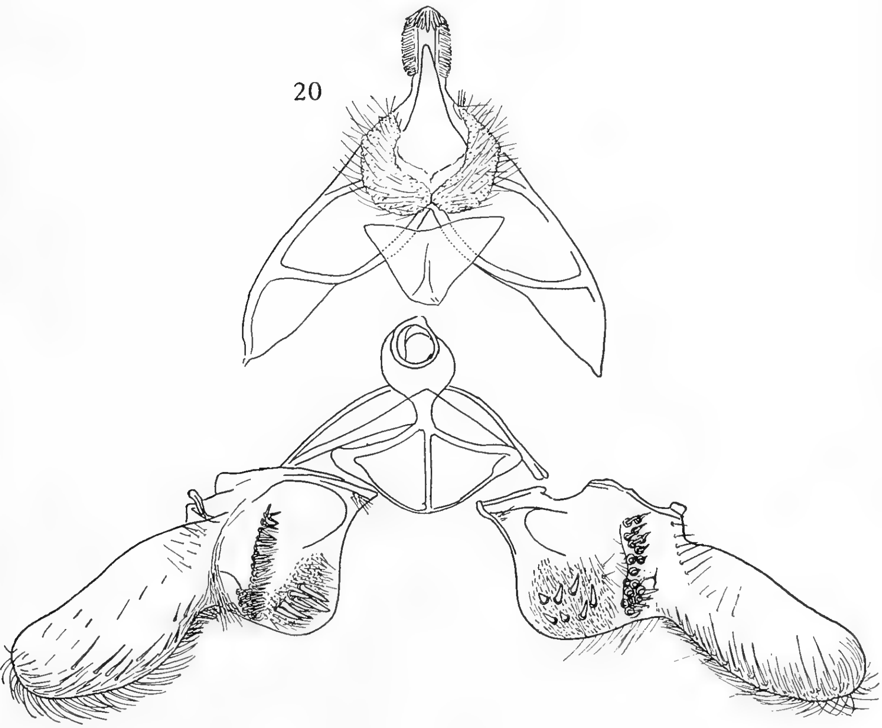

Bactra (Aphelia) egenana Kennel, 1900, non Haworth 1811, Iris, vol. 13, p. 264.

Bactra (Aphelia) fumosana Kennel, 1900, Iris, vol. 13, p. 263.

Bactra fumosana: Kennel, 1910, Palaearkt. Tortr., p. 472—473, t. 18, fig. 73a. — Rebel, in Staudinger & Rebel, 1901, Catal. Lep. Pal. Faun., vol. 2, p. 113.

Bactra (Bactra) fumosana: Diakonoff, 1956, Zool. Verh., no. 29, p. 16, fig. 16 (gen. ♀ type fig.).

Distribution. Northern Africa, Algeria, Morocco. Palaearctic region. Canada. Obviously introduced in Northern Africa from Europe.

Bactra (Bactra) graminivora Meyrick, 1922

Bactra graminivora Meyrick, 1922, Exot. Microl., vol. 2, p. 521 (♂ ♀, Bengal). — Fletcher, 1932, Life histories Ind. Microl., ser. 2, p. 24, t. 14 figs. a-d (biol., food-plants). — Diakonoff, 1950, Bull. Brit. Mus., Ent., vol. 1, p. 287, t. 6 fig. 24, t. 7 figs. 34, 36 (lectotype select., gen. ♂ ♀ fig.). — Amsel, 1958, Beitr. nat. Forsch. S.W. Deutschl., vol. 17, p. 76 (N. Arabia).

Bactra cyperana Amsel, 1951, Bull. Soc. Sci. Nat. Maroc, vol. 31, p. 68, fig. 4 (♂, Morocco).

Bactra mediterraneana Agenjo, 1952, Faunula Lep. Almeriense, p. 99, t. 4 figs. 32, 33, t. 12 figs. 6, 7 (♂ ♀, Spain, Almeria).

Bactra (Bactra) graminivora: Diakonoff, 1956, Zool. Verh., no. 29, p. 18, fig. 10. — 1959, Bijdr. Dierk., fasc. 29, p. 179, figs. 6, 7 (*cyperana, mediterraneana* syn.). — 1962. Zool. Verh., no. 59, figs. 1e, 18—20, 29, 30; t. III figs. 17—20. — 1963, Ann. Mus. Wien, vol. 67 (in press) (♂, Nubia).

Distribution. Canary Islands, South Spain, Malta, Algeria, Morocco, Egypt, Sudan, Nubia, Gambia, French Congo, Arabia, Iraq, Mesopotamia, Caucasus, Caspian region, Tadzhikistan, Bukhara, North Persia, Afghanistan, Hyderabad, Bengal.

This widely distributed Asiatic species apparently is a straggler in Africa. The incontinuous distribution suggests that it is rare and local.

The species is represented by the maculate form in the males with more or less pronounced discal markings characteristic for this species, while the females are, as usual, of the unicolorous form, with one exception, a vittate female, a form not familiar to me in *graminivora* so far.

Material studied. Transvaal Museum. Transvaal: Pretoria, 24.X.1915 (A. J. T. JANSE), 1 ♂, gen. no. 3785; 1 ♀, gen. no. 3415. Natal: Bela Vista, XI.1916 (C. J. SWIERSTRA), 1 ♀.

Vienna Museum. French Congo: Insongo, 27.III.1927 (WEIDHOLZ), 1 ♀, 4483. Sudan, Sungikai 19.III.1914 "*Bactra lanceolana* Hb., det. Meyrick", 1 ♀, 4484; Debri, 25.III.1914, 1 ♂, 4485 (as above); Rosti, 21.IV.1914 (do.), 1 ♂, 4486; Kororak, 31.III.1914, 2 ♀, 4487—8 (EBNER). In total 3 ♂, 5 ♀.

British Museum. West Africa: Gambia, Bathurst, XI.1884 (CARTER), WALSINGHAM Collection, no. 893, 1 ♀, gen. no. 3650.

Bactra (Bactra) crithopa Diakonoff, 1957
Fig. 20

Bactra (Bactra) crithopa Diakonoff, 1957, Mem. Inst. Sci. Madagascar, ser. E, vol. 8, p. 272, fig. 29, t. 8 fig. 20 (♂).

Distribution. Reunion.

The species of which only the single male is known, is easily recognisable by the Mc series formed not by hairs but by small spines, and by unusually large socii.

Subgenus **Chiloides** Butler, 1881

Chiloides Butler, 1881, Ann. Mag. Nat. Hist., ser. 5, vol. 7, p. 392. — Meyrick, 1885, Trans. New. Zeal. Inst., vol. 17, p. 142. — Fernald, 1908, Gener. Tortr., p. 44, 58. — Fletcher, 1929, Mem. Agr. Ind., Ent., vol. 11, p. 30, 46. — Diakonoff, 1956, Zool. Verh., no. 29, p. 19 (subgen. of *Bactra*).
Type-species, *Chiloides straminea* Butler, 1881.

For a short discussion of the subgenus may be referred to the introduction.

Bactra (Chiloides) jansei spec. nov.
Figs. 21—23

♂ 13—15 (holotype 15 mm). Head creamy. Antenna fuscous. Palpus pale ochreous. Thorax creamy, tegula infuscated, metathorax silvery-white. Abdomen pale ochreous, venter whitish.

Fore wing oblong, suboval, costa considerably curved throughout, apex pointed, termen sinuate, oblique. Creamy, rather densely dusted with purplish-brown, except an area in disc beyond cell extending halfway towards termen and limited by veins 3 and 8. Markings of the "tigroid" type, slightly reduced, tawny and brown. Costa with 6—7 thicker oblique strigulae, slightly undulate, some in the median portion of costa furcate towards wing margin (a very unusual feature; this furcation must be more or less incidental, as it is not congruent in right and left wings); these strigulae reach to cell and to vein 8, and alternate with minute shorter lines; penultimate costal streak forming a curved line across wing to tornus; basal fourth of wing rather strongly infuscated; first discal spot obliterate, second discal spot linear, a longitudinal dark fuscous strigula just above lower angle of cell; veins beyond cell finely streaked with brownish; a well-defined terminal streak, gradually dilated upwards, merging in a subtriangular and suffused subapical dark brown spot, being a reduced apical streak, including a small black streak through apex; a creamy spot on costa above apex. Cilia creamy with a suffused fuscous subbasal line.

Hind wing pale golden-fuscous, becoming very pale towards base, deeper fuscous towards apex, glossy. Cilia whitish, with a pale fuscous basal half.

The male series is rather variable, with more or less defined strigulation, some are pale fuscous, other pale ochreous tinged. One specimen (4327) is of the maculate type, with the fine strigulation noticeable but not conspicuous and with the both discal spots large, well-defined, fuscous, roundish, second spot larger and lighter than first. Sometimes (4322) the dorsal half of wing is suffused with purplish-fuscous. In paler specimens there is a contrasting black dot in apex.

♀ 13—17 mm (allotype 17 mm). Head and thorax fuscous mixed with creamy. Palpus pale ochreous, with an oblique median greyish stripe. Abdomen ochreous-fuscous.

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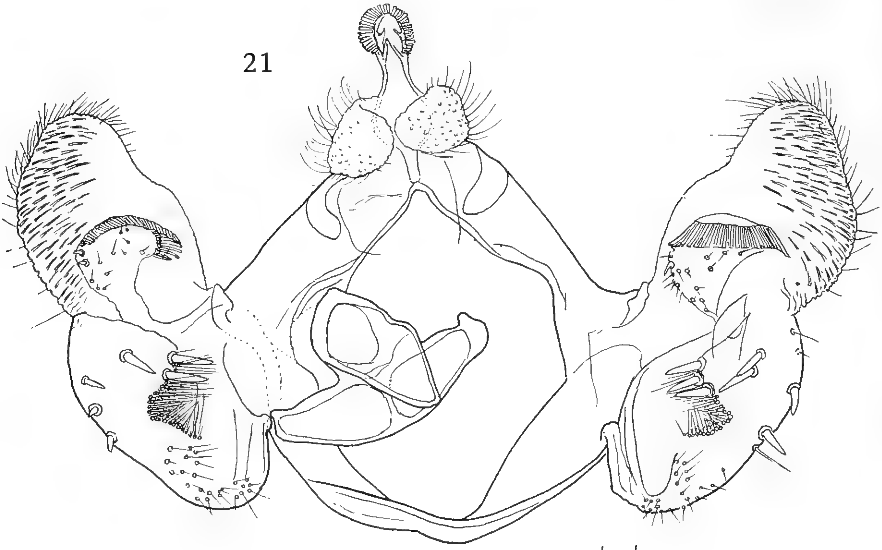

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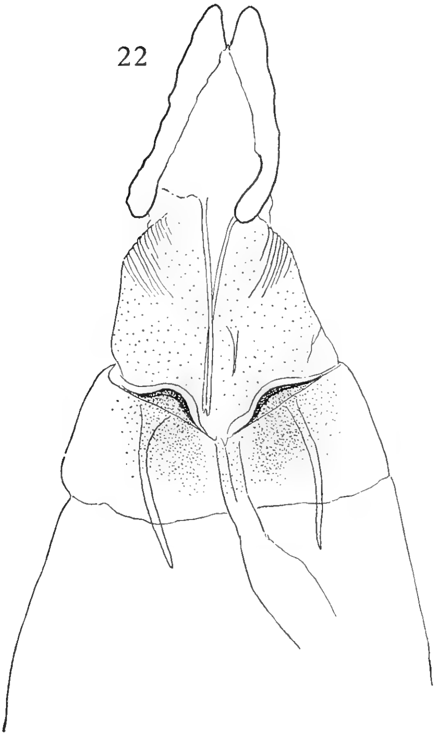

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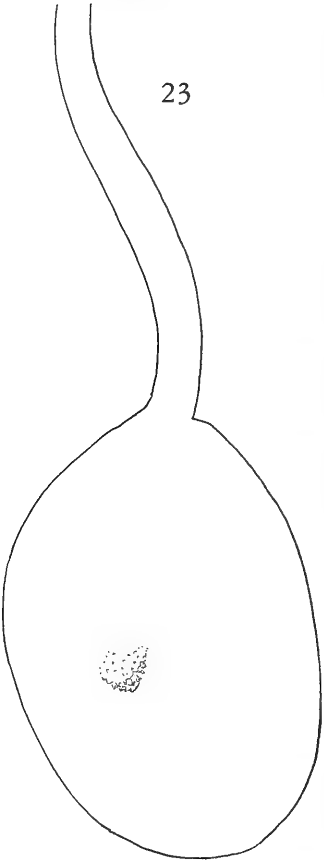

Fore wing as in male, costa slightly less curved posteriorly, apex more produced, termen ochreous-tawny. Costal strigulae slender, rather pale, except on costal edge where they are brown; streaks along veins beyond cell more contrasting, brownish; paler area beyond cell reduced to a narrow streak between veins 7 and 9; there is also a pale transverse spot along closing vein; lower edge of cell broadly suffused with tawny-brown; slight dusting with dark brown indicating first and second discal spots, terminal fascia narrow, black dot in apex present. Cilia tawny, densely dusted with purple, a purple supramedian and a slender submedian lines.

Hind wing glossy whitish-golden, veins pale yellowish, extreme apex infuscated. Cilia concolorous, towards apex clouded with fuscous.

Other females paler, straw-ochreous, one more greyish-fuscous tinged; every one has the characteristic black apical dot; one specimen (4300) is fasciate: whitish-ochreous, with strongly reduced strigulae and with a broad dark fuscous-grey median longitudinal streak.

Male genitalia. Resembling those of the Australian *psammitis* Turner, but with differently spined sacculus. Tegumen low and robust. Uncus moderate, top with corona small. Socius rather large. Vinculum band-like. Valva broad and short, suboval. Cucullus broad, rounded, sparsely spined. Valvula moderate, with two lateral spines beyond the corona. Sacculus large, ½, concave, with a semicircular series of 6—7 very strong spines, crossing the disc of the sacculus; punctulate area moderate, triangularly projecting laterad. Some fine setae scattered over base of sacculus. Aedeagus rather short, robust.

Female genitalia. Top of abdomen slender and elongate. Eighth segment rigid, sclerotized, compressed laterally (this does not show in fig. 38, does in fig. 41). Sterigma simple, a depressed-triangular lobe on each side of ostium, strongly sclerotized in middle, with a broad transparent upper edge; below each of the lobes, a rounded ill-defined sclerotization. Ostium not modified. Colliculum, a moderate, slightly sclerotized tube. Lobus analis slender and long, some wrinkles below foot of this lobe. Signum small, basket-shaped.

Material studied, in the Transvaal Museum. Males. South Africa, Transvaal: Mahuba's Kloof, 1050 m, 14.I.1925 (A. J. T. JANSE), 1 ♂, holotype, gen. no. 4364. Paratypes, the same locality and date, gen. no. 4361. Marieps Mtn. 3.I.1926 (G. VAN SON), gen. 4406. Pretoria, 4.XI.1909, gen. 4322; 8.XI.1909 (4327); Waterval-Onder, 10.X.1910 (4319) (A. J. T. JANSE).

In the British Museum. Pretoria, I.1910 (JANSE), paratype, ♂, gen. 3618. In total 7 ♂.

Females. South Africa, Transvaal: Barberton, 27.XII.1910 (A. J. T. JANSE), allotype, gen. no. 4306. Paratypes: the same locality and collector, 28.I.1911, gen. nos. 4300 and 4341. Natal: Sarnia, XI.1913 (Mrs. BURRY, Coll. JANSE), gen. no. 4289. Cape Province: Pt. St. Johns, 1-7.I.1931 (A. J. T. JANSE), gen. no. 4480. (In the Transvaal Museum).

Natal: Weenen, I.1925 (H. P. THOMASSET, MEYRICK Collection) 2 ♀, gen. nos. 2526 and 2527. (In the British Museum). In total 9 ♀.

Fig. 21. *Bactra* (*Chiloides*) *jansei* sp.n., ♂ holotype, genitalia. Fig. 22. The same of ♀, allotype. Fig. 23. The same, bursa

A rather small species of very variable and therefore confusing appearance. This material was identified by MEYRICK with *stagnicolana* ! The females are slightly larger. The pale hind wings in the two sexes are rather characteristic. The nearest relative, at present known to me, occurs in New Guinea and Australia (*B. (C.) scalopias* Meyr.).

Dedicated to Professor Dr. A. J. T. JANSE, the nestor of the South African Lepidopterology and collector of most of the present material.

Bactra (Chiloides) adelpha spec. nov.

Figs. 24—26

♂ 20 mm. Head and thorax fuscous. Palpus rather dark fuscous-grey. Abdomen pale greyish-ochreous.

Fore wing oblong, dilated, costa curved at base, almost straight posteriorly, apex moderately pointed, termen sinuate, oblique. Tawny-ochreous, densely dusted and suffused with fuscous and fulvous, veins streaked with darker, rows of ferruginous points between veins (superficially the wing seems to be rather evenly fuscous-fulvous coloured and almost devoid of markings). Costa with a series of very short dark greyish-fuscous suffused marks; a moderate brownish streak in posterior part of cell, sharply limited by stigma which is whitish, very slender and fasciate, actually being a strigula along closing vein, gently convex outwardly; a faint tawny-ferruginous suffusion along termen, dilated upwards. Cilia purplish.

Hind wing glossy pale grey, on apical $^2/_3$ tinged brownish-fuscous, with a faint bronze gloss. Cilia concolorous.

Male genitalia. Similar to those of the preceding species (*jansei*), but more robust, with larger socius and a more defined tuba analis. Valva less broad, especially cucullus. Sacculus with a fasciate and extended narrow punctulate area, with at the base a few small spines, and at the top of this area with some five slender and bristle-like spines; a similar single spine on top of right sacculus, left sacculus with four more robust apical spines. Aedeagus somewhat longer.

South Africa, Transvaal: Pretoria, 3.XII.1909 (A. J. T. JANSE), 1 ♂, holotype, gen. no. 2903.

♀ 23 mm (allotype). Head and thorax rather deep tawny, slightly suffused with fuscous and with faint fulvous gloss in certain lights; face and vertex in middle rather bright ochreous-tawny. Palpus long, pointed, slightly rough along upper edge, terminal segment almost concealed; dark brown. Abdomen fuscous.

Fore wing elongate, rather narrow, costa curved at base, straight posteriorly, apex pointed, termen sinuate, oblique. Bronze-brownish, with slight traces of markings only. Costa suffused with fuscous-purple; an ill-defined broad median fuscous-purple streak from base to apex; a faint ochreous-yellowish streak from middle of upper edge of cell to apex; termen slightly mixed with brighter appearing tawny-orange in certain lights. Cilia (damaged) dark brown, with a series of whitish round spots along basal half, arranged on opposite ends of veins.

Hind wing light leaden-fuscous, with some yellowish tinge, dorsum as far as cell sordid pale leaden, without yellowish. Cilia whitish-leaden; along fuscous part, pale fuscous with a paler base and a fuscous subapical band.

Female genitalia. Sterigma simple, showing only a weak rhomboidal or sub-

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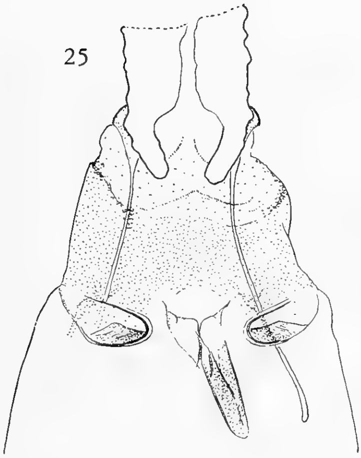

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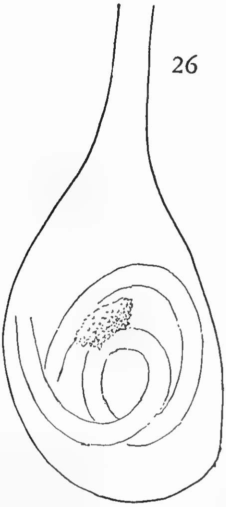

Fig. 24. *Bactra (C.) adelpha* sp.n., ♂, holotype, genitalia. Fig. 25. The same of ♀, allotype. Fig. 26. The same, bursa.

pentagonal ostium. This is, however, flanked by characteristic structures, being semioval impressions, open laterally, with a sclerotized edge that is margined by a hyaline substance. Colliculum, a slender, simple tube, slightly spindle-shaped, with several longitudinal folds. Postapophyses not perceptible. Signum moderate, basket-shaped, rather shallow.

South Africa, Transvaal: Tweefontein (near Bronkhorstspruit), 13.I.1907 (in JANSE's hand, 1 ♀, allotype, gen. no. 4476.

The species is much larger and not at all similar to *jansei* superficially, but judging from the genitalia, closely allied.

Bactra (Chiloides) simpliciana Chrétien, 1915

Bactra simpliciana Chrétien, 1915, Ann. Soc. ent. France, vol. 84, p. 302 (larva and pupa, on *Cyperus conglomeratus* Rottb.). — Amsel, 1951, Bull. Soc. Sci. Nat. Maroc, vol. 31, p. 68.

Bactra (Chiloides) telaviviana: Amsel, 1951, Beitr. nat. Forsch. S.W. Deutschl., vol. 17, p. 76, fig. 18 (♂ N.E. Arabia).

Bactra telaviviana Amsel, 1935, Zoogeographica, vol. 2, p. 46, 123 (nom. nud.). — 1935, Mitt. Zool. Mus. Berlin, vol. 20, p. 291, pl. 11, fig. 89 (Tel Aviv, Palestine). — 1935, Veröff. Deutsch. Kol. Uebers. Mus., vol. 1, p. 261, no. 230.

Bactra lactosana Turati, 1922, Atti Soc. ital. Sci. nat. Milano, vol. 61, p. 172 (Cyrenaica; sex?). Syn. nov.

Bactra pauperrima Turati, 1934, loc. cit., vol. 73, p. 196, t. 3 fig. 24 (Cyrenaica, sex?). Syn. nov.

The two species described by COUNT TURATI remained enigmatic, since the types are either lost or not accessible. All my informations concerning the fate of TURATI Collection did not provide any results. The collection seems to be in the possession of the TURATI family, but my inquieries addressed there were never answered.

The description of the two species and the figure of *pauperrima* concur in detail with those of *simpliciana*. Therefore it is apparent that we may sink both former names as synonyms of the latter, the present species being quite characteristic.

Bactra (Chiloides) sordidata spec. nov.

Fig. 27

♂ 18 mm. Head and thorax grey-fuscous. Palpus moderate, strongly dilated, triangular; dark fuscous with a pale greyish median streak, terminal segment very short, almost concealed, blackish. Abdomen fuscous.

Fore wing oblong, rather broad, costa gently curved throughout, apex obtusely pointed, termen gently sinuate, little oblique. Glossy purplish-fuscous, rather dark, slightly dusted with pale grey. Markings dull and therefore contrasting, ferruginous-tawny, more or less olive-tinged, limited (or partly rubbed?). Costal strigulae numerous, narrow and oblique, anteriorly not reaching cell, posteriorly some continued so as to form three or four more or less complete curved lines, running across wing between cell and termen, ending in tornus and lower part of termen; anterior part of wing except costa less densely strigulated, interrupted into short fragments; first spot small, dark fuscous, oval, in fold well beyond $^1/_3$; a roundish suffused ferruginous spot filling out space just beyond cell, another similar but smaller end transverse mark halfway between preceding and apex. Cilia (imperfect) ferruginous-fuscous.

Hind wing pale grey with a pinkish-bronze gloss, dorsal third whitish. Cilia concolorous but paler.

Male genitalia. Very similar to those of *rhabdonoma,* differing as follows. Socius larger. Vinculum broad and flattened. Cucullus much narrower, not attenuated, top broadly rounded. Valvula with a smaller corona, stalk distinctly extended in middle, with only a couple of spines. Sacculus broad and concave, but simple, top truncate, without spines. Punctulate area slightly elongate. Juxta larger. Caulis longer. Aedeagus thicker, less curved and sclerotized, slightly shorter; cornuti, two adjacent dense patches of long spines.

South Africa, Natal: St. Lucia Lake, 18.XII.1932 (H. W. Bell Marley), 1 ♂, holotype, gen. no. 4403. Unique.

Bactra (Chiloides) tylophora spec. nov.

Figs. 32—34

♂ 21 mm. Head whitish-ochreous, sides of vertex infuscated. Palpus rather long, slender at base, abruptly triangularly expanded posteriorly, edge rough; terminal segment short, obtuse, semiconcealed; ochreous-whitish, a dark grey oblique suffused median band, on lower angle of top of apical tuft this band becoming black; terminal segment blackish, tip pale. Thorax fuscous (greasy), tegula pale ochreous dusted with dark fuscous. Abdomen light fuscous.

Fore wing suboblong, broadest at $^3/_4$, costa gently curved throughout, apex pointed, termen slightly sinuate, oblique, long. Pale ochreous, partially touched with pale yellow, sharply strigulated and marked with dark fuscous. Base of costal edge slightly infuscated; anterior half of costa with numerous fine strigulae reaching to cell, more or less interrupted; posterior half with much more oblique, almost horizontal strigulae and with indistinct pairs of pale marks, obscured by numerous very short dark strigulae; an irregular streak of coarse dark fuscous marbling below cell from about $^1/_5$ to lower angle; dorsum dark-marbled, its edge dark dotted; a dark fuscous suffusion along termen, reaching beyond middle of distance towards cell, above reaching to apex, below to lower part of termen; less obscure ground colour forming a streak from middle of cell to costa just before apex; this streak containing sharp and fine lines along edges of cell and along most veins; an area between posterior half of costa and dorsum similarly unobscured, pale ochreous; stigma snow-white, cutting dark line along lower parting vein and vein 6 in two parts; an interrupted line along lower half of termen. Cilia pale ochreous, an antemedian, a postmedian line and tips of cilia fuscous.

Hind wing rather dark fuscous-grey, paler towards base, with a faint bronze gloss. Cilia pale fuscous, mixed with whitish, a darker fuscous subbasal band.

Male genitalia. Tegumen moderate. Uncus rather short and broad. Socius large. Valva moderate, cucullus broad, simple, suboval, costal edge hardly sinuate; valvula rather short, stalk slender, top broad; sacculus deeply concave, devoid of spines, towards smoothly rouded top a submarginal longitudinal patsch of minute hairs; only median posterior angle of the inner edge of sacculus extended into a strong characteristic process, with top blunt and slightly laminate; an oblique transverse band of small hairs across sacculus above its base. Juxta robust, rather small. Vinculum normal. Aedeagus broad, rather short, bent. Cornuti, several (11) strong spikes and a patch of smaller spines.

South Africa, Transvaal: Waterval-Onder, II.1912 (Bonnekamp, Coll. A. J. T. Janse), 1 ♂, holotype, gen. no. 4292. Orange Free State: Bloemfontein, 23.XI.-1925 (H. E. Irving), 1 ♂, paratype, gen. no. 4365. 2 ♂.

A robust species with finely dark-marbled and lined fore wings. Allied with

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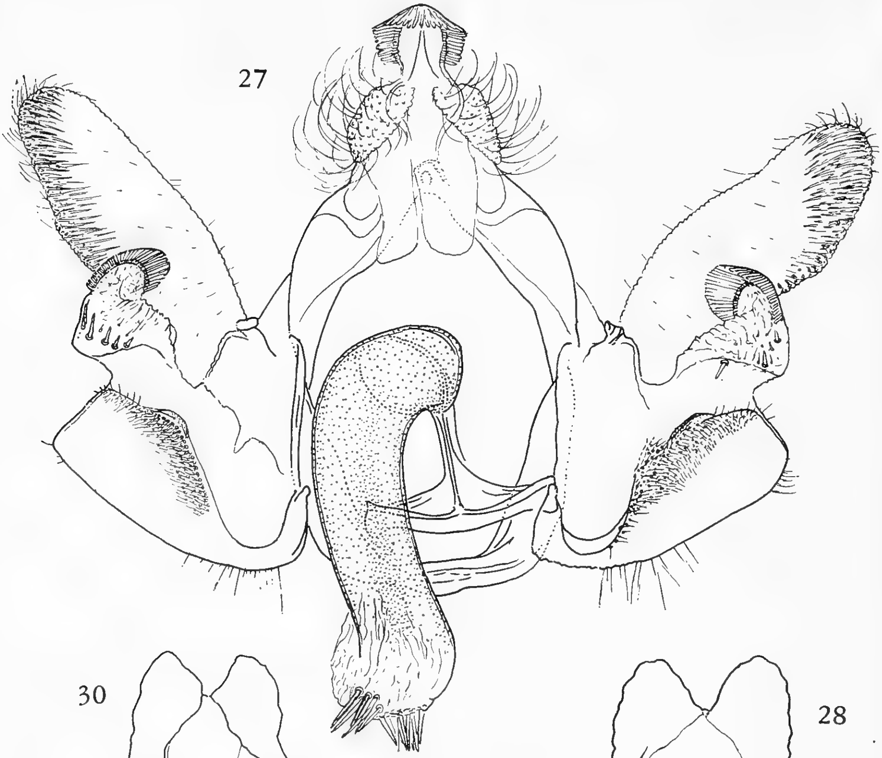

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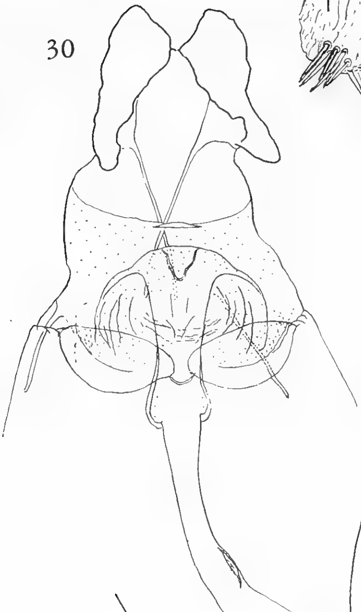

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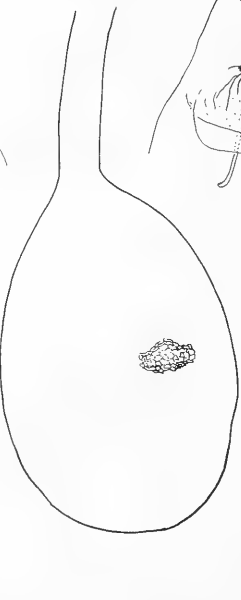

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fasciata where a process of the internal edge of sacculus is already developed but short.

♀ 20 mm. Head, palpus and thorax pale tawny, but brighter than in male, palpus with an oblique dark grey streak laterally. Fore wing as in male but costa a trifle less curved. Whitish-ochreous, strigulated with pale ochreous-tawny, on anterior half of wing markings interrupted in series of numerous short strigulae, on posterior half markings obliterate, being obscured by a brighter tawny suffusion from cell to termen, between veins 4—7; costal markings minute, dark brown, short, first discal spot indicated by a dark fuscous vertical strigula, second discal spot, by a suffused fuscous rounded spot below lower angle of cell; a whitish short streak along bases of veins 3—5, veins themselves finely brown; a terminal streak and a suffusion below apex, brownish.

Hind wing slightly paler, especially towards apex where it is tinged ochreous.

Female genitalia. Sterigma, a moderate but strong rounded sclerite, with the upper edge truncate, the lower narrowed and truncate or folded over. Ostium in centre of this sclerite, strongly sclerotized, rather small, colliculum, a narrow rather long tube, appearing as a narrow sclerotized band on each side, each band with hyaline edges. Signum basket-shaped.

South Africa, Transvaal: Waterval-Onder, 23.XI.1910 (A. J. T. JANSE), 1 ♀, allotype, gen. no. 4348. 1 specimen.

The female is more ochreous tinged than the male and less sharply marked, but otherwise very similar.

Bactra (Chiloides) endea spec. nov.

Figs. 28—31

♀ 11—14 mm (holotype 12 mm). Head and thorax creamy, vertex pale tawny. Palpus strongly dilated, with a rough edge; creamy, infuscated except at apex, terminal segment exposed, slender, fuscous. Abdomen glossy whitish.

Fore wing suboval, costa rather curved throughout, apex pointed, termen gently sinuate, considerably oblique. Creamy-white, minutely strewn with brown (tips of scales!), markings narrow, well-defined, dark brown. Anterior part of costa with a series of short marks, posterior part with about five very distinct oblique and long streaks, on costa dark brown, below costa becoming olive-tawny and narrowed; these streaks alternating with minute dark brown transverse marks; basal patch indicated by a curved, slightly outwards-oblique line, from before $^1/_4$ of costa to well beyond $^1/_3$ of dorsum, oblique above, becoming less oblique below, in fold including the dark brown conspicuous first discal spot; this spot elongate, acute anteriorly, tolerably rounded posteriorly; second discal spot large, tawny touched with olive, crescentic-suboval, arranged longitudinally, edges somewhat suffused; anterior arm of this spot connected with the first costal streak originating from slightly before middle of costa, posterior arm very short; stigma creamy, elongate-oval, not conspicuous; apical streak brownish mixed with purple

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Fig. 27. *Bactra (C.) sordidata* sp.n., ♂ holotype, genitalia. Fig. 28. *B. (C.) endea* sp.n., ♀ holotype, sterigma and ovipositor. Fig. 29. The same, bursa. Fig. 30. The same, ♀ paratype, gen. no. 3520, sterigma and ovipositor. Fig. 31. The same, part of bursa with signum.

dusting, extended into an elongate shade, becoming darker posteriorly; an elongate black dot in apex; terminal edge with a tawny marginal streak; dorsum with a series of slender dark brown transverse marks. Cilia creamy, densely dusted with purplish, so as to form several narrow darker lines.

Hind wing creamy with a golden gloss, posterior half gently infuscated. Cilia concolorous, along termen and around apex infuscated, and with a subapical fuscous band. The paratypes are all rather uniform and similarly marked; only one specimen (3651) is moderately infuscated all over the wing.

Female genitalia. Sterigma very delicate, only lightly sclerotized. Ostium bursae and colliculum trumpet-like, top dilated laterally and rather mushroom-shaped, under this "hood", a series of semicircular folds. Edge of seventh segment modified into two oval plates (less distinct in holotype). Ductus bursae abruptly narrower than colliculum. A small sclerite is present representing a cestum. Signum, rather small, basket-shaped.

West Africa, Gambia: Bathurst, XI.1884 (Carter), 1 ♀, holotype, gen. no. 3652; the same, 1884, 1 ♀ paratype, gen. no. 3656; the same XI.1884, 1 ♀, paratype, gen. no. 3651; the same, XI-XII.1885, 2 ♀, paratypes, gen. no. 3617, 3636. Nyassaland: Mt. Mlanje, 28.I.1914 (S. A. Neave), "*Bactra pythonia* Meyr., teste Meyr. 683", 1 ♀, paratype, gen. no. 3520. 6 ♀.

The species is extremely close to *B.* (*C.*) *angulata* Diak., from Borneo, Java, Moluccan and Palau Islands. The slender species have the same facies and markings. The genitalia, however, differ sufficiently to justify the separation of *endea.* The ostium bursae in *angulata* is stronger, at top more compressed so as to form a median and two lateral spout-like folds, plates at the foot of ostium are standing upright and are much more sclerotized, the caudal edge of the eighth segment is more distinctly modified.

The males are so far unknown.

Bactra (Chiloides) rhabdonoma spec. nov.

Figs. 35—37

♂ 13—17 mm (holotype 17 mm). Head creamy with a faintest pinkish tinge on vertex. Palpus moderate, strongly dilated, fuscous-grey. Thorax creamy, tegulae touched with pinkish, with a pinkish-lilac gloss in certain lights. Abdomen fuscous.

Fore wing pointed-suboval, rather broad, costa considerably curved throughout, apex pointed, termen hardly sinuate, oblique and long. Pale creamy-ochreous, anterior half faintly pinkish, posterior yellowish tinged. Costa with numerous oblique dark strigulae, anteriorly dark brown and short, along more than posterior half becoming extended by slender tawny appendages; interspaces anteriorly grey, posteriorly forming the usual paired silvery-white marks; a subcostal streak of pale ochreous ground colour, not obscured or marked, extending from base of wing to apex, extending downwards anteriorly to middle of cell, posteriorly sharply delimited by apical streak; first discal spot large, very irregular, fuscous, connected by some irroration with the second discal spot; this spot conspicuous, deep brown, semicircular, top of anterior arm extended basad by a short strigula; stigma somewhat irregular, oblique, ochreous-white; apical streak dark brown, gradually dilated

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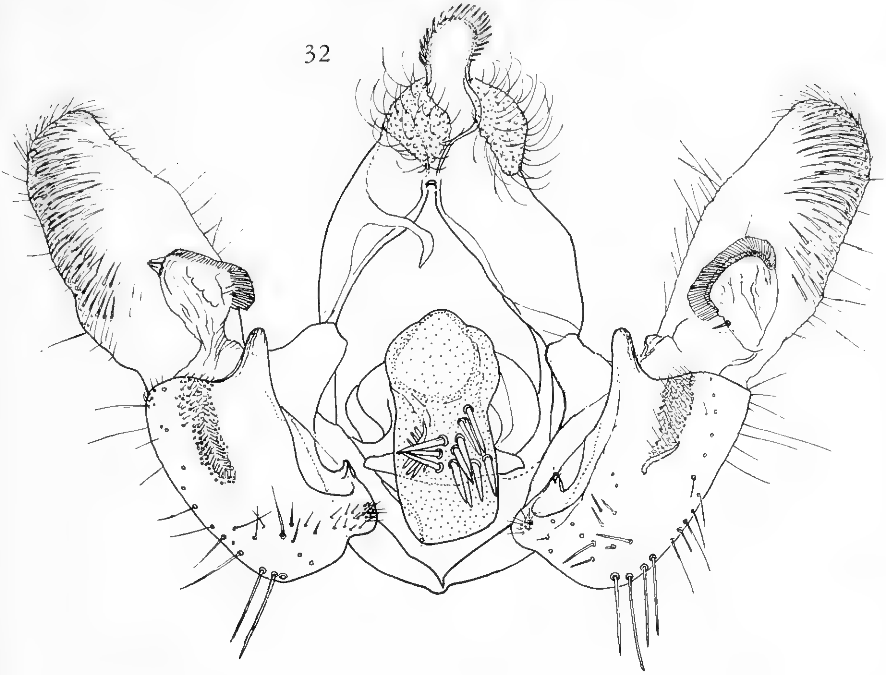

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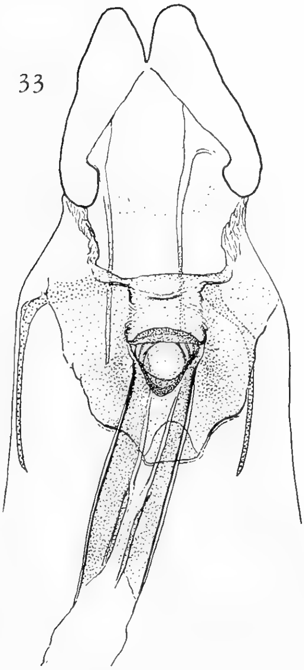

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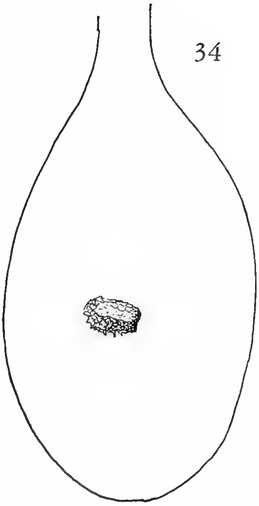

Fig. 32. *Bactra (C.) tylophora* sp.n., ♂, holotype, genitalia. Fig. 33. The same, ♀, allotype, sterigma and ovipositor. Fig. 34. The same, bursa

posterad, lower edge ill-defined, merging into grey suffusion occupying entire termen as far as cell; this suffusion mixed with tawny and transversely strigulated with brownish, but very faintly; a complete band and a subbasal, a postmedian, and an apical black lines.

Hind wing whitish-ochreous or whitish-tawny, pale, slightly infuscated towards apex. Cilia whitish, infuscated except towards dorsum, with a whitish basal line.

Male genitalia. Tegumen and uncus normal, moderate. Socius rather small. Vinculum erected, V-shaped. Valva with a broad cucullus, costa rounded and prominent beyond base, top narrowed and rounded, a rounded moderate prominence in the middle of lower edge. Valvula rather short but broad, corona, stalk with a slightly oblique dense row of spines. Sacculus thickened and concave, rather simple, outer edge with fine bristles, top rounded-truncate, with a small patch of rather short spines, punctulate area oval, moderate. Juxta rather small. Caulis developed. Aedeagus sclerotized, robust and long. Cornuti, some 6 scattered moderate spines, and a subapical very large patch of extremely dense spines.

South Africa, Transvaal: Nelspruit (C. J. S.), XII.1917 (in MEYRICK's hand), "*Bactra stagnicolana* Zell.", 1 ♂, paratype, gen. no. 3469 (in the British Museum). The same locality, II.1918 (H. G. BREIJER), 2 ♂, paratypes, gen. no. 4242 and 4244. Marieps Mtn., 10.XII.1925 (G. VAN SON), 1 ♂, holotype, gen. no. 4286. The same locality and collector, 5-8.XII.1925, 9 ♂, paratypes, gen. nos. 4388, 4390—4397. 13 ♂.

♀ 11.5—22 mm (allotype 15.5 mm). Head and thorax whitish-ochreous, thorax faintly spotted with grey, a grey subapical spot on each tegula. Palpus abruptly and strongly dilated, roughish; pale ochreous, median segment with a black point in middle of inner edge and a fuscous shadow opposite this on the outer edge. Abdomen light fuscous.

Fore wing suboval, rather broad, costa gently curved throughout, apex pointed, termen straight, oblique. Pale grey or whitish with a distinct bluish-leaden gloss. A longitudinal supramedian streak from base to apex, dull creamy-white. Other markings dark fuscous and pale tawny. Costal strigulae distinct, moderate, rather distant from each other (about 9 in total), alternating with minute dark marks, both dark brown; median strigula faintly reaching to second discal spot, penultimate strigula reaching to termen; a black dot in apex; first discal spot distinct, fasciate, transverse, direct, beyond $^1/_3$, blackish, slightly mixed with olive-tawny; this spot preceded by a series of three similar, blackish spots; second discal spot incomplete, only inner arm being present and forming an oblique blotch, dark fuscous mixed with olive-tawny; stigma suffused, white, small; apical streak incomplete, formed by a small, ill-defined tawny spot beyond cell and a larger one of irregular fuscous suffusion, before termen; ocellar area centred with an elongate transverse dot, cut in two by vein 3; a dark fuscous terminal fascia, attenuated downwards and interrupted between veins 5—7. Cilia dark fuscous, dusted with white.

Hind wing pale grey, extreme apex suffused with darker grey. Cilia concolorous.

Female genitalia. Seventh sternite sclerotized, forming two large oval plates with a hyaline outer edge; their caudal edge is wrinkled, two areas of fine wrinkles flanking the ostium. Ostium small, triangular, simple. Colliculum, a moderate,

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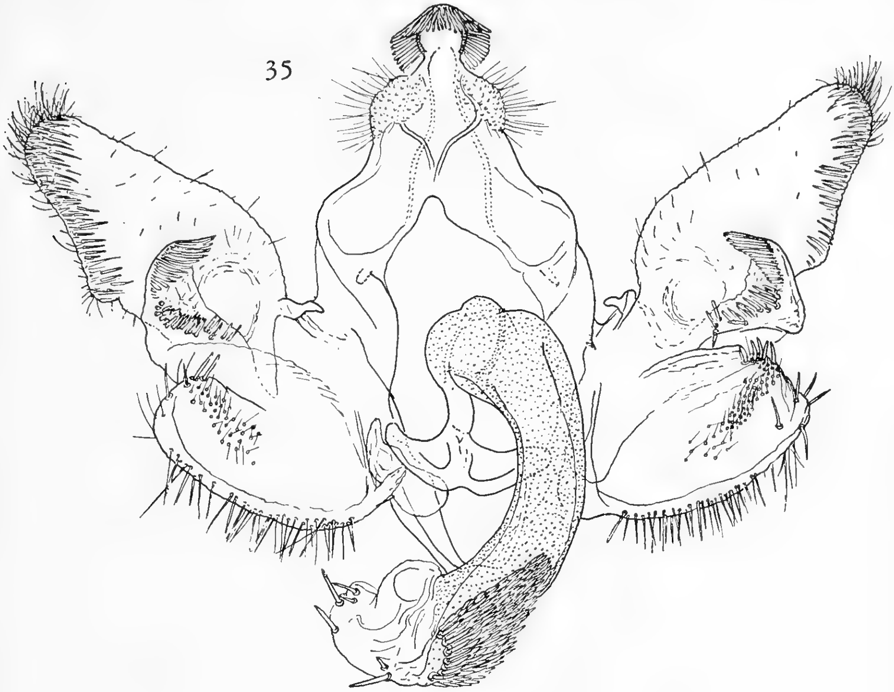

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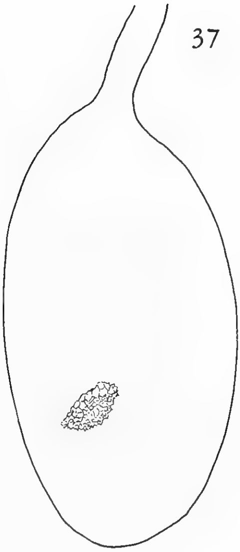

Fig. 35. *Bactra* (*C.*) *rhabdonoma* sp.n., ♂, holotype, genitalia. Fig. 36. The same, ♀ allotype, sterigma and ovipositor. Fig. 37. The same, bursa

slightly narrowed tube. Cestum, a small oval sclerite. Signum, a shallow basket.

A variable series, as to the colouring as well as to the size. Larger specimens are more tawny-tinged, smaller, pale greyish. The markings are rather similar and appear superficially as a narrow median streak interrupted by the stigma, a very narrow suffusion along costal margin, and the minute ocellar dot.

Material studied. In the British Museum. South Africa, Transvaal: Waterval-Onder, 18.XI.1910 (A. J. T. JANSE) (label in MEYRICK's hand, in MEYRICK Collection), 1 ♀, gen. no. 3613. In the Transvaal Museum. Transvaal: Barberton, 17.I.1911 (A. J. T. JANSE), 1 ♀, allotype, gen. no. 4316. The following are all ♀ paratypes. Natal: Umkomaas, 10.I.1914, gen. no. 4374; 17.I.1914, gen. nos. 4287 and 4457; 24.I.1914, gen. no. 4456 (all by A. J. T. JANSE). Transvaal: Marieps Mtn., 8.XII.1925 (G. VAN SON), gen. no. 4398. 6 ♀.

The species apparently is intermediate between the *coronata* and the *venosana* groups, linking them together; the male seems closer to the latter species, while the female seems related to *coronata* ♀.

Bactra (Chiloides) stagnicolana Zeller, 1852
Figs. 38—41

Bactra stagnicolana Zeller, 1852, Lepid. Micropt. Caffr., p. 84, ("Caffraria"). — Meyrick, 1913, Ann. Transv. Mus., vol. 3, p. 275 (*siccella* Walk., synonym). — 1920, Voyage Allaud & Jeannel, Lep., p. 63 (E. and S. Africa). — Diakonoff, 1958, Ent. Tidskr., vol. 78, suppl., p. 77, text fig. 7, tab. fig. 7 (type redescr., gen. ♂ fig.).

Tortrix stagnicolana: Walker, 1863, List Lep. Het. Brit. Mus., vol. 28, p. 326 (S. Africa).

?Ancylolomia siccella Walker, 1866, l.c., vol. 35, p. 1750 (♀, Cape).

?Aphelia lanceolana Walsingham, 1881 (nec Hübner), Trans. Ent. Soc. Lond., p. 231 (Natal, Spring Vale, Dec., March, April)

Distribution. South and East Africa.

It is not possible to ascertain whether "*siccella*" is a synonym of *stagnicolana,* because the unique type specimen of WALKER seems to be lost. It could not be located neither in the British Museum nor in the Oxford Museum. Neither am I able at present to make out the identity of the material which LORD WALSINGHAM studied in 1881. At that time he regarded *Bactra* all over the world as belonging to a single species, *lanceolana*; the three specimens he saw from Spring Vale may have been as many different species.

For a redescription and figure of ZELLER's male holotype may be referred to my earlier paper (1958).

The species is variable; the following types may be discriminated.

(1). Maculate type. The ground colour pale purplish-grey, the markings ferruginous-fuscous. The costal strigulae are numerous and rather slender. The first discal spot rounded, fuscous, across fold at $^1/_3$; the second distal spot broad, semioval, along lower angle of cell; pretornal mark well defined, moderate, transversely-oval, closer to preceding than to tornus; apical streak almost black, well-defined, running from middle of wing across stigma and more or less obscuring it, to apex; sometimes there is a distinct circular thick brown line from middle of vein 8 to and along lower third of termen; sometimes veins beyond cell more or less narrowly dark-streaked. This is the common type, in males as well as in females.

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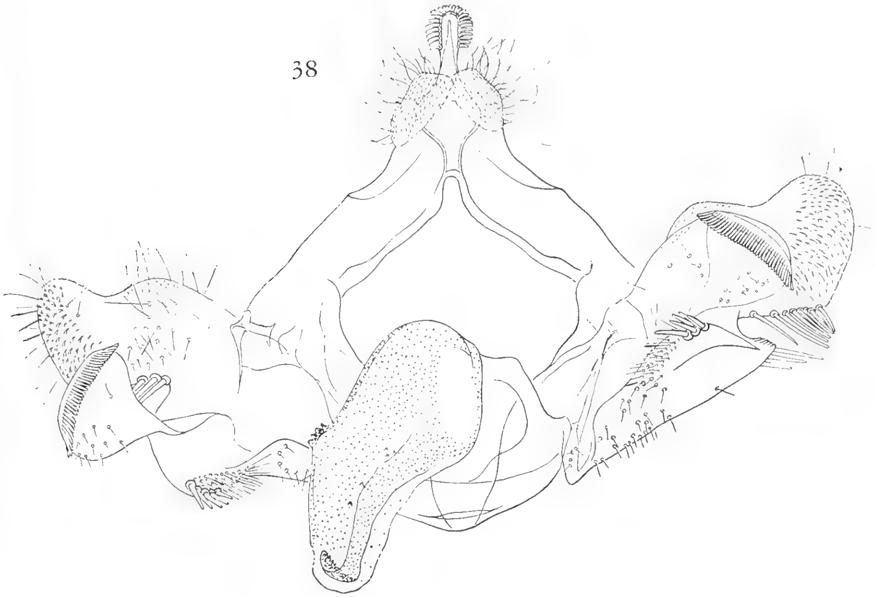

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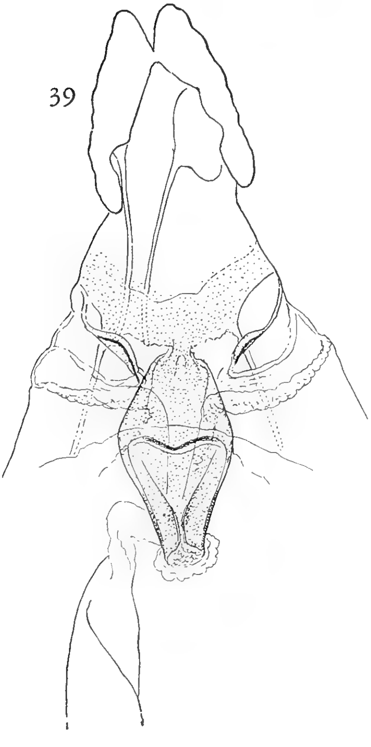

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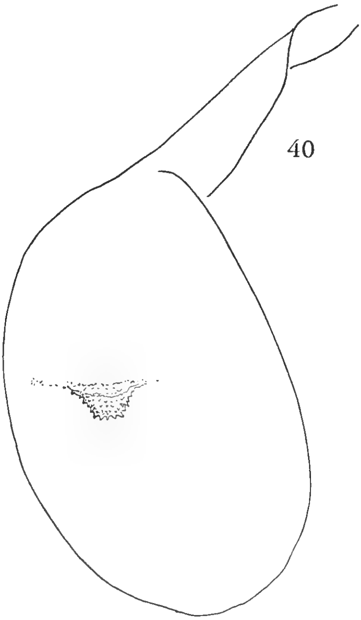

Fig. 38. *Bactra* (*C.*) *stagnicolana* Zell., ♂ holotype, genitalia. Fig. 39. The same, ♀ allotype, ovipositor and sterigma. Fig. 40. The same, bursa

(2). Suffused type, is similar to preceding, but with the wing evenly suffused with dark grey, so that all discal markings disappear and sometimes only marginal strigulae remain; stigma minute, but distinct. Also common in males, less common in females. The holotype belongs here.

(3). Unicolorous type, only females. Pale ochreous, sometimes more or less darker infuscated along edge of wing, with traces of costal strigulae; sometimes also a faint infuscation of centre of disc.

(4). Vittate type, only females. Ground colour pale ochreous, costal markings very short and faint, apical streak dark brown, including the clear white stigma, and connected with the base of wing by a fuscous suffusion along middle of disc; pretornal mark reduced to two short horizontal black strigulae.

Hind wing invariably whitish-ochreous, pale, slightly infuscated towards apex, seldom gently suffused with pale grey all over. Hind wing in female paler than in male.

The female has never been described. Therefore a female neallotype is selected herewith, gen. slide no. 3798. This specimen is of the vittate type, 20 mm, and is labelled thus: Pretoria, 21.XII.1911 (A. J. T. Janse).

Male genitalia. Tegumen rather broad, lower part rounded, top high and slender. Uncus moderate, slender. Socius normal, rather small. Tuba analis large and distinct. Vinculum strongly dilated at the sides, normal below. Valva broad; cucullus characteristic, broad, with an obliquely rounded top; costa broadly prominent in middle; lower edge of cucullus above the primary incision with a dense corona of long spines and bristles; valvula with a broad top and a moderate stalk; sacculus deeply folded and concave, top forming a short, prominent and serrulate crest; a strongly sclerotized subtriangular tumescence subapical on the inner edge of sacculus, crowned with a group of 5—6 moderate spines, anterad from these a patch of small hairs. Aedeagus peculiar and therefore very characteristic, sclerotized, base spherical, above base aedeagus laterally flattened, broad, narrowed towards top, upper edge with a postmedian prominence bearing three small teeth; ventral side of aedeagus formed by a separated slender sclerite, at top bent sideways and denticulate.

Female genitalia. Lobus analis long and rather narrow, postapophyses long. Eighth segment erected-conical, moderately sclerotized; anapophyses moderately long. Lamella postvaginalis shaped as a moderate transverse band, being the caudal portion of the eighth sternite. Colliculum attached to its middle, very large, spindle-shaped, with slightly strengthened upper wall and below middle thickened walls, in the middle a narrow, strongly sclerotized, lip-like and sinuate transverse fold. Ostium membraneous, rather wide. Ductus bursae wide, moderately long. Corpus bursae large, with a finely scobinate wall. Signum moderate, basket-shaped. (Slide figured, 3798).

Material studied. In the British Museum. Comoro Islands: Mayotte (L.), V.1911, 2 ♂ (3523, 3525), 2 ♀ (3522, 3524). Nyassaland: Fort Johnston, (R.) III.1906, 1 ♂ (3616). South Africa, Cape Province: Ceres (R. E. Turner), III.1925, 1 ♀ (3641). Transvaal: Barberton, VI.1911 (A. J. T. Janse), 1 ♀ (3463). Natal: Weenen, XII.1926 (H. P. Thomasset), 1 ♀ (3626). Madagascar: Ampoza, IX.1929 (E. J. White) (B.M. 1930—26), 1 ♀, gen. no. 3075.

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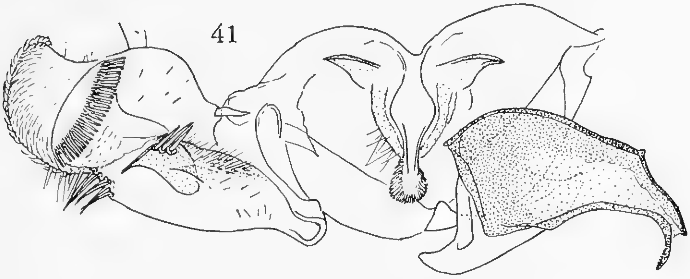

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Fig. 41. *Bactra* (*C.*) *stagnicolana* Zell., ♂ holotype, part of genitalia, showing the compressed aedeagus (after Diakonoff, 1958). Fig. 42. *B.* (*C.*) *aletha* sp.n., ♂, holotype, genitalia

In the Transvaal Museum. Southern Rhodesia: Bulawayo, Zimbabwe. Transvaal: Pretoria. Natal: Nkwaleni, Magude, New Hanover, Karkloof, Umkomaas. Cape Province: Willowmore, Kokstad, Grahamstown, Stella Bush. From October untill June (A. J. T. JANSE, C. J. SWIERSTRA, F. SIMONS, HARDENBERG, C. G. C. DICKSON, G. C. CLARK, J. OMES-COOPER, VAN DER MERWE). 18 ♂, 20 ♀. Gen. nos. ♂ 3790, 3798, 3804, 4232—33, 4237, 4253, 4267, 4294, 4337, 4349, 4351, 4358, 4405—6, 4644 T.M. ♀, 3801, 3805, 4235, 4249, 4250, 4251, 4277, 4297, 4343, 4450, 4471, 4473—74, 4478, 4481.

In Leiden Museum. Mauritius, Moka, 1 ♂, gen. no. 2880; Mauritius, 1 ♂, gen. no. 2892 (J. VINSON).

A big species, often conspicuously dark-coloured (melanistic). Judging from the male genitalia, related with *venosana.*

Bactra (Chiloides) punctistrigana Mabille, 1900
Figs. 43—45

Bactra punctistrigana Mabille, 1900, Ann. Soc. ent. France, vol. 68 (1899), p. 751 (Madagascar). — Viette, 1947, Mem. Inst. Sci. Madagascar, ser. A, vol. 1, p. 54. — 1954, ibid., ser. E, vol. 5, p. 379 (lectotype select.). — Diakonoff, 1959, Rev. franç. Ent., vol. 26, p. 177, figs. 20—21, t. 2 fig. 10 (type redescr., fig.).
Distribution. Madagascar.

For the description of the female type specimen may be referred to my above cited paper (1959). That specimen is melanistic, while the female specimen at hand (gen. no. 4234) is brighter coloured and marked. It may be redescribed thus.

♀ 20 mm (right pair of wings missing). Head pale ochreous, thorax greyish-tawny (palpi missing). Abdomen light fuscous. Fore wing slightly broader than in the type, dilated, costa gently curved, apex pointed, termen distinctly sinuate, little oblique. Pale ochreous, rather densely suffused with fuscous-grey, except a pale streak between cell and costa; costa narrowly dark fuscous, transverse markings pale ochreous; median longitudinal fascia interrupted anteriorly, grey-fuscous and cloudy along cell, ill-defined, posteriorly forming a dark brown, well-defined apical streak; stigma, small white, rounded; a dark brown terminal fascia, rather broad, attenuated below, almost interrupted between veins 5—6; a longitudinal dark brown mark in centre of ocellus. Cilia pale tawny with a whitish basal line and a postmedian dark line, on lower part of termen and in tornus cilia unicolorous light tawny.

Hind wing ochreous-whitish with a silky gloss. Cilia glossy, creamy.

Female genitalia are described in my 1959 paper. They show such a close resemblance to those of *venosana* that at first I regarded MABILLE's species as a subspecies of the former, no males being available at the time. Now I am satisfied that *punctistrigana* is a perfectly distinct species, although closely related with *venosana,* as the genitalia of the two sexes show.

Material studied. South Africa, Southern Rhodesia: Zimbabwe, 6-10.IV.1934 (A. T. J. JANSE), 1 ♀, gen. no. 4234. Madagascar: Sumbiran Plantation, 1911 (R.), MEYRICK Collection (in the British Museum), 1 ♀ gen. no. 3615.

♂ neallotype, 19 mm. Head and thorax dark fuscous, metathorax silvery-grey. Palpus rather long, strongly dilated triangularly, densely and tolerably smoothly scaled; dark fuscous, terminal segment almost entirely concealed. Abdomen glossy greyish-white.

Fore wing oblong-subtruncate, costa rather strongly curved along anterior half, straight along posterior, apex subobtuse, termen hardly concave, almost straight, little oblique. Dark fuscous, markings faint, ferruginous. Costa with numerous little curved transverse strigulae edged on both sides and accentuated with faint leaden-purplish; costal strigula at $^4/_5$ of costa longer than other, straight, almost to termen below apex; a ferruginous terminal streak, along extreme margin of wing finely dusted with whitish. Cilia with basal half dark fuscous, apical half paler fuscous, base with a narrow pale line, a postmedian blackish line.

Hind wing glossy pale greyish, posterior half slightly infuscated, apex darker suffused with grey. Cilia glossy pale grey, base with a narrow dull ochreous line, followed by a dark grey band.

Male genitalia. Of the *venosana* type. Tegumen high and rather narrow. Socius large. Tuba analis perceptible. Vinculum, a strong, broad band, mesially rounded-prominent, smooth. Valva broad. Cucullus broad, broadest above base, top oblique and attenuated, costa being strongly sinuate. Sacculus extremely large, extended and deeply impressed from the outside, so that it is not possible to open and flatten both valvae without dislocating them; outher surface smooth except for an extremely dense basal patch of strong slender spines, upper angle of the inner edge of sacculus with a short, curved blade; inner surface with a narrow strip of punctulations (in left valva showing through, in right plainly visible), and a continuation of the basal patch of spines, partly on an elevated short ridge. Juxta and caulis strong. Aedeagus long and curved, with a slender longitudinal sclerite dorsally, on the right side beset with strong cornuti.

Material studied. Central Madagascar: Imerina Plateau, Tsimbazaza Park, 1200 m, 11.I.1952 (P. VIETTE), 1 ♂, neallotype, gen. no. 2611. In the Paris Museum. Unique.

Obviously this is the sex partner of the species of which the female was described by MABILLE. The facies, colouring, locality, and above all the character of the ♂ ♀ genitalia point in this direction.

Bactra (Chiloides) venosana (Zeller, 1847)

Phoxopteris venosana Zeller, 1847, Isis, p. 738.

Aphelia venosana: Herrich-Schäffer, 1849, Syst. Bearb., vol. 4, p. 244.

Bactra venosana: Rebel, 1901, in Staudinger & Rebel Catal., vol. 2, p. 113. — Kennel, in Spuler, 1910, Schmett. Eur., vol. 2, p. 273. — Kennel, 1910, Pal. Tortr., p. 472, t. 18 fig. 73. — Diakonoff, 1956, Zool. Verh. no. 29, p. 33, figs. 31—33.

Bactra (Chiloides) venosana: Diakonoff, 1956, Zool. Verh., no. 29, p. 33, figs. 31—33. — 1959, Bijdr. Dierk., part 29, p. 184 (Palestine, Sardinia). — 1963, Ann. Mus. Wien, vol. 67 (in press; *banosii, truculenta* syn.).

Bactra truculenta Meyrick, 1909, Journ. Bombay Nat. Hist. Soc., vol. 19, p. 586. — 1922, Exot. Microl., vol. 2, p. 521. — Meyrick in Caradja, 1934, Iris, vol. 48, p. 33. — 1935, Mater. Microl. chin. Prov., p. 57. — Diakonoff, 1950, Bull. Brit. Mus., Ent., vol. 1, p. 289, t. 5 fig. 16, t. 7 fig. 30. — 1956, Zool. Verh., no. 29, p. 27, figs. 28—30. Syn. nov.

Bactra (Chiloides) truculenta: Diakonoff, 1956, Zool. Verh., no. 29, p. 27, figs. 28—30. — 1959, Bijdr. Dierk., part 29, p. 184.

Bactra scythropa Meyrick, 1911, Proc. Linn. Soc. N.S. Wales, vol. 36, p. 284.

*Bactra gerarop*a Meyrick, 1932, Exot. Microl., vol. 4, p. 147.

Bactra banosii Gozmany, 1960, Ann. hist.-nat. Mus. Hung., vol. 52, p. 416, figs. 3A-D. Syn. nov.

Distribution. Northern Africa, Southern Europe, Southern Asia, Pacific, Australia.

Bactra (Chiloides) trimera spec. nov.

Figs. 55—57

♂ 13—16 mm (holotype 16 mm). Head, palpus and thorax creamy-whitish,

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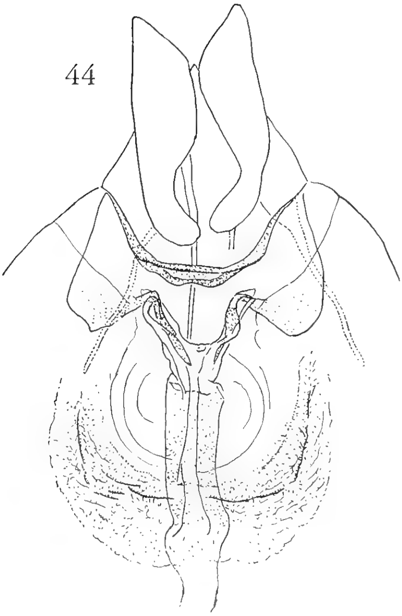

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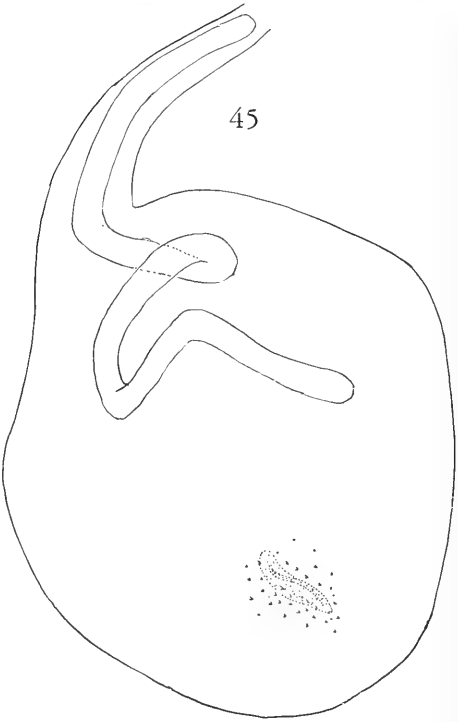

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median segment of palpus with an oblique rather narrow light fuscous transverse fascia; lower edge of palpus roughish. Abdomen fuscous.

Fore wing elongate, dilated, broadest beyond $^3/_4$, costa gently curved at extremities, rather straight in middle, apex obtusely pointed, termen gently sinuate above, little convex below, oblique. Glossy whitish, suffused with pale tawny. Markings dark fuscous. Costal edge dark fuscous, broken in numerous short marks by pairs of thick pale transverse strigulae, along posterior portion of costa becoming silvery; first discal spot longitudinally extended, ill-defined, irregular-oblong or fasciate, from well beyond base towards second discal spot, but twice interrupted before latter; second discal spot rather well-defined, V-shaped, anterior arm broader; stigma moderate, white; apical streak short, black, from below apex halfway towards cell, edged above with grey; some grey suffusion below this streak, reaching to cell and more or less extending over terminal part of wing; ocellar area centred with a wedge-shaped, ill-defined mark parallel to termen, cut twice by black; apex with a dark brown dot; a dark brown terminal line: a transverse narrow preapical line, from penultimate dark costal space to termen below apex. Cilia dark fuscous dusted with pale ochreous, with three dark lines.

Hind wing creamy-white, more or less suffused with pale grey, more so on posterior half, deeper suffused towards apex.

Male genitalia. Tegumen high. Uncus moderate, curved. Socius rather large. Vinculum moderate, smooth. Cucullus long, moderately broad, bent and slightly sinuate over its whole breadth at $^1/_3$ of length, not narrowed, top gradually rounded; valvula rather long, stalk swollen in middle, top bent, corona rather small; sacculus concave, strongly flattened dorso-ventrally, top subobtuse with strong inequal spines, three right, two left, an external submarginal row of short and slender bristles, internal flattened side with a large patch of long spines at and above outer lower angle and a second smaller but much denser patch of smaller spines proximad of the first; haired area from below apex of sacculus to spine patches, narrow above, in a shallow depression, flanked by two rounded prominences of the inner edge of sacculus; this hairy area much extended below. Aedeagus moderate, strongly sclerotized, moderately attenuated and curved, without cornuti.

The rather pale species makes a superficial impression of having three longitudinal slender dark stripes: costal, median, and dorsal. The five males available are rather uniform, one somewhat more distinctly marked than the other. Male no. 4264, however, has a fine and sharp dark fuscous marbling upon pale ground, with veins marked by fine dark lines ("tigroid" type of markings).

Material studied. South Africa, Transvaal: Minastone (= Louis Trichardt), 16-25.II.1919 (H. G. BREIJER), 1 ♂, holotype, gen. no. 4240. Paratypes: Transvaal: Waterval-Onder, 10.XI.1910, 1 ♂, gen. no. 4321. Natal: Nkwaleni, 10.I.1916, 1 ♂, no. 4463 (both: A. J. T. JANSE). Transvaal: Marieps Mtn., 3.I.1926 (G. VAN SON), 1 ♂, no. 4389; Cape Province: Umtata, 20 miles E, 8-11.I.1931 (A. J. T. JANSE), 1 ♂, no. 4264. 5 ♂.

Fig. 43. *Bactra* (*C.*) *punctistrigana* Mab., ♂ neallotype, genitalia. Fig. 44. The same, ♀ holotype, sterigma and ovipositor. Fig. 45. The same, bursa. (Figs. 44 and 45 after Diakonoff, 1959).

♀ 18—20 mm (allotype 18 mm). Head, palpus and thorax pale ochreous-tawny, palpus spotted with pale grey laterally. Abdomen fuscous.

Fore wing oblong, moderately broad, little dilated, costa gently curved troughout, apex subobtuse, termen tolerably straight, oblique. Pale ochreous-tawny, in disc moderately suffused with that colour; costal strigulae numerous, on costal edge dark brown; those along posterior part of costa tending to form sinuate transverse strigulae, anterior reaching to dorsum before tornus, posterior strigulae running to termen; a small pale spot on costa before apex; first discal spot before $^1/_3$, arrowhead-shaped, preceded by several irregular smaller spots along and around fold; second discal spot very narrow, fasciate and transverse, with a strigula along closing vein, stigma absent; a suffused tawny terminal streak attenuated above, edged along extreme margin of wing with dark brown dusting; a series of dark brown dots along dorsum. Cilia dark fuscous, finely dusted with pale ochreous, with a narrow whitish basal line.

Hind wing glossy whitish-golden, cilia concolorous.

Female genitalia resembling those of the Asiatic *optanias*. Sterigma strongly sclerotized, forming a convex subtriangular, rather three-lobed plate; also the eighth tergite is sclerotized. Ostium bursae rather ill-defined, its outer rim sclerotized and curved. Colliculum asymmetrical, strong, clavate. Signum rather small, basket-shaped.

Material studied. South Africa, Natal: Mtunzini, 30.XI.1953 (L. VÁRI), allotype, gen. no. 4378. Umkomaas, 15.I.1914 (A. J. T. JANSE), 1 ♀, paratype, gen. 4305. Cape Province: Kleinmond, IV.1942 (V. G. DICKSON), 1 ♀, paratype, gen. 4296. Pt. St. Johns, 1-7.I.1931 (A. J. T. JANSE), 1 ♀, paratype, gen. 4375.

The female is rather larger than the male. The genital characters strongly suggest that the sexes belong together, in analogy with the nearest allied Asiatic species, *Bactra* (*C.*) *optanias* Meyr.

Bactra (Chiloides) aletha spec. nov.

Fig. 42

♂ 11.5 mm. Head, thorax and palpus fuscous (rubbed!). Abdomen sordid whitish.

Fore wing oblong, rather narrow, costa gently curved anteriorly, hardly curved posteriorly, apex moderately pointed, slightly projecting, termen distinctly sinuate, little oblique. Pale fuscous, clouded with darker (strongly rubbed). Cilia lacking.

Hind wing pale greyish. Cilia missing.

Male genitalia. Belong to the type of *boschmai* Diakonoff. Tegumen high. Uncus short and rather broad. Socius moderate. Vinculum strong, V-shaped. Valva rather slender. Cucullus slender and long, not dilated, costa not prominent, top rounded; spines small. Valvula rather short, ventral edge with 3—6 rather strong spines. Sacculus strongly concave, strongly bent rectangularly at base, inner edge emarginate in middle, strong and partly beset with long bristles, its upper angle

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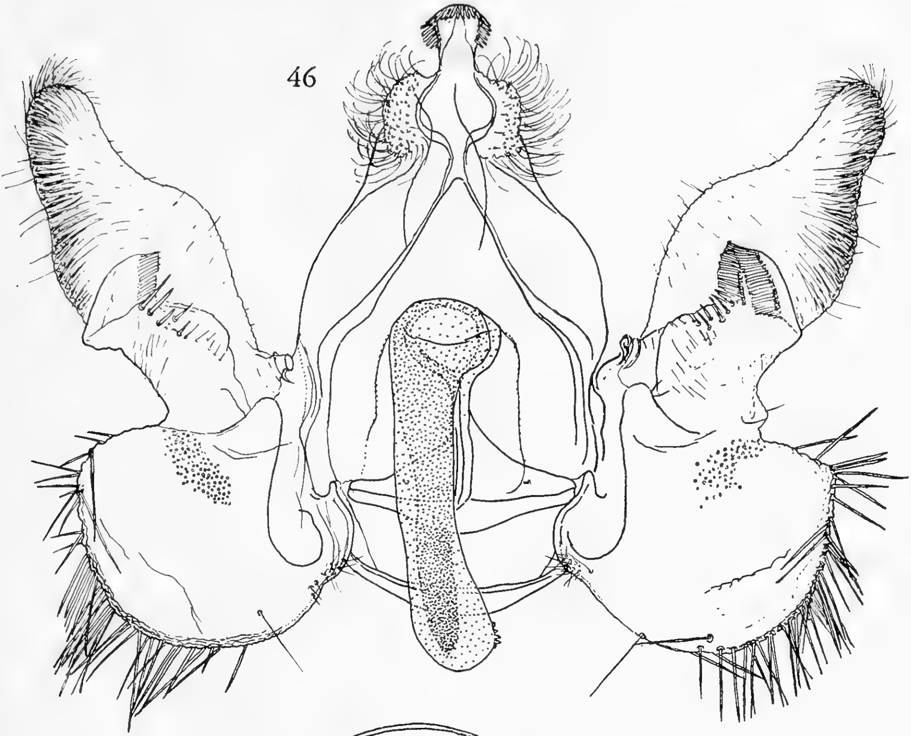
Fig. 46. *Bactra* (*C.*) *fasciata* sp.n., ♂ holotype, genitalia. Fig. 47. The same, paratype, aedeagus in lateral aspect, gen. no. 3459. Fig. 48. The same, ♀ allotype, sterigma and ovipositor. Fig. 49. The same, bursa



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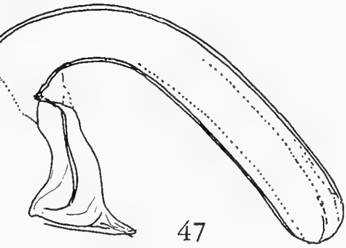

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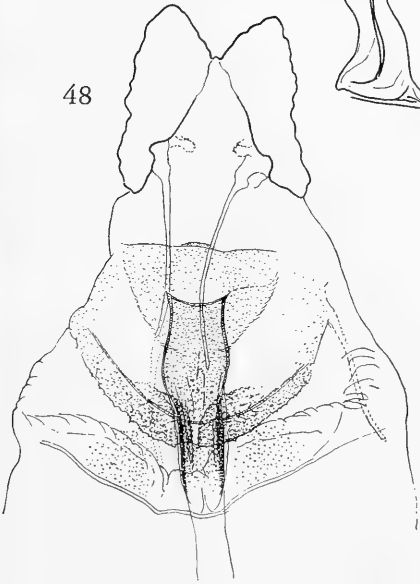

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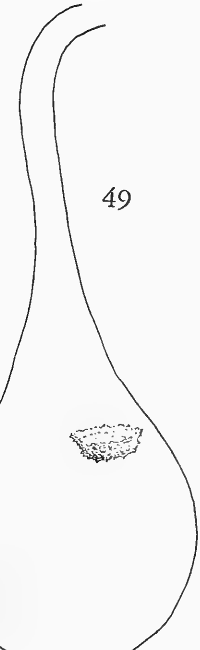

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forming an acute strong cusp (not so long as in *clarescens* or in *boschmai*); top of sacculus with 5—6 strong spines of moderate length; base of sacculus with a group of robust shorter spines. Juxta and caulis robust. Aedeagus long, curved. Cornuti apparently absent.

Material studied. West Africa: Kumasi, IX.1911—IV.1912 (J. D. G. Sanders), 1912—481, 1 ♂, holotype, gen. no. 3635. Unique. (In the British Museum).

Although the small insect is badly rubbed, the genitalia are distinct and allow description.

Belongs to the *boschmai* group of species.

Bactra (Chiloides) salpictris spec. nov.

Figs. 53—54

♀ 13—15 mm. Head, thorax creamy. Palpus whitish, with a finest dark dusting. Abdomen pale ochreous.

Fore wing oblong, suboval, pointed, termen hardly sinuate, oblique. Creamy, with a golden gloss, suffused in disc rather bright ochreous. Markings ochreous and tawny, becoming dark brown on edges of wing. Costa with the usual strigulae, very short along anterior half, zigzagged along posterior half, forming some reticulation or marbling in terminal portion of wing; these markings more or less interrupted by a longitudinal streak of pale ground colour running along upper edge of cell and thence to costa before apex; a little distinct median longitudinal streak from base to termen, formed by ochreous suffusion and markings beyond cell; terminal area also suffused with pale leaden-grey; first discal spot narrow, fasciate, transverse, second discal spot small, irregularly semicircular, suffused, enclosing a very small white stigma; a dark terminal line, an ochreous strigula before apex; a black dot in apex. Cilia whitish sprinkled with dark brown or purplish, and with a submedian and an apical dark lines.

Hind wing white, slightly suffused with pale ochreous and greyish towards apex and costa posteriorly. Cilia whitish, grey opposite apex.

Female genitalia. Eighth sternite, a broad, sclerotized band. Ostium bursae, a pear-shaped large opening extending almost over the breadth of the band; further not modified. Colliculum very large and tubular, sclerotized, lower half with a longitudinal median split, with less sclerotized sides. Signum, a large, shallow denticulate cup. A pair of peculiar small sclerites apparently belonging to the anal opening, are visible between the lobi anales.

Material studied. South Africa, Cape Province: Pt. St. Johns, 1-7.I.1931 (A. J. T. Janse), 1 ♀, holotype, gen. no. 4303. Umtata, 20 miles E, 8-11.I.1931 (A. J. T. Janse), 1 ♀, paratype, gen. no. 4366. 2 ♀.

The paratype is dark, brown-fuscous, a stripe of tawny-ochreous colour from base to apex, occupying the costal third of wing except the extreme costal edge.

The exact position of the species is uncertain without the knowledge of the males. It may belong to the *boschmai* group and then be nearest to *aletha*.

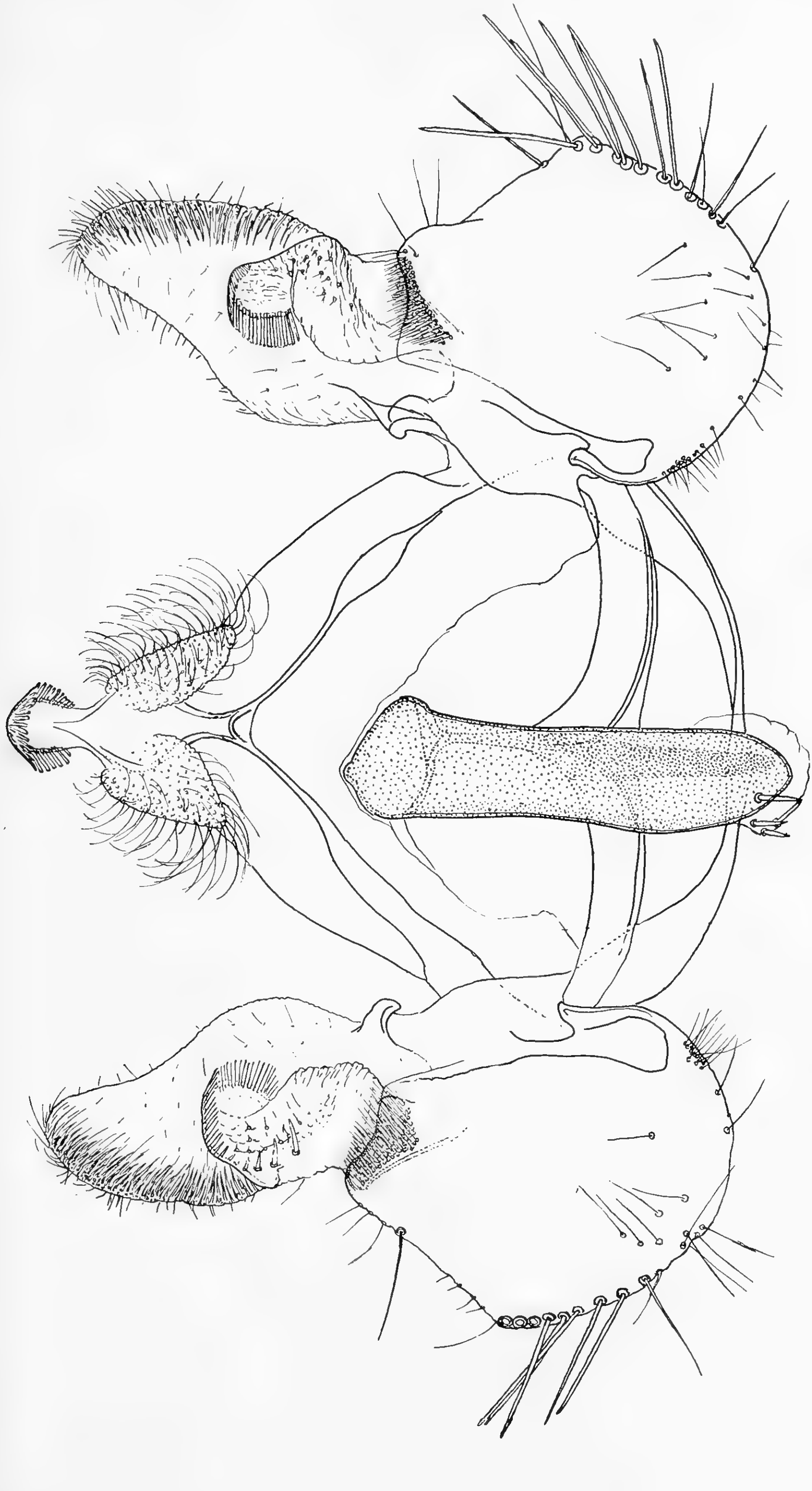


Fig. 50. *Bactra (C. sinassula* sp.n., ♀, holotype, genitalia

Bactra (Chiloides) fasciata spec. nov.
Figs. 46—49

♂ 15.5 mm. Head pale ochreous, face and vertex roughly scaled, scales divided along middle of face. Palpus thickened, obtuse; pale ochreous above and internally, dark fuscous elsewhere. Thorax pale ochreous with two pairs of faint fuscous marginal spots, tips of tegulae fuscous. Abdomen pale ochreous, anal tuft dark fuscous-grey.

Fore wing elongate-suboval, rather broad, dilated, broadest at $^2/_3$, costa considerably curved, strongly at base, apex moderately pointed, termen gently sinuate, concave above, oblique. Pale leaden-grey mixed with whitish, partially suffused with pale ochreous. Anterior half of costa darker leaden-grey, with several slender dark fuscous strigulae edged with ochreous suffusion; posterior half of costa with four pairs of oblique white strigulae, ultimate pair longest, followed by a vertical single white bar and then by a white smaller triangular dot just before apex; these white markings converging in one point below costa; anterior half of wing suffused with pale tawny-ochreous and mixed with some deeper tawny spots; first discal spot blackish-brown, bent, transverse, across fold just beyond $^1/_3$, obtusely pointed posteriorly and rather irregular; second discal mark fasciate, from middle of wing, encircling lower half of stigma, thence to apex, thus giving rise to a conspicuous apical streak; stigma transverse, conspicuous; apical streak edged above by a strongly contrasting white streak, from $^2/_5$ of disc, gradually dilated to preapical costal white spot, faintly traversed by minute ferruginous interneural lines and by two transverse similar lines from costa between the second and third and third and fourth pairs of white strigulae; the latter two lines gradually curving across wing to $^2/_3$ and $^1/_2$ of termen, respectively, merging there in a dark brown terminal line; ocellar area large, oval, leaden-grey centred with a brown obliquely-oval dot. Cilia dark grey, slightly dusted with white, with a fine white basal line and three black lines alternating with white.

Hind wing dirty whitish, touched with grey towards apex, veins slightly darker ochreous, cubital pecten grey. Cilia pale fuscous with a darker fuscous subbasal shade.

Male genitalia. Tegumen high. Uncus moderately long, slender. Socius moderate. Vinculum strong, flattened, smooth. Valva long; cucullus with a slender top and base, dilated in middle, costa prominent above middle. Valvula with a long, swollen stalk which has a rounded prominence in middle, and a series of moderate spines, decreasing in size basally; top of valvula moderately broad; sacculus strongly dilated and flattened, semicircular, moderately concave, simple; a small patch of punctulations above centre and a dense corona of long and slender spines along outer edge. Juxta small and strong. Aedeagus very long, hooked downward, sclerotized.

♀ 13—19 mm (allotype, 16 mm). Head, palpus, and tegula as in male, thorax tawny. Abdomen ochreous-fuscous.

Fore wing slightly narrower and longer, otherwise of the same shape, costa slightly less curved, apex and termen similar. Markings of the allotype which is slightly rubbed, are similar, except that the ground colour appears paler, whitish, perhaps due to rubbing, while there is never a trace of the ocellus nor of its central dark dot.

Hind wing similar to that in male, apex variably suffused with greyish.

Sometimes the entire wing in the female suffused with bright ochreous-tawny, apical streak deep brown, connected with base of wing by a suffused fuscous streak, containing a dark fuscous first discal spot; stigma conspicuous (e.g., ♀ paratypes nos. 3794, Karkloof, and 3646, Kimbolton).

Female genitalia. Lobus analis triangular, pointed, inner edge below middle with an excision. Postapophyses long and slender, anapophyses considerably shorter. Sterigma moderately sclerotized mesially, margin of sclerotization ill-defined towards rostral edge which is triangular-truncate; above this edge a gradually curved strong tubular fold with irregularly denticulate structure. Ostium shaped as a triangular funnel, sclerotized; colliculum, a strong tube, beginning immediately below the edge of the rather small lamella antevaginalis, calyciform above, with thin wall, cylindrical below, with thicker wall. Cestum present, a small triangular sclerite. Corpus bursae normal. Signum basket-shaped, rather shallow.

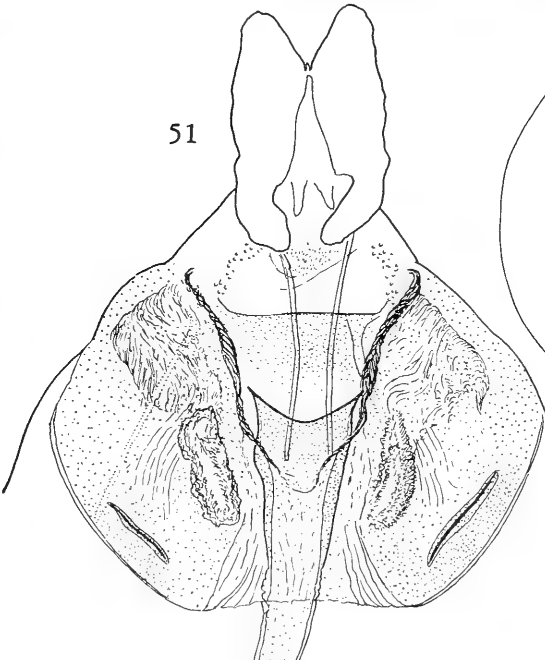
Material studied. South Africa, Transvaal: Pretoria, 30.I.1910, holotype, ♂, gen. no. 4295; allotype, ♀, 31.I.1910, gen. 4273. Paratypes, the same locality, 29.II.1907 (2904 ♂); 25.III.1910, gen. no. 3459 ♂ (British Museum); 27.I.1910, (4284 ♂); 29.II.1909 (4274 ♂); 8.I.1910 (4239 ♂); 12.II.1910 (4276 ♂); the same locality, 28.II.1910 (4275 ♀); 20.III.1909 (4288 ♀) (A. J. T. JANSE). Nelspruit, 1 ♂, XII.1917 (4238) (H. G. BREIJER). Natal: Weenen, Kimbolton Estcourt, 1892, 1 ♂, gen. no. 3640; 2 ♀ 3645 and 3646 (HITCHINSON) (British Museum). Nkwaleni, 2 ♂, 10.I.1916, 4285 and 12.I.-1916, (4272); 2 ♀, 10.I.1916, 4268 and 4269 (A. J. T. JANSE); Magude, IV.1918 4293 ♂ (C. J. SWIERSTRA). Karkloof, 11.I.1917, 1 ♀, 3794 (A. J. T. JANSE). Indaleni, II.1951 1 ♀, 4231 (J. W. HUNT). Cape Province, Umtata, 20 miles E, 8-11.I.1931, 1 ♂, 3793; 1 ♀, 3799 (A. J. T. JANSE). In total 12 ♂, 10 ♀.

Allied with *B.* (*C.*) *coronata* Diak., from Java, Borneo and the Philippine Islands.

Bactra (Chiloides) sinassula spec. nov.
Figs. 50—52

♂ 19—21 mm (holotype 18 mm). Head and thorax tawny-fuscous; palpus rather long, abruptly dilated; tawny, infuscated. Abdomen fuscous.

Fore wing oblong-subtriangular, costa gently curved at extremities, apex pointed, termen clearly sinuate, oblique. Rather pale glossy purplish-fuscous. Markings fine, dark fuscous, partly edged or suffused with tawny-olive. Costal markings narrow, dark, along anterior half short, along posterior very slender, termen from apex to dorsum with a dark fuscous line; first discal spot indistinct, represented by a whole series of transverse fuscous marks more or less interconnected so as to form zigzag marks, second discal spot obliterate; all veins on posterior half of wing very finely streaked with dark fuscous; upper half of posterior portion of cell rather distinctly filled out with brighter tawny-ochreous; entire wing with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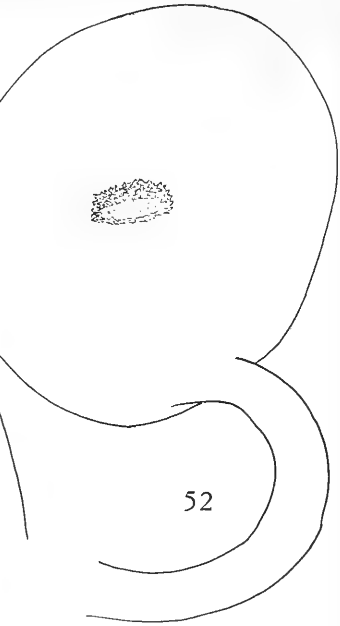
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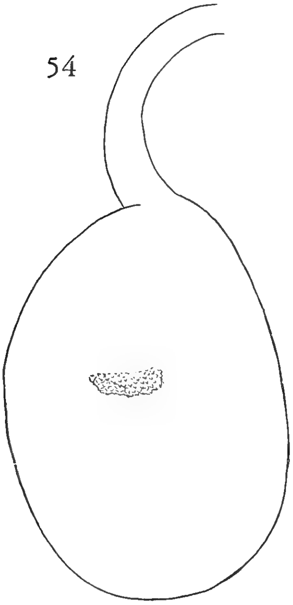
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minute transverse strigulae between the veins. Cilia (imperfect) concolorous, with an antemedian fuscous line.

Hind wing pale fuscous becoming whitish towards dorsum; deeper fuscous towards apex. Cilia glossy whitish-fuscous.

Male genitalia. Tegumen and vinculum very broad, the latter smooth. Valva with cucullus moderately broad, sinuate, costa strongly prominent and rounded beyond base, top of cucullus gradually narrowed, spines moderate. Valvula rather long with blown up stalk, bearing some five spines below the corona which gradually become longer. Sacculus extremely large, over $^1/_2$, dilated and extended, lower edge gradually rounded, its outer half with a single row of very long, slender spines; punctulate area small, at the base of valvula. Juxta very broad. Caulis moderate. Aedeagus long, sclerotized, bent downward.

The series is rather variable. One paratype (4482) is paler, suffused with tawny-olive and tawny-ochreous, with a whitish-ochreous faint supramedian streak from base to apex, along fold edged below with cloudy dark fuscous suffusion. Two males (3802, 3803) are melanistic, more or less densely infuscated throughout. Finally the male no. 4252 is similar to the type but has a distinct second discal spot and indications of a pale stigma.

Material studied. South Africa, Transvaal: Pretoria, 15.XII.1911 (A. J. T. JANSE), holotype, ♂, gen. no. 4472. The same locality and collector, I.1918, 1 ♂, paratype, no. 3602; the same, 16.II.1909, 1 ♂, paratype, gen. no. 3803. Natal: Magude, IX.1918 (C. J. SWIERSTRA), 1 ♂, paratype, gen. no. 4399; the same locality and collector, X.1918, 1 ♂, paratype, gen. no. 4252. Also one ♂, paratype: British East Africa (F. THOMAS), gen. no. 4482 (in the Vienna Museum). 6 ♂.

♀ 16—20 mm (allotype 19 mm). Head and thorax in middle creamy, laterally and on tegulae suffused with very pale fulvous-tawny. Palpus pale tawny with a whitish base and an oblique median dark grey shade. Abdomen fuscous.

Fore wing oblong, rather narrow, costa gently curved at base, apex pointed, termen sinuate, oblique. Pale ochreous, markings tawny, fuscous, and dark brown. Costa with a series of fine and short dark brown strigulae. An ill-defined longitudinal median suffusion, greyish-fuscous mixed with tawny and dark brown, extending to above dorsum; on anterior half this suffusion cut by several brown ill-defined inwards-oblique marks, anterior three of these representing the first discal spot; second discal spot shaped as some faint dark edging to lower half of stigma, which is white and little contrasting; the median streak considerably dilated and brighter tawny-brown beyond the cell; a pale creamy streak above cell from its middle to apex; veins finely streaked with brown; termen with a dark brown line; dorsum with a series of dark brown dots. Cilia tawny, strongly dusted with creamy, a subapical and an apical dark brown lines.

Hind wing and cilia glossy, creamy-white.

The series is rather variable, one specimen brighter pale ochreous with more

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Fig. 51. *Bactra (C.) sinassula* sp.n., ♀, allotype, sterigma and ovipositor. Fig. 52. The same, bursa. Fig. 53. *B.* (*C.*) *salpictris* sp.n., ♂, holotype, sterigma and ovipositor. Fig. 54. The same, bursa

extended costal strigulation and median streak brighter tawny ochreous; two other specimens more greyish-fuscous tinged, with a darker but interrupted median streak, containing one or both discal spots.

Female genitalia. Sterigma sclerotized, strongly folded at the sides, two longer folds flanking the ostium bursae which is calyciform and wide, with a pair of short parallel folds on each side above extensions of the edge of ostium. Colliculum, a very strong, straight tube, gently dilated above, with strongly thickened walls below dilatation, and complicated structures of the inner surface. Anapophyses are short, with peculiar rectangularly bent bases. On each side of the colliculum there is an oval tumescence. Postapophyses very long and slender. Signum large, basket-shaped.

Material studied. South Africa, Transvaal: Pretoria, 13.I.1916 (A. J. T. JANSE), 1 ♀, allotype, gen. no. 4270. Natal: Bela Vista, XI.1916 (C. J. SWIERSTRA), 1 ♀, paratype, gen. no. 4236; Tanganyika: Victoria Falls, 26.I.1918 (Coll. JANSE), 1 ♀, paratype, gen. no. 4291.

Comoro Ids.: Mayotte (L.), V.1911 (in MEYRICK's hand), 1 ♂ paratype, gen. no. 3600 (in MEYRICK Collection, in the British Museum).

It seems very likely that the sex partners are correctly chosen because the long and sclerotized aedeagus corresponds with the long colliculum.

A large and robust species, belonging to the *coronata* group.

Bactra (Chiloides) triceps spec. nov.

Figs. 58—60

♂ 15—17 mm (holotype 15 mm). Head sordid whitish, tinged creamy, tuft on vertex, which is rough and high, mixed with fuscous-tawny laterally. Palpus strongly dilated, with rough edges, fuscous-grey externally, creamy inside, terminal segment very slender, grey. Thorax pale ochreous, regularly spotted with fuscous, metathorax with a silvery gloss. Abdomen fuscous.

Fore wing oblong, little dilated, moderately broad, costa gently curved, more so along posterior half, apex rather obtuse, termen gently convex, almost straight, little oblique. Ochreous-white, with a faint gloss, partially clouded with pale fuscous-grey. Markings dull, ferruginous and dark fuscous. A conspicuous streak of pale ground colour from beyond base to above apex, rather well-defined, occupying about $^1/_6$ of wing breadth, gradually attenuated at extremities, running along upper edge of cell; remainder of wing clouded; costa along posterior part with distinct ferruginous little oblique strigulae, delimited by the white streak, along anterior part of costa obliterated; median longitudinal fascia irregular but complete, from base to apex, dark fuscous, obscuring discal markings; first discal spot discernible, second discal ill-defined, followed by two roundish dark brown suffused spots between cell and termen; an oblique-oval moderate spot forming the centre of ocellus; a narrow slightly undulate or dentate terminal streak, above connected by a curved slender line with costa. Cilia grey, with several faint darker lines, in tornus pale ochreous-grey, along costa pale ochreous.

Hind wing sordid whitish-ochreous, with a moderate gloss, slightly infuscated towards apex. Cilia pale ochreous, with a golden gloss around apex.

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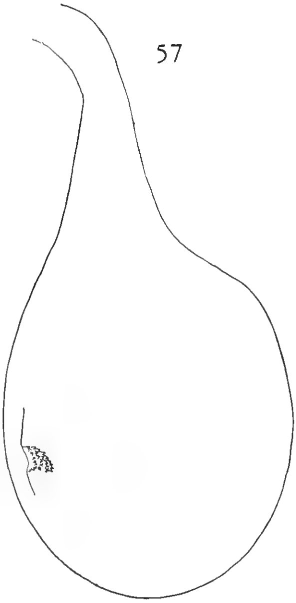


Fig. 55. *Bactra* (*C.*) *trimera* sp.n., ♂, holotype, genitalia. Fig. 56. The same, ♀, allotype, sterigma and ovipositor. Fig. 57. The same, bursa

Male genitalia. Very characteristic. Tegumen short and broad, vinculum widely V-shaped. Uncus rather short. Socius large. Valva peculiar, cucullus narrowed at base, costa rounded and strongly prominent below middle, top considerably attenuated, slender. Valvula moderate, with a large corona. Sacculus strongly concave, top extended so as to form a large triangular process, with 7—8 long spines along edge; base of sacculus narrowed, concave; punctulated area on an oblique transverse discal tumescence. Juxta large. Caulis short. Aedeagus robust, rather short, cornuti, some 5 long spines.

Material studied. South Africa, Natal: Bela Vista, XI.1914 (C. J. SWIERSTRA), 1 ♂, holotype, gen. no. 4243; Magude, IX.1918 (C. J. SWIERSTRA), 1 ♂, paratype, no. 4241. Transvaal: Woodbush Village, 1670 m, 11.I.1925 (A. J. T. JANSE), 1 ♂, paratype, no. 4367. 3 ♂.

The male from Woodbush is melanistic, with the fore wing strongly infuscated, but with discal markings, the discal spots, and the pretornal dot remaining distinct. The second paratype is similar to the holotype.

♀ 18—24 mm (allotype 22 mm). Head and thorax tawny-fulvous. Palpus pale fulvous, basal half of tuft of median segment blackish. Abdomen fuscous.

Fore wing oblong, rather narrow, costa curved towards extremities, straight in middle. Pale fuscous, glossy, evenly suffused except above tornus, with dull tawny. Costal markings reduced to minute dark purplish traces along extreme edge posteriorly; first and second discal spots indicated by some dark purple dustings; traces of some leaden transverse strigulae below costa posteriorly; termen with a tawny line dusted with purplish; part of wing below vein 7 and as far as cell rather well-defined and not suffused with tawny. Cilia purple, dull, dusted with whitish, a narrow basal and an indistinct subapical whitish lines.

Hind wing glossy, slightly suffused with grey. Cilia concolorous.

A variable lot. Except the allotype there are three tawny-greyish unicolorous specimens, two pale ochreous insects with a narrow grey median streak, faint and interrupted, and two pale ochreous specimens with well-defined dark fuscous-grey broad median streak, in one of them gradually dilated so as to occupy almost entire termen.

Female genitalia. Seventh sternite strongly sclerotized and plicate, outer rostrolateral margin stronger sclerotized and with a narrow dark fold on each side. Ostium rather wide, forming a strong funnel, its walls thickened along upper portion from below top. Anapophyses rather long and slender, postapophyses slender and long. Signum, a shallow basket.

Material studied. In the Transvaal Museum. South Africa, Natal: Karkloof, 23.I.1917 (A. J. T. JANSE), 1 ♀, allotype, gen. no. 4479. All other are ♀ paratypes: Transvaal: Tweefontein, 13.I.1907, gen. no. 4299; Pretoria, 7.I.1910, gen. no. 2879; 5.XII.1907, gen. no. 4354; the same, 15.II.1915, gen. no. 4302; the same, 6.XII.1917, gen. no. 4304. Barberton, 31.XII.1910, gen. no. 4307 (all by A. J. T. JANSE).

In the British Museum. Natal: Weenen, X-XI.1925 (H. P. THOMASSET), 1 ♀, paratype, gen. no. 3627. Transvaal: Pretoria, 2.XI.1907 (JANSE), gen. no. 3462 (MEYRICK Collection). 8 ♀.

Bactra (Chiloides) nesiotis spec. nov.
Figs. 61—62

♀ 19 mm. Head and thorax dark fuscous-grey. Palpus rather pointed, pale ochreous-tawny, with a well-defined median blackish line running to tip. Abdomen rather dark fuscous-grey.

Fore wing narrow, sublanceolate, costa rather curved along anterior half, almost straight posteriorly, apex acutely pointed, termen almost straight, gently convex, very oblique. Rather unicolorous dark fuscous-grey. Costa slightly lighter, slaty-grey with minute linear transverse black marks; basal third of wing tinged purplish-grey, darker; terminal portion of wing somewhat more tinged grey-olive, dorsum with a series of approximated triangular dark fuscous dots. Cilia sordid pale ochreous-fuscous mixed with fuscous, with slightly paler base and ill-defined subbasal line.

Hind wing dark fuscous with a bronze gloss, paler towards costa; in paratype hind wing dull fuscous-black, unicolorous. Cilia pale fuscous with a fuscous subbasal band.

Female genitalia. Lobi anales slender and elongate. Sterigma formed by a transversely oblong moderately sclerotized lamella postvaginalis, its upper edge with two triangular excisions, middle part rounded. Lower edge of this sclerite forming the ostium bursae, continued as a strong tubular colliculum, gradually dilated downwards, with a split in middle of lower third. Ostium flanked by slightly sclerotized plates, finely wrinkled along inner edge which is prolonged downwards. Signum basket-shaped.

Material studied. Madagascar: "Antananarivo", (M.), 1911, 1 ♀, holotype (rather worn, right fore wing and head missing), gen. no. 2158. Paratype, 1 ♀, the same data, without abdomen. (Labels in MEYRICK's hand. In MEYRICK Collection, in the British Museum).

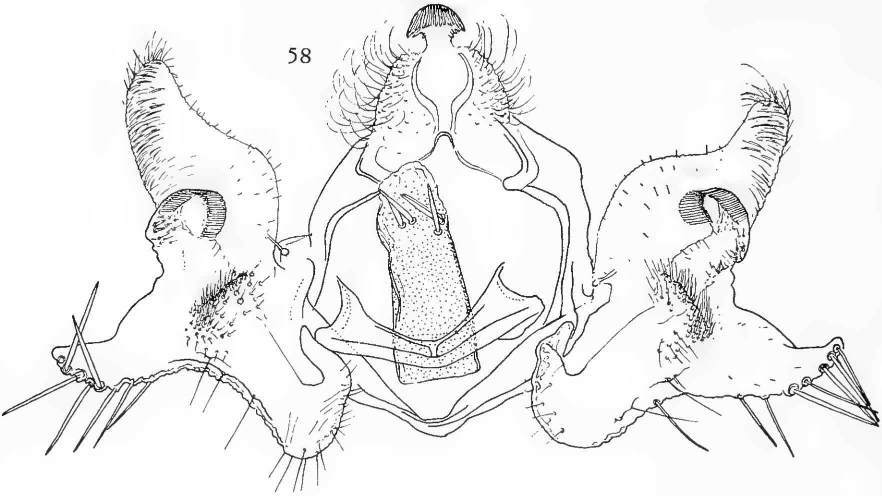
A conspicuously dark insect with strongly pointed fore wings. Superficially it resembles a *Nannobactra* and is, in fact, very similar to *B. (Nannobactra) sardonia* Meyr. Its position is obscure without the evidence of the male genitalia. The genitalia resemble slightly those of *contraria* Diak. from Borneo, but resemblance may be purely incidental.

Subgenus **Nannobactra** Diakonoff, 1956

Nannobactra Diakonoff, 1956, Zool. Verh., no. 29, p. 52 (subgen. of *Bactra*).

The subgenus differs from *Chiloides* by compact male genitalia with the valvula present and equally well-developed, but with the cucullus distinctly separated from the basal part of the valva by a transverse groove; this cucullus is usually rounded, sclerotized throughout and beset along its outer edge with one to three series of very large spines becoming smaller towards top of cucullus. The females possess a weakly sclerotized sterigma, formed by little modified, small and usually finely short-haired ridges, tumescences and folds. The signum is a small concave and denticulate sclerite, often weak, sometimes absent.

The species usually are small, with narrow and pointed wings, and with similar,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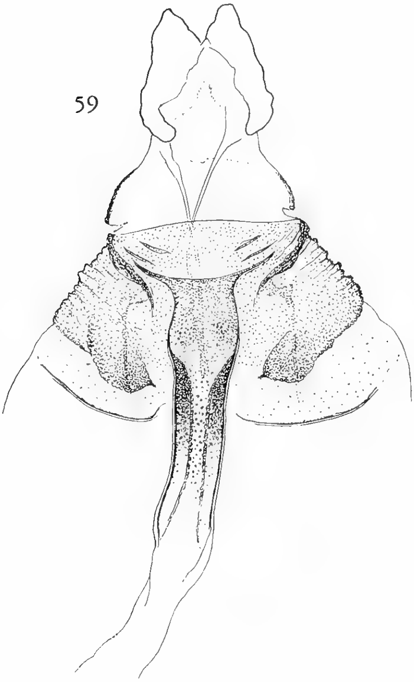
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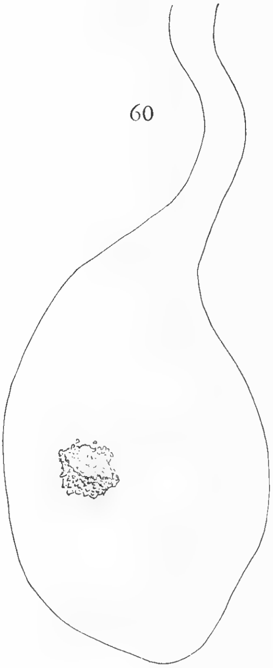
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Fig. 58. *Bactra* (*C.*) *triceps* sp.n., ♂, holotype, genitalia. Fig. 59. The same, ♀, allotype, sterigma and ovipositor. Fig. 60. The same, bursa

although variable markings. It is very easy to identify the subgenus, but the species usually are difficult of recogniton, especially the females. Although I am including the males in the key to the species, I am not able to do the same for the females, except for the very distinct *sardonia*. It is likely that only rearing of whole egg batches will allow certain identification and separation of the females of *Nannobactra* species; a key for that purpose is not possible at present.

To stress and elaborate certain differences of the structure of the male genitalia in this difficult group, I am introducing a few new (non-Latin) descriptive terms. The degree of the development of the gnathos, or at least, of structures which seem to be homologous with that part, is of specific importance. Sometimes a membraneous, complete transverse and band-like gnathos is present, more often it is obliterated in the middle and only its basal parts, shaped as triangular lobes at the tegumen, are visible; for these structures I use the therm "shoulder lobes". Sometimes they may be entirely absent. The large spines along the edge of the cucullus, are homologous with "cucullus bristles and spines", an indication used by me before, in the subgenera *Bactra* and *Chiloides*. In *Nannobactra* these spines are so large that they form a marginal corona; therefore the term "corona spines" is used for these structures. Often the ultimate and the penultimate 1—3 corona spines are much larger or differently shaped than the other; in this case they are termed "inequal". Seldom this difference is slight, then they are termed "subequal corona spines".

Bactra (Nannobactra) sardonia (Meyrick, 1908)
Figs. 64, 67—68

Pamplusia sardonia Meyrick, 1908, Proc. Zool. Soc. Lond., p. 718 (♂ ♀). — Clarke, 1955, Meyrick's Types, vol. 1, p. 277.

Bactra sardonia: Clarke, 1958, loc. cit., vol. 3, p. 315, t. 156 figs. 1—1a (lectotype select., fig.).

Distribution. Transvaal: N.E. Pretoria.

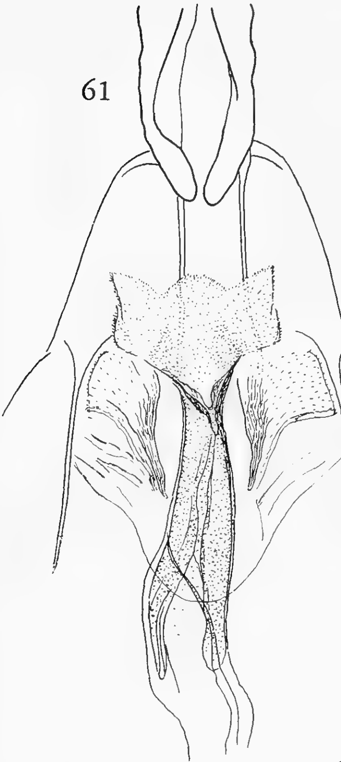
This apparently rare species has hitherto been known after the unique male lectotype, in the British Museum. By a lucky chance a single female specimen, in my opinion undoubtedly conspecific with the male, was found in the MEYRICK Collection. This female and the genitalia of the two sexes may be described as follows.

♀ 17 mm. Head and thorax pinkish-fulvous. Palpus whitish, upper edge and tip fulvous. Abdomen dark fuscous.

Fore wing sublanceolate, little dilated, costa gently sinuate, being curved along anterior half, slightly prominent before middle and hardly concave posteriorly, apex sharply pointed, termen gently concave, almost straight, very oblique. Evenly tawny-fulvous, only towards costa becoming paler, fulvous-greyish. Costa with numerous dark brown, small, wedge-shaped transverse marks, on posterior half of costa with whitish interspaces, which become pale pinkish before apex. Cilia pinkish-fulvous, mixed with whitish, with a pure white basal streak, a cloudy black bar opposite apex.

Hind wing dull dark bronze-fuscous, darker towards apex, paler towards dorsum. Cilia (imperfect) fuscous with a dark fuscous subbasal band.

Male genitalia. Tegumen broad, spherical. Uncus large; socius small. Gnathos indicated, very weak. Valva of the usual shape, but valvula very large and characteristic, corona being continued along the ventral edge of the valvula to its base. Sacculus small, with a large punctulate area, spined only in centre and to-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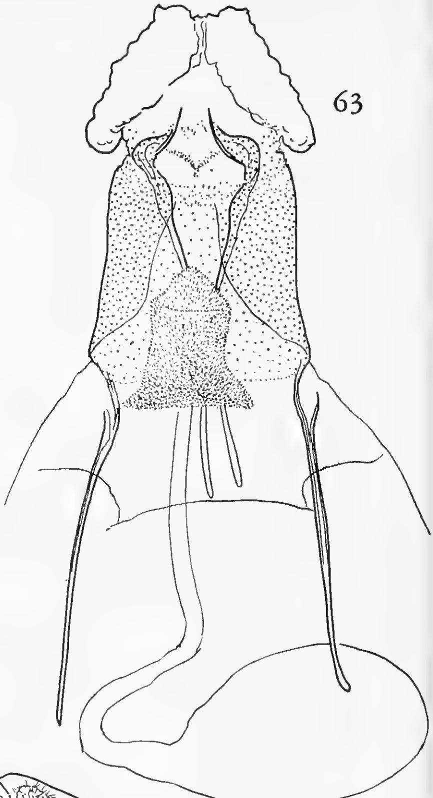
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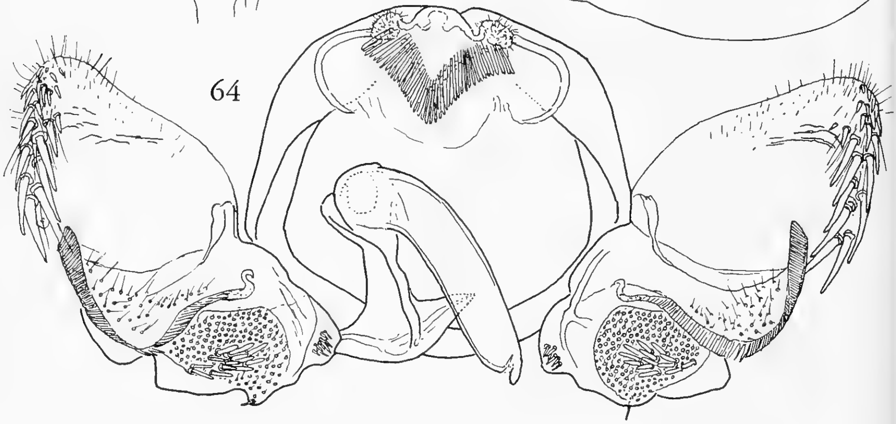
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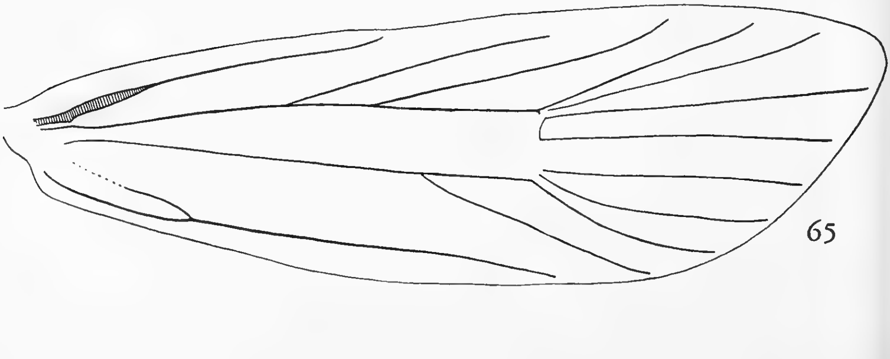
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wards the outer edge, spines moderate, not numerous. Aedeagus rather long.

Female genitalia. Eighth + ninth segment sclerotized, intersegmental membrane between this and lobi anales finely aciculate ventrally, naked laterally. Both apophyses pairs quite long. Sterigma well-modified, lamella posterior forming a rather narrow vertical prominence, densely aciculate, with a truncate top. Ostium bursae pear-shaped, its lower edge gradually rounded and thickened; lamella antevaginalis developed, a sinuate transverse band or fold with thickened edges, twice sinuate; curved downwards in the middle and again, less so, at the sides; strong folds running from the extremities of this lamella along edges of the genital segment, and becoming weaker and less sclerotized dorsad. Signum, a small concave sclerite, finely scobinate and denticulate.

Material studied. South Africa, Transvaal: N.E. Pretoria, 14.I.1907 (JANSE), ♀, gen. no. 3519. (In MEYRICK's hand; in MEYRICK Collection, in the British Museum).

Bactra (Nannobactra) legitima Meyrick, 1911
Figs. 68, 70—71

Bactra legitima Meyrick, 1911, Trans. Linn. Soc. Lond., vol. 14, p. 269 (♀). — Viette, 1947, Mém. Inst. sci. Madagascar, ser. A. vol. 1, p. 54. — Clarke, 1955, Meyrick's Types, vol. 1, p. 183. — 1958, loc. cit., vol. 3, p. 312, t. 155 fig. 1 (type figured).

Bactra (*Nannobactra*) *legitima* : Diakonoff, 1961, Ann. Soc. ent. France, vol. 130, p. 70 (Mahé, ♂ neallotype).

Distribution. Seychelles: Silhuette Id, Mahé Id.

Material studied. South Africa, Natal: St. Lucia Lake, X.1920 (H. W. B.), 1 ♂, gen. no. 4379; New Hanover, 26.XII.1915 (A. J. T. JANSE), 3 ♂, gen. nos. 3792, 4335, and 4339. Southern Rhodesia: Salisbury, 1.I.1920 (A. J. T. JANSE), 1 ♂, gen. no. 4543 TM. Bulawayo, 15-23.XII.1919 (A. J. T. JANSE), 1 ♂, gen. no. 4370.

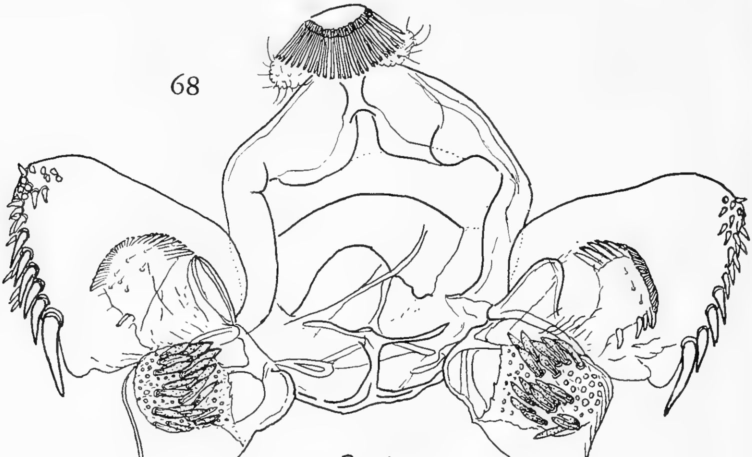
Besides, a ♀, with a label in MEYRICK's hand: "Silhouette, Seychelles I., X.09" (MEYRICK Collection, in the British Museum), gen. no. 2157. A worn specimen without head, but with an intact abdomen, obviously conspecific with the female type specimen (without abdomen) in the British Museum and, very probably, being the paratype. Female genitalia may be described as follows.

The genital segment moderately and evenly sclerotized throughout; this segment discending on each side of sterigma, so as to form slender smooth bands, each ending in a small free lobe level with the ostium; these bands sharply delimiting the sterigma proper which is weak and not sclerotized but recognisable by fine aciculation (while the bands are naked); lamella postvaginalis with a curved upper edge; ostium wide and regular; colliculum well-defined but neither sclerotized, nor aciculate and rather shallow.

Bactra (Nannobactra) minima Meyrick, 1909

Bactra minima Meyrick, 1909, Journ. Bombay Nat. Hist. Soc., vol. 19, p. 586 (♂ Barberyn Island, Ceylon). — Diakonoff, 1950, Bull. Brit. Mus., Ent., vol. 1, p. 288, pl. 6

Fig. 61. *Bactra* (*C.*) *nesiotis* sp.n., ♀, holotype, sterigma. Fig. 62. The same, signum. Fig. 63. *Lobesia* (*Lomaschiza*) *quadratica* (Meyr.), ♀, holotype, genitalia. Fig. 64. *Bactra (Nannobactra) sardonia* Meyr., ♂, holotype, genitalia. Fig. 65. *Lobesia (Harmosma harmonia* (Meyr)., neuration of right fore wing



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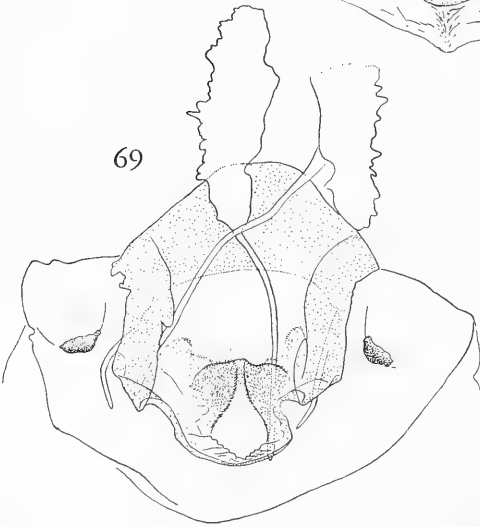

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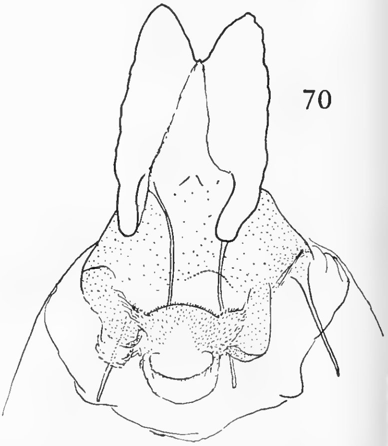

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fig. 25 (lectotype designated, gen. ♂ descr. and fig.). — 1956, Zool. Verh., no. 29, p. 55, figs. 52—53 (*phaeopis* syn.).

Bactra phaeopis Meyrick, 1911, Proc. Linn. Soc. N.S. Wales, vol. 36 p. 254 (♂ ♀, Sudest Island, New Guinea). — Diakonoff, 1950, Bull. Brit. Mus., Entom., vol. 1, p. 288, pl. 6 fig. 28 (gen. ♂), pl. 8 fig. 41 (gen. ♂) (Lectotype designated, gen. ♂, ♀ descr. and fig.).

Distribution. Ceylon (Barberyn Island); New Guinea (Sudest Island); Solomon Islands; Marianas Islands.

Canary Islands, Tenerife, IV.1884 (LEECH) (WALSINGHAM Collection), gen. no. 3697, ♂ (no. 62294), 3700 ♂ (78866), 3701 ♂ (78865) and 3705 ♀ (78864). All in WALSINGHAM Collection, British Museum.

It is surprising to find *minima* "so far from home". This species must be widely distributed, but must have escaped attention of collectors due to its modest colouring and size.

The male genitalia of the present material agree in all details with those of the Asiatic specimens. The female has an exactly similar sterigma, but the genital segment is somewhat more sclerotized. However, this feature is subject to some variation throughout the subgenus.

Bactra (Nannobactra) dasioma spec. nov.

Figs. 69, 73

♂ 16 mm. Head creamy, vertex suffused with pale tawny. Palpus whitish above, creamy, mixed with light brown, laterally. Thorax creamy, spotted with fuscous. Abdomen light grey, anal tuft pale ochreous.

Fore wing rather broad, oblong, costa curved at extremities, straight in middle, apex moderately pointed, termen straight, oblique. Creamy-white, glossy. Markings light tawny-brown, fuscous and blackish, well-defined. Costa along anterior half with not numerous dark fuscous wedge-shaped small marks, posterior half of costa contrastingly different: with six broad, light tawny transverse spots; first of these median and trapezoidal; second narrow, fasciate; third to fifth, wedge-shaped; sixth apical, rounded; spaces between these spots formed by glossy pairs of white costal marks, each pair with a minute separating median dark line; fourth costal mark continued by a straight streak to upper part of termen; first discal spot arrowhead-shaped, black, continued below as an inwards-oblique streak across wing to above dorsum; second discal spot semioval, longitudinal, dark tawny-fuscous, on middle of its upper edge a small tawny suffusion indicating rest of transverse fascia; stigma small and pale, upper half absent; a slightly inwards-oblique short fuscous streak between cell and tornus; a pair of irregular curved ochreous-tawny marks on upper part of termen, united into a suffused triangular fuscous marginal line from apex to tornus. Cilia creamy, mixed with pale ochreous, a pale ochreous antemedian line, a dark fuscous small blotch opposite apex.

Hind wing glossy pale ochreous, considerably suffused with light purplish, more so towards apex.

Fig. 66. *Bactra (N.) legitima* Meyr., ♂, neallotype (after Diakonoff, 1961). Fig. 67. *B. (N.) sardonia* Meyr., ♀, gen. no. 3519. Fig. 68. The same, signum. Fig. 69. *B. (N.) dasioma* sp.n., ♀, allotype, sterigma and ovipositor. Fig. 70. *B.* (*N.*) *legitima* Meyr., ♀, gen. no. 2157. Fig. 71. The same, signum

♀ 16 mm. Exactly similar to the male but with all markings somewhat darker, fuscous, costal spots narrower, pretornal mark broader, touching dorsum before tornus, first discal spot continued to dorsum. Hind wing suffused with darker purple, except towards base.

Male genitalia. Comparable with those of *phaulopa* Meyrick from Asia, but clearly differing by the presence of shoulder lobes which are slightly rounded and aciculate. Valva of normal shape, corona spines large and long, in two oblique series, punctulate area with only few thick and rather short spines (10 left, 11 right), and a few fine teeth on the inner edge; lower part of sacculus extended into a broad blade, rounded below, forming a short triangular cusp above.

Female genitalia of *phaulopa* type, but more similar to those in *verutana* Zell. The genital segment sclerotized, lamella antevaginalis with upper and lower edges distinct and sclerotized. Small lateral sclerites present, separate and very dark. Signum minute.

South Africa, Cape Province: Stella Bush, 28.II.1915 (A. J. T. JANSE), 1 ♂, holotype, gen. no. 4477. Natal: Umkomaas, 29.I.1914 (A. J. T. JANSE), 1 ♀, allotype, gen. no. 4459. (In the Transvaal Museum).

Cape Province: Umtata, X.1904 (LEIGH), 16411, 1 ♂, paratype, gen. no. 3655 (WALSINGHAM Collection, in the British Museum). 2 ♂, 1 ♀. A brightly marked species with, for the subgenus *Nannobactra,* unusually broad fore wings.

Bactra (Nannobactra) aciculata spec. nov.

Fig. 72

♂ 14 mm. Head, palpus and thorax whitish, shoulder fuscous. Abdomen fuscous.

Fore wing sublanceolate, dilated, broadest at $^3/_4$, costa gently curved troughout, more so along its posterior fourth, apex acutely pointed, termen tolerably straight, oblique. Creamy-white with a silky gloss, markings dark fuscous (rather worn). Anterior part of costa narrowly suffused with dark grey and with a series of dark fuscous transverse marks; basal patch not defined, transverse fascia indicated by a moderate transverse fuscous spot on middle of costa, below costa extended into a fasciate longitudinal small tawny suffusion, continued across wing by a very faint pale yellowish colour; first discal spot longitudinal, fasciate; second discal spot irregularly semioval, rather well-defined, dark fuscous, its ends acutely produced, stigma represented by a small excision of its upper edge; apical streak faint anteriorly, posteriorly blotchy and emitting a vertical bar to lower part of termen; a jet-black oval spot in apex; faint transverse marks along dorsum. Cilia dark fuscous (damaged).

Hind wing and cilia pale fuscous (imperfect).

Male genitalia of *phaulopa* type. There is a distinct membraneous and band-like gnathos. Cucullus with a broadly rounded top, corona spines in two series, moderately curved and subequal (ultimate 3—4 spines hardly different in shape and size), pointed. Sacculus as large as cucullus, lower edge with a moderate, gradually rounded blade, becoming narrower above, cusp blunt; punctulate area with a moderate number of strong pointed spines, situated towards top and outer edge; inner edge of this area with several inequal, very acute teeth.

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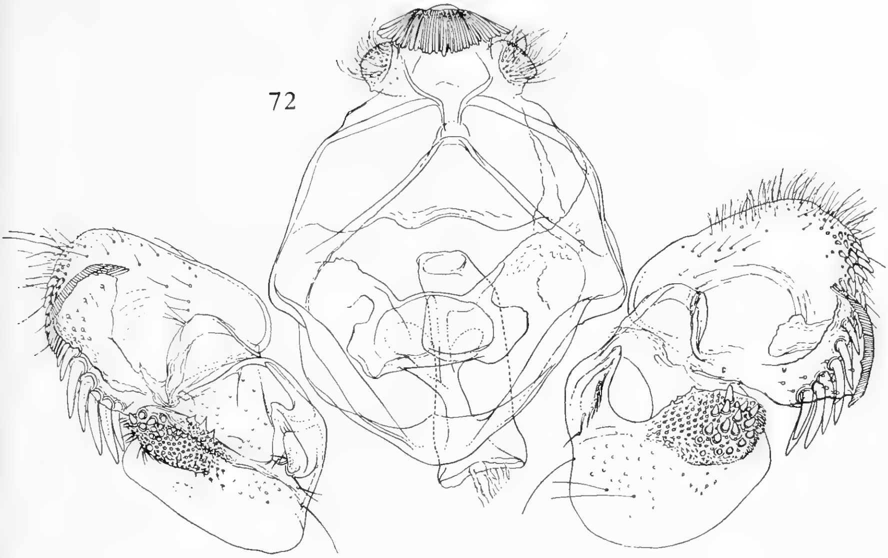

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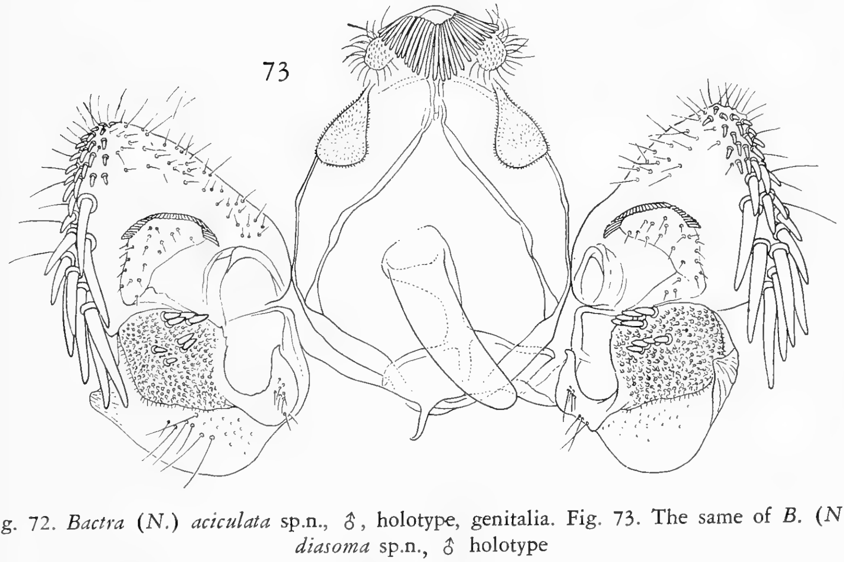

Fig. 72. *Bactra* (*N.*) *aciculata* sp.n., ♂, holotype, genitalia. Fig. 73. The same of *B.* (*N.*) *diasoma* sp.n., ♂ holotype

Distinct by strongly rounded cucullus, subequal corona spines, position of sacculus spines and dentate inner edge of punctulate area.

Material studied. South Africa, Southern Rhodesia: Selukwe, 27.XII.1919 (A. J. T. JANSE), 1 ♂, holotype, gen. no. 4466. Unfortunately a single specimen available; the species, however, is sufficiently distinct.

Bactra (Nannobactra) spec.

The following six female specimens of *Nannobactra* must remain unidentified for the present, due to their poor condition and to the considerable variability of the sclerotization of the genital segment in the species of this subgenus.

3788, Mazoo (S. R.), I.1920 (Coll. Janse). 4329 and 4330, Barberton (T.), 15.I.1911 and 31.XII.1910 (A. J. T. Janse). 4335, Durban (C. P.), 13.XII.1916 (v. d. Merwe, Coll. Janse). 4369, Bulawayo (S. R.), 15-23.XII.1919 (A. J. T. Janse), and 4402, Lorenzo Marques, 23.II.1930 (A. C. Daintree).

APOCRYPHAL SOUTH AFRICAN *BACTRA* SPECIES

Two following species have been originally described as, or subsequently transferred to, *Bactra.*

Lobesia Guenée, 1845

Harmosma subgen. nov.

Fig. 65

With superfical characters of *Lobesia* but with veins 9 and 10 moderately sinuate, approximated posteriorly, then slightly diverging again; pterostigma ill-defined.

Male genitalia with tegumen weak, rounded. Gnathos membraneous, a weak curved transverse rod. Tuba analis ill-defined. Valva rather narrow, sclerotized throughout, cucullus slender, narrowed, covered all over, but not densely, with slender spines; sacculus strongly thickened, with a transverse deep groove (scalloped), separating Spc_1 and Spc_2 completely; both these spine clusters large, elongate, formed of extremely dense spines, those on the ventral end of Spc_1 very long, forming a projecting sheaf.

Female genitalia with sterigma shaped as a long, entirely free, rising tube, narrowed towards the top which is spinulose. Signum, a small denticulate concave sclerite.

Type-species, *Polychrosis harmonia* Meyrick, 1908. An interesting form, derivable from the Palaearctic subgenus *Lobesiodes* Diakonoff, 1954.

Lobesia (Harmosma) harmonia (Meyrick, 1908) combin. nov.

Fig. 65

Polychrosis harmonia Meyrick, 1908, Proc. Zool. Soc. Lond., p. 716 (♂ ♀, Transvaal: Pretoria). — 1911, Ann. Transv. Mus., vol. 2, p. 63 (transferred to *Bactra*). — Clarke 1955, Meyrick's Types, vol. 1, p. 153.

Bactra harmonia: Clarke, 1958, Meyrick's Types, vol. 3, p. 311, t. 154 figs. 2—2a (lectotype selected, figured).

Distribution. South Africa; Madagascar.

The genitalia, as described for the subgenus above.

Lobesia (Lomaschiza) quadratica (Meyrick, 1912) combin. nov.

Fig. 63

Bactra quadratica Meyrick, 1912, Ann. Transv. Mus., vol. 3, p. 63 (♀, Natal: Nkwaleni). — Clarke, 1955, Meyrick's Types, vol. 1, p. 267. — Anonymous, 1958, List Types S. & E. Afr. Museums,vol. 1, p. 57 (holotpe indicated).

Distribution. South Africa.

APPENDIX

After the manuscript of the present paper has been sent to the printer, I was entrusted with a small collection of *Bactra* species, collected in Sudan, which were kindly sent to me for identification by Dr. KLAUS SATTLER of the Munich Museum, Germany. It seems worth while to add these latest data to my paper, for the sake of completeness.

Bactra (Bactra) graminivora Meyrick, 1922

This paper, p. 312

Sudan, Ed Damar, Hudeiba, 1.X—18.XI.1961 (R. REMANE), 2 ♂, 14 ♀, genitalia nos. ♂ 4615, 4622; ♀ 4604—4608, 4610—4614, 4616—4618 and 4621.

Bactra (Chiloides) venosana (Zeller, 1847)

This paper, p. 331

Sudan, Ed Damar, Hudeiba, 18.XI.1961, 15.III.1962; Blue Nile Province, Wad Medani, 3.VIII.1962 (R. REMANE), 3 ♂, 1 ♀, genitalia nos. 4542 ♂, 4620 ♂, 4609 ♀.

Bactra (Chiloides) tornastis Meyrick, 1909

Bactra tornastis Meyrick, 1909, Journ. Bombay Nat. Hist. Soc., vol. 19, p. 586 (♂ ♀ Ceylon; Coorg). — Diakonoff, 1950, Bull. Brit. Mus., Ent., vol. 1, p. 289, t. 5 fig. 18 (lectotype select., genit. figured). — Clarke, 1955, Meyrick's Types, vol. 1, p. 312. — 1958, loc. cit., vol. 3, p. 315, t. 156 figs. 3—3a (lectotype illustr.).

Distribution. India: North Coorg; Ceylon; Pakistan.

Sudan, El Damar, Hudeiba, 18.XI.1961, gen. no. 4619 ♂. Blue Nile Province, Wad Medani, 3.VIII.1962, gen. no. 4624 ♂ (R. REMANE). 2 ♂.

The discovery of this Indian species in Africa is a complete surprise. The species is intermediate between *fasciata* and *triceps,* but all three are entirely distinct. In my key *tornastis* would run to no. 14, *triceps*. However, the male genitalia differ by the sacculus being less extended laterad, having a more rounded and less prominent point, beset with a much longer series of distinctly shorter spines. The genitalia agree with those of my Asiatic examples of *tornastis* closely. There is no doubt of this being the same species.

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Index to species

Synonyms are in italics

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De *Entomologische Berichten* worden eveneens door de Nederlandsche Entomologische Vereeniging uitgegeven en zijn bestemd voor de publicatie van kortere artikelen, van faunistische notities etc., alsmede van de Verslagen der Vergaderingen en van mededelingen van het Bestuur. Zij verschijnen twaalf maal per jaar in een aflevering van 16 of meer bladzijden. Deze 12 afleveringen vormen samen een deel.

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Text references to this list might be made thus:

"Mosely (1932) says...." or "(Mosely, 1932)".

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DEEL 106 AFLEVERING 8 1963

TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSCHE ENTOMOLOGISCHE VEREENIGING

INHOUD:

B. M. Lensink. — Distributional ecology of some Acrididae (Orthoptera) in the dunes of Voorne, Netherlands, pp. 357—443, fig. 1, plates 2—5, 2 graphs.

Tijdschrift voor Entomologie, deel 106, afl. 8. Gepubliceerd 2-XII-1963

Nederlandsche Entomologische Vereeniging

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DISTRIBUTIONAL ECOLOGY OF SOME ACRIDIDAE (ORTHOPTERA) IN THE DUNES OF VOORNE, NETHERLANDS

BY

B. M. LENSINK

Oostvoorne

CONTENTS

GENERAL INTRODUCTION

Experience in making an inventory of a given region has consistently shown that a species is not equally distributed over the area in which it occurs. In some places it is completely absent and in others its numbers vary greatly from place to place. In approaching this phenomenon from the point of view of the ecology of distribution, attention is given on the one hand to the structure of the animal, its physiological characteristics and behaviour, and on the other hand to the environmental factors, both biotic and abiotic. At this point the student encounters an extremely complex network of relationships. For the present it is impossible to investigate the whole of such a network or even the whole of one of its parts. We are forced to limit ourselves to the investigation of some of the relations between some of these factors. This may, however, make it possible to distinguish the nature of the totality of the mutually operative relations.

A systematic approach is nevertheless indispensable. This type of investigation can usually be divided into three phases. First, the places in which a particular species occurs in the area are established; second, in a field study the factors are determined which might be responsible for the restriction of the species to that environment; and third, a laboratory investigation is made to determine whether the reaction of the animals to various factors is such that what has been observed in the field can be understood.

The distribution of three species of grasshoppers, *Myrmeleotettix maculatus* (Thunb.), *Chorthippus biguttulus* (L.) and *Chorthippus albomarginatus* (de Geer), found on the island of Voorne (4°.5′ W, 51°.54′ N) in the Netherlands was investigated between 1953 and 1955. Of the three investigational phases mentioned above, only two could be fully carried out. The newly-built field laboratory was not yet properly equipped, which meant that the third phase could only be realised for a few factors with very simple procedures. Nevertheless, this situation did not detract from the fact that a comparative investigation into the distribution of the three species of grasshoppers over a small area of the dune region made it possible to understand the situation observed in the field, this in turn providing an understanding of the nature of the relationships between the various entities.

A study of the factors in the environment which determine localization requires the analysis of the very complex totality of relationships affecting life. Such analysis can only be productive when it is possible to select an environment without too large variations or too strong extremes.

On the basis of these considerations, distribution was studied in a small area, in this case a section of older stabilized (landward) dunes (measuring 1.5 hectare) which was almost entirely covered with grass. This had advantages over a study made in an area with a great variety of vegetational structures. It not only simplified the technical aspects of the study but also permitted a more intensive study of the mutual dependence of the distribution of the species in all their developmental stages and the various environmental factors. In addition, the apparently limited variation in this vegetation proved to be a crucial factor for organisms spending their entire lives in that vegetation without many possibilities to escape from it (UVAROV, 1928 and CLARK, 1948). This region had the further advantage that the three species of grasshoppers are all present on the same terrain and could thus be investigated simultaneously. Differences and agreement between phenomena offer the observer increased opportunity to penetrate to the basic relationships between animal and environment.

This region was chosen after a rough inventory had been made of the dune area on Voorne (p. 374).

A special sampling technique was developed for the investigation into the distribution of the three species of grasshoppers, with particular view to the local circumstances (p. 378). With this technique, the distribution could be studied from the initial egg stage to the adult.

For this investigation a large number of quadrats was chosen in the various types of vegetation and sampled during the season (from April to November) with our method. Although no difficulty was encountered in identifying the adults of the three species, practicable field-characteristics had to be chosen for distinguishing the immature stages of each of the species and the corresponding stages of all three (p. 376).

During the three years in which the study was carried out, an attempt was made to establish as accurately as possible when the various stages appeared in the field and when they disappeared from it. The relationship between this annually recurring phenomenon and the climatic factors at the time was also studied (p. 398).

In addition to the attention given to distribution during the season, observations were also made of the activities of the animals during the period of a day under various weather conditions (p. 427). It is particularly this latter kind of study which, by observation of the animal from minute to minute, greatly increases the understanding of an animal. It reveals the manner in which the animals move about in the vegetation, where their courtship occurs, where and for how long they sun themselves, what diet they choose, how and where the eggs are laid, how they react to all kinds of enemies, etc.

In this picture, the vegetation is extremely important and very complex. It serves not only as a source of food but also as a place in which to live. The vegetation, which has a patchy distribution is characterized not only phyto-cenologically but also structurally (p. 364). Special attention has been given to the structural changes which occur during the year and from year to year. Periodic changes in the vegetation produce changes in the character of the animal's habitat. Such changes may create conditions under which the animals cannot live, and this may result in migration.

The vegetation is subject to climatic influences. But it is the vegetation and the structure of the soil (which in its turn is also partially influenced by the vegetation) that create the peculiar phenomenon of the microclimate. VESTAL (1913) refers to this point, and UVAROV (1928), FRANZ (1931), STROHECKER (1937) and CLARK (1948), among others, emphasize the importance of microclimatological investigation in the study of the distribution of grasshoppers.

The investigation of this extremely important microclimate could not be carried out because the proper instruments were lacking. STOUTJESDIJK (1961) later investigated, in the same locality, on a number of points the variations in microclimate within the vegetation in the course of a day and the season. These data and the general pattern of the microclimate in the various types of vegetation are described (p. 372). The investigation of the activities of the insects during the day revealed very clearly how sensitive they are to changes in climatological conditions. FRANZ (1931, 1933) stresses this sensitivity by calling the Orthoptera climate indicators.

THE VEGETATION OF THE LANDWARD DUNES AND THE MICROCLIMATE

THE VEGETATION

Introduction

The vegetation occupies an important place in the lives of the grasshoppers. It is not only a source of food, it also forms a predominant part of the environment of these insects. For this reason, much attention was paid to the characteristics of the vegetation present in the area in which the investigation was carried out.

As a source of food, the composition of the vegetation has little influence on the distribution of the grasshoppers because their primary preference is for grasses and sedges. These plants are present in the entire field in which the study was made, some even dominating the grass cover.

As environment, however, the vegetation is very important for the distribution of the grasshoppers. They seek those places that agree with their vital requirements such as locomotion, protection against predators, protection against climatic extremes, and the maintenance of reasonable heat and water economy.

This environment is determined by the structure of the vegetation and the microclimate prevailing in it. These two aspects are very closely related. The structure of the vegetation is determined by the qualitative and quantitative characteristics of the various parts of which it is composed, and shows differences from one place to another that are dependent of the botanical composition and habitat factors. The structure of any given place will also in the majority of cases vary rather strongly in the course of a year (seasonal dynamics, BOERBOOM, 1957a) and may differ from year to year depending on annual changes in the macroclimate.

During the investigation, as many data as possible concerning the vegetation were collected and the most striking changes noted. Samples were made at many points, and the development of the various layers in the vegetation and the height of the most important plants was followed.

In the plant growth of the landward dunes, eight communities and vegetations are distinguished. However, this characterization does not express the seasonal dynamics of the vegetation. The vegetation, in all its variations, is therefore described in a different manner which reveals peculiarities in the structure that may be important to the life cycle of the grasshopper. On the basis of the finer nuances in the vegetation, a number of types are distinguished, each with a specific structure and annual development. For each of these types the grasshopper population was estimated several times during the season in a number of 3 sq.m quadrats.

The nomenclature used in this work for the higher plants is taken from HEUKELS & VAN OOSTSTROOM (1956) and for the mosses from VAN DER WIJK & MARGADANT (1947). The infraspecific taxa of many plants characteristic for the dunes were chosen, after consultation with E. VAN DER MAAREL who has investigated the vegetation of the dunes of Voorne, in agreement with BOERBOOM (1957b). The phyto-cenological nomenclature is borrowed primarily from WESTHOFF, DIJK, PASSCHIER & SISSINGH (1946).

General description of the terrain

The grassy and slightly rolling landward dunes on the border of the municipalities of Oostvoorne and Rockanje comprise two parts separated by market gardens, hedges and a road. The investigation was carried out in the part of the terrain lying furthest to the west (Plate 2). This part of the dunes is bordered on the west, north, and east by market gardens. The only connection between this part and the younger dunes is by a small path through a wood. The dunes are separated from the market gardens by a thick and in some places quite high hedge of hawthorn trees. To the south is the Tenella-plas, an educational public garden surrounded by trees of medium height. The entire terrain is therefore completely isolated from all other dune regions in which grasshoppers are found. Migration from these regions is practically excluded; grasshoppers are seldom seen in the market gardens.

The maximal difference in elevation between the highest and lowest ground is 3 metres. The more elevated parts of the otherwise rather flat field are relatively dry. The lower parts are rich in humus and moist; particularly in the winter and early spring of the years in which the investigation was done, these places were spongy and in some spots even covered with water.

The landward dune formerly served as pasture land for goats and horses, and this fact probably gave the present vegetation the chance to develop. A large number of plant species is found, more than 60 species being present.

The area may be generally characterized as dry and more or less densely covered grassland. Wide differences in structure occur, partially caused by the stand. The higher parts are covered with a thin vegetation, often rich in herbs, with a highly-developed moss layer that partially or entirely covers the soil. Where the moss does not entirely cover it, the sandy soil is visible. In the transitional areas between the higher and lower parts, the grass cover is thicker and the moss covers less of the surface. In the lower spots the grass cover is very thick and locally rich in herbs. In late spring the grass in this vegetation becomes fully developed.

Locally, *Salix repens* penetrates the grass cover from the hedges. A high, thick growth of grass is sometimes found between the low shrubs.

Botanical description of the vegetation

The vegetation of the terrain in which the investigation was carried out comprises a complex of communities belonging primarily to the Koelerion albescentis, but also in part to the Corynephorion canescentis.

The characteristic species and the species occurring frequently among the Koelerion are: *Lotus corniculatus* var. *ciliatus, Taraxacum rubicundum, Ranunculus bulbosus, Ononis repens* var. *mitis, Erigeron acer, Arenaria serpyllifolia, Erodium glutinosum, Phleum arenarium, Thymus pulegioides, Plantago lanceolata* var. *sphaerostachya.*

In addition there are few species from the Bromium erecti: *Potentilla tabernaemontani* and *Helictotrichon pubescens.*

The species from the Corynephorion are: *Corynephorus canescens, Aira praecox, Polytrichum juniperum, Festuca ovina, Polygala vulgaris,* and *Poa pratensis* var. *humilis.*

A few different species are: *Galium verum* var. *maritimum, Carex arenaria,* and *Leontodon nudicaulis.*

In this complex, eight communities and vegetations are to be distinguished. They are to a great extent determined by the stand.

(1) Tortuleto-Phleetum arenarii, an open vegetation on the south slope with an incomplete moss layer of *Tortula ruraliformis* and *Phleum arenarium, Erodium glutinosum, E. cicutarium, Myosotis hispida,* and *Veronica arvensis.* Two transitions of this community are found:

(a) A transition to Taraxaco-Galietum, consisting of a vegetation with a half closed to entirely closed moss layer of *Hypnum cupressiforme*, in which *Galium verum* predominates, and

(b) A transition to Violeto-Corynephoretum dunense, in which tussocks of *Corynephorus canescens* occur.

(2) Taraxaco-Galietum, a vegetation with a closed moss layer of *Hypnum cupressiforme* with *Galium verum* var. *maritimum, Thymus pulegioides, Poa pratensis* var. *humilis, Lotus corniculatus* var. *ciliatus, Carex arenaria,* and *Festuca rubra* subvar. *arenaria.* The herbs form a low, dense and closed layer. This vegetation occurs on the slightly higher parts of the terrain.

(3) Festuceto-Galietum maritimi. Of these a poor form occurs with *Festuca ovina* in tussocks and rosette plants of *Leontodon nudicaulis, Hieracium pilosella,* and a moss layer of *Hypnum cupressiforme* and *Cladonia* species. This vegetation covers a large flat part of the southernmost part of the terrain.

(4) An incompletely developed Violeto-Corynephoretum dunense, without *Viola canina* and with few *Cladonia* species. This vegetation is found in only a few places.

(5) A vegetation of *Sedum acre* and *Plantago coronopus.* This is found along paths and around depressions. It probably develops where calcareous sand has worked its way to the surface.

(6) A vegetation of *Festuca rubra* subvar. *arenaria* and *Carex arenaria,* a form with *Calamagrostis epigejos*; in this vegetation *Calamagrostis* can dominate so

strongly locally that facies-formation occurs. This vegetation occurs only locally and spreads from the borders of the terrain.

(7) A vegetation of *Sieglingia decumbens* and *Gentiana campestris baltica.* This form of vegetation is found at the transition from the higher parts to the lower. Grasses such as *Sieglingia decumbens, Anthoxanthum odoratum,* and *Holcus lanatus* predominate here, forming a grassy cover on rather moist ground.

(8) A vegetation with *Lythrum salicaria* and *Lysimachia vulgaris.* This vegetation grows on the moist soil, rich in humus, of the lowest parts of the terrain. It often forms a growth rich in herbs with such species as *Achillea millefolium, Potentilla erecta, Hydrocotyle vulgaris, Potentilla anserina, Holcus lanatus, Sieglingia decumbens, Anthoxanthum odoratum, Plantago lanceolatum* var. *sphaerostachya,* and *Carex flacca.*

Vegetational types and structural changes

A list of the plant-communities and vegetations found in the landward dunes will give plant ecologists and biocenologists a clear impression of the nature of the overgrowth, but as a description of the habitat of the grasshopper it is not adequate. Even the samples of the various vegetations would fail to provide a real insight into the habitat and the changes taking place in it. A more detailed description of the structure is required. This point is often neglected by animal ecologists. Several botanists have offered a type of structural description which has very attractive aspects for the field ecologist. DANSEREAU (1951) made use of symbols expressing many characteristic peculiarities of the plants in a vegetation. The structure of the vegetation is thus symbolized by a diagram which, however, fails to reflect the natural situation. Each symbol reflects the relative space occupied by a plant type in the community. It serves both for individuals of one species and for individuals of various species. Such a diagram, however, always requires an accompanying description.

Although the value of this method was not underestimated for the present study (it would, for instance, be extremely serviceable for comparisons of vegetations at different geographical latitudes), it was considered to offer too few possibilities in a physiognomically simple vegetation such as the growth on the landward dunes. The use of symbols as proposed by DANSEREAU provides an over-generalized picture and also fails to reflect periodicity.

For the present study, in characterizing the vegetation of the field a detailed description is first given of the various types of growth to be distinguished in it. This is illustrated by a number of drawings of these types (fig. 1). These drawings, however, refer exclusively to the natural situation in the month of June.

A structural description requires in the first instance the distinguishing of as many vegetational layers as possible and the indication of the cover in per cent. In consultation with E. VAN DER MAAREL who made a study of the structural description from the botanical point of view, the following surface vegetation layers were tentatively distinguished: the moss layer, the rosette layer, the carpetting layer, the high herb layer and the low shrub layer.

These layers may be briefly described first as follows.

(1) The moss layer. The mosses often cover a large part of the soil; in denser vegetations they remain more in the background.

(2) The rosette layer. Under this term is understood the layer of herbs that form rosettes in the moss layer and barely project above it, such as *Hieracium pilosella, Taraxacum* spec., *Hypochaeris radicata, Leontodon nudicaulis* and typical low-growing creepers such as: *Potentilla tabernaemontani* and *Ranunculus repens.* Only the flower stalks of these species project above this layer.

(3) The carpetting layer. A large number of herbs show a strong horizontal spread and form a low cover above a highly developed moss layer. These species are: *Lotus corniculatus* var. *ciliatus, Galium verum* var. *maritimum, Polygala vulgaris, Ononis repens* var. *mitis, Cerastium holosteoides, Cerastium arvense, Veronica arvensis,* and a few creeping species such as: *Thymus pulegioides* and *Sedum acre.* Between these herbs a few of the low grasses such as *Agrostis stolonifera* and *Bromus mollis* var. *nanus* occur.

(4) The high herb layer. This layer is formed by the more vertical plants, the grasses in particular dominating. The layer includes: *Festuca rubra* subvar. *arenaria, Festuca ovina, Corynephorus canescens, Sieglingia decumbens, Calamagrostis epigejos, Carex arenaria, Helictotrichon pubescens, Poa pratensis* var. *humilis, Anthoxanthum odoratum, Luzula campestris, Holcus lanatus, Carex flacca, Achillea millefolium,* and *Erigeron acer.* This layer occurs in various forms. A number of grasses such as *Festuca ovina* and *Corynephorus canescens* grow in tussocks, which creates a characteristic structure. Other grasses and *Carex arenaria* influence the structure of the vegetation by their dominancy. In addition, differences in the density of this layer are caused by variations in the amount of horizontal spread of the species present.

(5) The low shrub layer. This layer is formed by *Salix repens,* small shrubs 40 to 80 cm in height. Locally, and in the summer barely projecting above the high herb layer, *Rosa pimpinellifolia* (25—40 cm) occurs.

On the basis of typical differences in the share taken by these layers in the vegetation, I have distinguished seven structural types. Type I through type VI are grass vegetations, type VII comprises the *Salix repens* shrub that spreads into the terrain from its borders and between which a dense grass cover is sometimes present. Type VII was not sampled systematically.

Type I. The vegetations belonging to this structural type are open and low (Plate 3). The moss layer covers the soil only partially (coverage 0—10%); *Hieracium pilosella* very locally, sometimes forms facies. The herbs appear only to a small extent, and the sparsely distributed grasses and herbs in the high herb layer cover the soil to a very limited degree. *Festuca rubra* subvar. *arenaria* and *Carex arenaria* dominate in this layer. Locally, tussocks of *Corynephorus canescens* occur on an otherwise very scantily covered soil.

In the course of the year, the aspect of the vegetation changes appreciably. The period of the greatest vegetative expansion falls in the winter and the early spring. The moss cover is then saturated with moisture and as a result shows a fresh green colour. The superficial sandy soil is moist and firm. A number of annual herbs occur in the moss layer (winter annuals), such as *Erophila verna, Saxifraga tridactylitis, Aira praecox, Phleum arenarium,* and *Vicia lathyroides.* The perennial species are still small and of a yellowish-green colour. The green grass cover is 5—10 cm high. Scattered over the soil are dead leaves of grass and flower stalks.

Later in the spring, in April and May, the winter annuals flower and fructify. They are not numerous and most of them barely project above the moss layer. In this period the remaining herbs develop.

In the early summer the bare sandy soil becomes dry and develops a crust, or where it is walked over, is very loose. The moss cover also becomes very dry, changes to a yellowish-green colour and shows splitting. Of the winter annuals only dried remnants can be found. Some of the other species come to the fore. Rosette plants develop and creeping plants spread horizontally over the moss cover. In the summer during flowering, some of these plants add colour to the vegetation. The grasses and the sand sedges flower and fructify with stalks as high as about 20 cm. Their vegetative part does not grow higher than 10 cm. A few plants such as *Senecio jacobaea* shoot up very high during the flowering period.

In late summer and in the autumn, more and more dead leaves and stalks appear and are pressed down on the moss cover by the wind. The mosses become greener again and the winter aspect gradually asserts itself. The vegetations described here occur on the southern slopes and belong to transitions from the Tortuleto-Phleetum arenarii to the Taraxaco-Galietum maritimi and the Corynephoretum dunense. They also occur, distributed over the field, in places where the vegetation was damaged before and during the Second World War, having originally belonged to the Taraxaco-Galietum maritimi.

Type II (Plate 3). The vegetations of this type have a well-developed moss cover (coverage: 60—100%). The soil is entirely covered by the mosses and herbs so that the sandy surface is not visible. In the rosette layer many rosettes of *Hieracium pilosella* are found, a species which is often extensively represented in this type and even forms facies, in which case its coverage is 50—100%. The carpetting layer is better developed than in type I, especially *Galium verum* var. *maritimum* and *Thymus pulegioides* predominating. The grasses *Festuca rubra* subvar. *arenaria, Agrostis tenuis,* and the sedge *Carex arenaria* form a thin layer to a height of about 10 cm.

The appearance of type II changes less in the course of the year than that of type I. The moss layer is saturated with moisture in the winter and early spring. Winter annuals are far less frequent. In the early summer the mosses become dry but continue to form an unbroken layer. Locally, the activity of ants brings some sand to the surface. The remaining species in the carpetting layer develop and flower. They cover only a small part of the surface, however (— 50%). The high herb layer becomes higher during flowering because of the flower stalks (20 cm). In the autumn many dead leaves and stalks are seen on the moss layer. These vegetations occur on the highest parts of the terrain and may be assigned to transitions from the Tortuleto-Phleetum maritimi to the Taraxaco-Galietum maritimi.

Type III. The vegetations belonging to type III correspond closely to the overgrowth described for type II. Instead of free-standing grasses in the high herb layer, tussock grasses are predominantly seen, which creates the typical structure of this type (Plate 4).

The moss layer covers 30—50% of the surface; the rosette layer and the carpetting layer do not grow higher than 5 cm and cover 30—60% of the surface. In the high herb layer tussocks of *Festuca ovina* occur, covering 30—50% of the surface. In the period in which the grass flowers, a great number of flower stalks grow up above the vegetative part of the plants (10 cm), to a maximum height of 25 cm.

These plants cover a large part of the terrain and belong to the Festuceto-Galietum maritimi.

Type IV. In the moderately dense to dense low vegetation, the moss layer is well developed (coverage: 60—100%). A rosette layer is almost entirely absent: it blends into the carpetting layer which is dense but not higher than 5 cm. Both layers combined cover 60—100% of the surface. They include: *Lotus corniculatus* var. *ciliatus, Galium verum* var. *maritimum, Thymus pulegioides, Cerastium* c.f. *tetrandum, Plantago lanceolata* var. *sphaerostachya, Potentilla tabernaemontani, Luzula campestris,* and *Achillea millefolium.* The high herb layer constitutes a grass cover covering a maximum of 30% of the soil. The vegetative parts are 10—15 cm high, the flower stalks growing up 20—30 cm. A few of the species in this group are *Festuca rubra* subvar. *arenaria, Agrostis tenuis, Carex arenaria, Festuca ovina, Poa pratensis* var. *humilis,* and *Achillea millefolium.* In various places along the borders of the terrain or near vegetations composed of a high, thick grass cover, the flower stalks of *Calamagrostis epigejos* rise up to a height of 40 cm in this type.

The changes in the vegetation over the year are again less marked than for the previously described types. In the course of the summer the cover provided by a number of the most frequently occurring species in the carpetting layer is increased; the plants in the high herb layer begin to flower. The latter cause little change in the structure of the very dense carpetting layer.

The vegetation of this type belongs to the Taraxaco-Galietum maritimi and occurs over a large surface on the higher parts of the terrain.

Type V. The vegetation included in this type are distinguished by the higher proportion of grasses in the high herb layer. The structure of the higher layers is consequently much denser than in the corresponding layers of the other types.

The moss layer is of little importance. *Rhytidiadelphus squarosus* predominates. There is no rosette layer, the rosette plants do not spread their leaves horizontally on the soil. The carpetting layer shows a transition to the high herb layer.

Two different forms can be distinguished within this type. The first is a vegetation occurring on the transitional slopes between the highest to the lowest parts of the terrain. It consists of a moderately dense to very dense, gentian-rich grass cover, in which among others are present: *Anthoxanthum odoratum, Sieglingia decumbens, Festuca rubra* subvar. *arenaria, Holcus lanatus, Agrostis tenuis,* and *Gentiana campestris baltica.*

The vegetation covers 80—100% of the surface and its vegetative part is 10—15 cm high; in the flowering period the many flowering stalks may reach a height of up to 25 cm. Locally, a vegetation is also found that is rich in *Rosa* *pimpinellifolia,* small shrubs 25—40 cm high; these roses, which bear numerous small leaves in summer, cover 80% of the surface and cast much shade on the underlying layers. The higher herb layer covers 20—100% of the soil. Many plants occur in this layer: *Achillea millefolium, Cerastium tetrandum, Luzula campestris,* and a number of rosette plants such as *Ranunculus bulbosus, Taraxacum* spec., and *Plantago lanceolata* var. *sphaerostachya.* The grasses *Helictotrichon pubescens, Festuca rubra* subvar. *arenaria, Agrostis tenuis, Calamagrostis epigejos,* and *Carex arenaria* are numerous between the dune roses.

In winter and spring this vegetation, excluding the dune roses, is 15—20 cm in height and consists of the vegetative parts of the herbs. In spring the grasses grow quickly, especially *Helictotrichon pubescens.* The weather conditions prevailing in this period are of great importance for the extent of this growth. Most of the herbs do not grow much higher than 20 cm, with the exception of a few flower stalks (*Achillea millefolium*). In the summer and autumn the dry stalks of many grasses, which have already finished flowering, fall to form a dead layer in the high herb layer. The dune roses shrubs are leafless in the winter, in the summer they come more to the fore in and above the high herb layer. It is striking, lastly, that in some parts of this vegetation the structure is less dense because of the large numbers of rosette plants that spread their leaves between the grasses.

Type VI. Type VI includes the vegetation of the lowest parts of the terrain and its edges along the hedgerows. It comprises densely covering grass vegetation, rich in herbs in the parts with the most moisture (Plate 5).

The moss layer is either absent or very fragmentary. The soil is covered with a layer of dead grass and flower stalks, sometimes as much as 10—15 cm thick. The carpetting layer on the wettest spots is 10 cm high and covers 60—100% of the surface. It includes: *Achillea millefolium, Ranunculus bulbosus, Taraxacum* spec., *Prunella vulgaris, Plantago lanceolata* var. *sphaerostachya, Galium uliginosum, Potentilla anserina, Lotus corniculatus, Hydrocotyle vulgaris.*

Growing to a height of about 40 cm in the high herb layer are: *Lythrum salicaria, Lysimachia vulgaris, Pulicaria dysenterica,* and *Achillea millefolium.* The grasses that frequently occur in this layer are: *Holcus lanatus, Calamagrostis epigejos, Festuca rubra* subvar. *arenaria, Agrostis stolonifera, Sieglingia decumbens, Anthoxanthum odoratum,* and the sedges *Carex flacca* and *Carex arenaria.*

On higher spots in the terrain a high, dense grass cover is found locally in which *Calamagrostis epigejos* dominates. The non-grassy herbs are forced into the background. This vegetation shows strong growth in the summer and its flower stalks reach a height of a metre in some cases. The soil is covered with a 20 cm thick layer of dead plant material, only the surface of which dries out in summer.

The appearance of this vegetation varies greatly, due especially to the grasses. At first the vegetative parts of the plants are not higher than 20 cm, but in the course of the summer some species show rapid growth to an appreciable height as a result of which the structure becomes very dense. In the autumn and winter most of the grasses collapse and their dead parts accumulate on the ground.

Type VII. The dwarf shrubs, consisting of *Salix repens* and a moderately dense to dense grass cover, comprises this type of vegetation. The shrubs reach a height of 40—80 cm with a coverage of 60—100%. The grasses grow rapidly in early

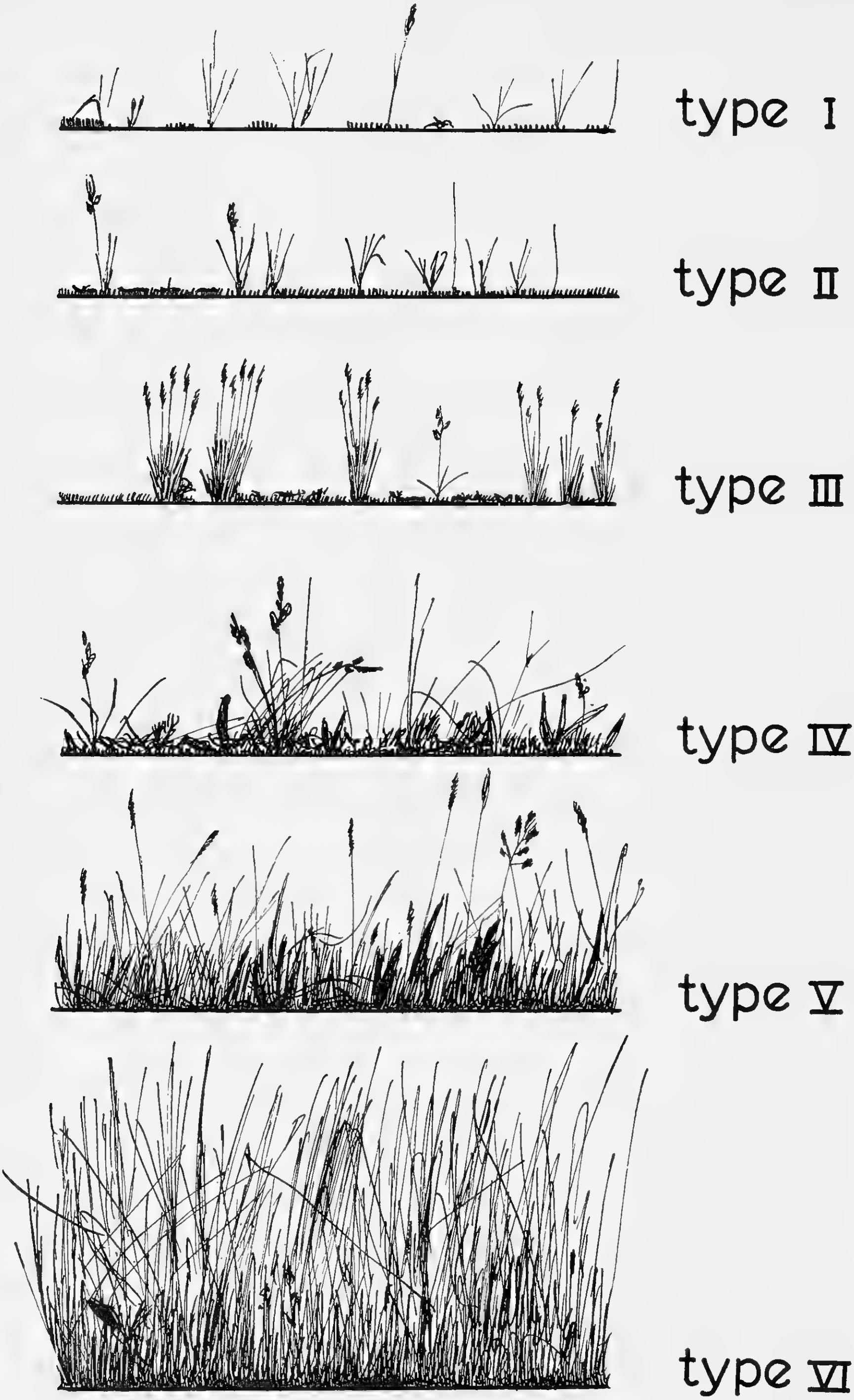


Fig. 1. The vegetation types I—VI

Table 1. Data concerning the vegetation of the terrain. The amount of coverage and the height of the various layers in the seven types of vegetation in per cents and centimetres, respectively.

Type	I	II	III	IV	V	VI		VII
						m	d	
Moss layer	30—95 %	60—100%	30—50%	60—100%	< 10%	—	—	—
Rosette layer	0—10 % 50—100% 1)	50—100% 5 2)	30—60% 5 2)	60—100% 5—10 2)	—	—	—	—
Carpetting layer	10% 5 2)				80—100% 10—15—25 2)	80—100% 10—40	80—100% 20—100	100% 40—80
High herb layer	10% 5—10—20 2)	10—30 % 10—20 2)	30—50% 10—25 2)	20—30% 10—15—30 2)				
Low shrub layer	—	—	—	—	*Rosa* 80% 25—40	—	—	60—100% 40—80

1) with facies-formation by *Hieracium pilosella*
2) height of the flower stalks

m = low, moist areas
d = higher, dry areas

summer, causing a strong increase in the density of the vegetation among the shrubs.

In addition to the developmental changes in the various layers of the vegetation in the course of the year, differences are observed from year to year in the appearance of the vegetation. For instance, in May and June, 1955 the grasses showed a more luxuriant growth than in the same months in 1953, 1954, and 1956. This vigorous growth was probably induced by heavy rains, in particular in May, 1955. Although the grasses had developed more fully throughout the terrain in which the investigation was carried out, the structural differences were strongest in the vegetations belonging to types V and VI, which occur in the driest areas. As a consequence, in 1955 the structure of these vegetations was high and dense at an earlier date than in other years, and in addition the grass cover spread towards the less dense vegetation. It is self-evident that observations of such vegetational changes from year to year are very important to the estimation of the distribution of the grasshoppers.

Changes in the vegetation were also established in succeeding years. In addition to a marked spreading of the shrub, *Calamagrostis epigejos* was observed to show local predomination.

The increase in shrub components on the landward dunes accompanies a loss of characteristic peculiarities of the landscape.

The data concerning the description of the vegetation are arranged in Table 1, in order to give a general impression. An illustration of the various types is given in fig. 1, the drawings representing the situation in the month of June.

The choice and distribution of the quadrats

The choice of the quadrats in the early summer of 1953 was based on the differences in the structure of the vegetation. Fifty quadrats measuring three sq.m were selected, and the grasshopper populations were investigated in 1953, 1954, and 1955. In 1955, another group of quadrats was laid out for more detailed investigation of certain activities of the grasshoppers. For each of the types of vegetation, the quadrats were chosen in the most densely populated locations. In 1954, 55 additional quadrats measuring one sq.m were sampled for the investigation of the hatching sites. Table 2 gives the number of three sq.m quadrats systematically sampled from 1953 through 1955 in each type of vegetation.

Table 2. Number of quadrats sampled from 1953—1955.

Type	I	II	III	IV	V	VI	
1953—1954	7	3	8	9	8	11	quadrats
1955	7	1	0	6	3	6	quadrats

Two of the group of 50 quadrats were found to be transitions between two types and two other quadrats were later found to lie in an area very frequently visited by people. These four quadrats were excluded from the investigation.

THE MICROCLIMATE

The microclimatological conditions are important not only for the rate of development of the insects and their condition in the various stages, but also for all the activities of the insects. In the places where grasshoppers occur, attention must be given to such factors as temperature and moistness of the immediate surroundings in addition to the factors of the macroclimate. Lack of suitable instruments and the impossibility of obtaining them in time for the investigation, and the fact that the taking of the samples proved to require all the available working time, prevented serious investigation of the microclimate. However, starting in 1956, at Weevers' Duin Biological Station in Oostvoorne, Dr. PH. STOUTJESDIJK carried out microclimatological measurements for biological purposes in many types of vegetation found in the dunes of Voorne (STOUTJESDIJK, 1961), including the terrain used in the present study. Using these data and others from the microclimatological literature (BRUNT, 1945, GEIGER, 1950, SUTTON, 1953), a general discussion can be given concerning the course of the microclimate in the various types of vegetation, as distinguished by me, in the periods of the year that are of importance for the grasshoppers. An attempt is also made to roughly characterize the ecological factors of the environment.

In general it may be stated that the various microclimatological factors manifest themselves quite differently above a soil surface covered with vegetation than above a surface with no plant cover. Even a very sparse growth introduces changes that moderate the climate immediately above the soil. In this sense, for example, a surface with no plant cover may reach very high temperatures on warm, sunny days, while the same values are appreciably lower when some cover is present. This factor alone is sufficient to produce wide direct and indirect differences in the microclimate.

The microclimate is formed by the influence of the climate as a whole, by the nature of the soil, exposure, and all kinds of particularities of the vegetation. The combinations of species and the height and density of the plants are of importance. The denser the vegetation, the cooler it is during the day near the ground. The solar radiation is taken up by the leaves and stalks of the grasses and other plants, creating deep shade in the layers below. The thick absorption layer (soil and vegetation) distributes the heat in such a way that high temperatures do not occur as they do immediately above a bare or sparsely covered soil. A thick grass cover with a layer of dead leaves contributes to the occurrence of low nocturnal temperatures within and above it, especially on clear, windless nights with high radiation. This cooling process is accentuated by the slightness of the horizontal air currents and the fact that little heat is radiated by the soil.

In the terrain in which the study was carried out the microclimate is subject to great variation caused by differences in elevation as well as by the vegetation, which shows distinct structural differences from place to place. The grasshoppers which live in this vegetation must therefore make a choice during the season and in the course of a single day throughout their development. The following material contains some considerations concerning the microclimate in the various types of vegetation distinguished in this study.

Type I. The vegetations included in type I are very thin in structure; above an incompletely developed moss cover there is a very scanty grass cover. The microclimate in this extremely open vegetation often shows extreme variations. On sunny days, a large part of the solar radiation is absorbed by the surface of the soil. Under favourable conditions high surface temperatures can develop, which lie 20—30° C above the air temperature at a height of two metres (STOUTJESDIJK, 1959, 1961). In addition, as a consequence of the limited flow of moisture from this type of vegetation, the relative humidity of the air is low.

One cm above the ground the temperature is appreciably lower. STOUTJESDIJK states that the air temperature one cm above the soil is even much lower than the soil temperature at a depth of two cm. It was also found that directly above the surface there is very wide fluctuation in temperature. In addition, after sunset the temperatures of the surface layers of the soil drop sharply; the sand can become very cold, especially on very clear, windless nights. It is in just this layer with wide temperature variations that the grasshoppers occur.

In general, the nocturnal temperature of the air layers immediately above the soil and of the soil itself remains a few degrees higher than the temperature at a height of two metres, which points to heat radiation by the soil. The same picture holds in general for the spring season, although the absolute values lie lower than in the middle of the summer.

Type II. The vegetations of type II differ from type I in the development of the moss layer. The entire soil surface is covered with a well-developed moss cover. The microclimate in this type shows strong agreement with that in type I, but in this case the moss layer, which dries rapidly, absorbs most of the radiation and therefore reaches high temperatures. The soil temperature under the moss is appreciably lower.

Type III. The vegetations of type III are characterized by tussocks of grasses between which a more or less closed moss cover occurs. The microclimate above the moss cover is comparable to that of type II, although the values may lie somewhat higher because the cooling effect of the wind is greatly reduced by the grass tussocks. In the tussocks themselves the highest temperatures are found just under the tops of the plants, because the solar radiation is taken up by the leaves and flower stalks of the grasses. The temperature will be only a few degrees higher than the air temperature just above the plants. The tussocks also cast shade on the moss cover, especially when the sun is lower in the sky. In this type of vegetation, consequently, opposite extremes may occur quite close together, i.e., maximum temperatures may occur as high as those occurring on the surface in type II, but the average temperatures lie lower.

Type IV. The vegetations of this type are open forms, rich in grass and other plants, in which rosette plants occur frequently in the approximately five cm thick carpetting layer. Due especially to the presence of the rosette plants, the solar radiation can penetrate deep into the vegetation locally. Since the grasses and herbs decrease the drying effect of the wind above the moss cover, high temperatures occur in some spots. The local humidity of the air is high as a result of the high transpiration of the plant cover and evaporation from the soil, which has a relatively high humus content. Shady spots occur beside many plants, with the result that in this vegetation too, mild conditions are found next to heat.

Type V. The vegetations of type V are rich in grasses and herbs, with low, closed growth. Solar radiation penetrates the vegetation less deeply. The highest temperatures, which are not very high because of the strong transpiration of the many leaves, are found above the soil between the tips of the leaves. Deeper in the vegetation the temperature is lower, and a relatively large amount of shade is created by the layer of leaves above. Later in the year there is more shade because the sun is lower in the sky; the temperatures in the vegetation are lower than in July, even during the warmest part of the day.

In the early morning, dew often forms in this vegetation, because the moist air between the higher grass exposed to the cooling effect of the radiation does not receive sufficient heat from the lower layers. This phenomenon is not seen in the more open growths of types I, II, and III until later in the season.

Type VI. Type VI includes the high, dense grass vegetation found especially in the lower areas of the terrain. A number of remarkable observations have been made by STOUTJESDIJK (1961) in this type of vegetation on the same terrain. In a closed, high stand of *Calamagrostis epigejos* varying between 45 and 75 cm in height, the highest temperatures were recorded at the level of the lowest of the leaf tips. Most of the solar radiation is absorbed there and converted into heat and evaporation energy. On 10 July, 1959, with an air temperature of 22° C a temperature of 24° C was measured between the tops of the leaves; the temperatures in this vegetation are therefore not very high. The soil is much cooler and receives heat from the top layer. On the afternoon of the same day (reduction in the radiation intensity and more shade in the vegetation), the temperature gradient was still slight and the fluctuations in temperature were also small. During the clear evening which followed, however, the lowest temperature was found at the level of the lowest tops (reading at 9:10 p.m.). Both above and below this level the temperature was several degrees higher. The wind velocities in this dense vegetation are very low.

In less uniform vegetation of this type, consisting of tussocks of *Calamagrostis epigejos* between which layers of flattened grass or low herbs occur, the temperature profile is very different between the tussocks. The highest temperature is measured a few millimetres above the surface of the dead leaves. On 11 July, 1959, at 12:00 noon the average local temperature was about 23° C higher than at a height of one and a half metres. The fluctuations in temperature are very large: STOUTJESDIJK observed temperature extremes at a height of three mm, ranging over a 15° C difference during an observation period of about one minute. The fluctuations remain large at even greater heights between the tussocks.

On still, clear nights the vegetation takes heat from the air, causing a drop in temperature of about 30° C at a height of 3 mm, while at a height of one and a half metres the temperature drops only a few degrees. The formation of dew draws a great deal of moisture from the air, and this withdrawal of heat together with moisture during the entire night causes very low temperatures and vapour pressure to develop. On 12 June, 1959, at 4:07 a.m. a temperature of −7° C was measured at the soil surface as a result of very favourable conditions: the dry, rather cold air on a clear, still night; the inability of the cold air to escape from the low spots in the terrain; and, perhaps the most important factor, the unusual heat economy of the soil which is covered with an insulating layer of dead grass.

This situation occurs in many of the spots where quadrats were chosen for sampling. In May, low temperatures are still recorded in the vegetation, and it is self-evident that such microclimatological conditions have very definite consequences for the grasshoppers.

THE GRASSHOPPERS

THE GRASSHOPPERS IN THE DUNES OF VOORNE AND THE CHOICE OF THE WORKING TERRAIN

Investigation of the Acrididae in the dunes of Voorne showed that eight species occur. These species are: *Myrmeleotettix maculatus* (Thunb.), *Chorthippus biguttulus* (L.), *C. brunneus* (Thunb.), *C. mollis* (Charp.), *C. albomarginatus* (de Geer), *C. parallelus* Zett., *Omocestus viridulus* (L.), and *Oedipoda coerulescens* (L.).

An understanding of the distribution of these species indicates why a given area with a given number of species was the obvious choice as working terrain for this investigation. The density of the population and the variegation of its composition are factors affecting this choice. The density and variegation depend to a large extent on the vegetation. In this connection it has been found (VAN DER MAAREL, 1960) that the amount of shrubs in its various developmental phases, with its heavy to medium heavy growth, excludes a grasshopper population in many places. The small grassy areas occurring here and there between the shrubs are too small to permit more than a limited grasshopper density. Open spots, thinly covered dune slopes, and the verges of the many foot-paths are also lightly populated. The most suitable environment is offered by terrains with a grass cover, such as are found in the landward dunes.

The inventory made in 1953 supplied the following data.

(1) *Myrmeleotettix maculatus* occurs in varying densities throughout the dune region. In the small open spaces between the *Hippophae*-shrubs and along the paths, the numbers are small. On the coastal ridge, a few specimens are found here and there; the local climate, being extreme, apparently prevents a population increase. The landward dunes, with extensive grassy surfaces, show the highest density. In the direction of the polder, *M. maculatus* is rarely found because of the increasing amount of woodland and farms.

(2) *Chorthippus biguttulus* occurs only locally, especially in the old dunes, in the low, thick grass cover of the driest areas and in low *Salix repens* and *Hippophae* shrubs or near them.

(3) *Chorthippus brunneus* is distributed over the entire dune region, but in limited numbers. It prefers dry, sunny places such as those along the paths in the dunes. This species is frequently seen in the grass verges of the roads in the landward dunes and in ruderal places. If only this grasshopper is present it is

found in only a few spots. Frequently, *C. brunneus* and *C. biguttulus* are present simultaneously. PERDECK's experience (1957) concerning the choice of habitat by these species agrees completely with mine. *C. biguttulus* prefers denser and often somewhat more humid vegetations than *C. brunneus.*

(4) *Chorthippus mollis* is found in the dune region locally; this species lives in the dry, dense vegetations in which a low *Hippophae*-shrub, *Salix repens* and *Ligustrum vulgare* form an element. *C. mollis* is often found as sole species in the dunes of Oostvoorne. Here and there this species lives, like *C. brunneus,* together with *C. biguttulus* (but in limited numbers).

(5) *Chorthippus albomarginatus* lives in the dense, often high grass cover of the dune meadows in the relatively damp parts of the dunes. It apparently prefers the old parts of the dunes over the younger ones. It increases in number in the direction of the polder, and is often seen in the polder itself.

(6) *Chorthippus parallelus* is found in large numbers in only one place, namely in a meadow in the woods called the Mildenburg, in the municipality of Oostvoorne. Outside the dunes this species is found on the ramparts of Brielle. Up to the present it has not been observed between the two places.

(7) *Omocestus viridulus* was observed only once (in 1954) in an Agropyretum-vegetation on the Kruininger Gors along the Brielse Maas river.

(8) *Oedipoda coerulescens* is seen in the dunes only in small numbers; it prefers warm, dry places.

It is apparent that, in connection with the vegetational factors discussed in the preceding chapter, the density of the grasshopper population in the dune region proper is limited. The grassy landward dunes on the border between Oostvoorne and Rockanje, however, show larger concentrations, particularly of *M. maculatus, C. biguttulus,* and *C. albomarginatus.* These landward dunes were chosen for the working terrain, a choice which offered many advantages. In the main, the three species are the only ones occurring there, and the nymph stages of these species (with the exception of the first instar) are easily distinguished from each other. In addition, the vegetation of this terrain is extremely suitable for quantitative sampling. Its location is also very favourable, particularly with respect to the Weevers' Duin Biological Station.

In very small numbers, three other species occur: *C. brunneus, C. mollis,* and *O. coerulescens. C. brunneus* was observed on only a few occasions and during the three-year study *C. mollis* was seen only once (1954), in a part of the landward dunes lying outside the working terrain. *O. coerulescens* occurs only on thin vegetation; it is easily distinguished so that confusion with the other species is excluded. The instars of *C. brunneus* and *C. biguttulus* are difficult to distinguish from each other in the field. Because the latter occurs on this field in such small numbers, the doubtful cases were very limited in number and did not affect the quantitative investigation.

In 1953 two grasshoppers were heard and seen whose song deviated from that of *C. biguttulus.* PERDECK investigated one of these and identified it as a hybrid (*C. biguttulus* x *C. brunneus*). The song contained elements of that of *C. brunneus.*

THE IDENTIFICATION OF THE INSTARS

At the beginning of the investigation, only a guess could be made as to which species of grasshoppers inhabited the chosen terrain. In order to become familiar with the immature stages of these species as rapidly as possible, nymphs were collected in the field directly after hatching and raised in the laboratory to adulthood. Experience has shown that observation of the insects during rearing is absolutely necessary for recognition in the field. Descriptions in literature can convey only an impression. The appearance in 1954 of RICHARDS & WALOFF's publication provided an opportunity to check my experience against their table for the identification of the various instars and their determination table for the nymphs of a large number of species, including *M. maculatus* and *C. albomarginatus*. My experience is in agreement with the characteristics established by these authors for both species.

However, for the recognition of the individual instars, their material gave little support for my work. Measurements and counts of the insects in the field cannot be made if it is necessary to release the nymphs directly after ward. The nymphs in the field were not distinguished as to sex, since in the first instar this requires too close an examination during which it is almost impossible to avoid damaging the insects and consequently causing an unnecessary increase in mortality.

The rearing of nymphs is not easy. It often involves high mortality, which requires beginning with large numbers. The collection of the first instar in the field must consistently be done with the greatest care, especially because of their fragility. Catching them with the hand or sweeping net damages them so badly that only a few survive. They can best be caught in a glass tube. The tube is placed over the nymph, which usually jumps up into the tube. The insect can then be transferred to a glass bottle, the bottle being filled with dead grass to prevent the insect from killing itself by jumping against the glass. Direct sunlight must be avoided, because of the fatal effects of too much heat and moisture. When such precautions are taken, laboratory culture is much more successful: the mortality drops to about ten per cent.

For rearing the nymphs are transferred to a glass cylinder, ten cm long and two cm in diameter, open at both ends. One end is covered with gauze and the other plugged with a cork. Fresh grass must be fed daily. Before the last instar moults, the insects must be transferred to a larger tube with a diameter of four cm, containing a twig. Rearing experiments done by Miss A. S. C. SCHIJFSMA in Leiden showed that the last mould is more successful if the insect can inflate its wings while hanging from a twig. This behaviour is often observed in the field as well.

All the tubes were held in a large glass container, with a relative humidity of about 75%, and about the same air temperature as the laboratory. The widely varying surface temperatures measured in very thin vegetation do not usually occur in laboratory rearing, and as a consequence the development of the nymphs is retarded as compared to that in the field. Because these observations were required before work in the field could begin, in 1953, field sampling could not be started before the season was half over, causing us to miss the period from hatching to the occurrence of the youngest nymphs.

Thorough observation of the various cultured instars yielded several characteristics that were very useful for recognition of the insects in the field. The first and second instars are easily distinguished from those of the third and fourth instars: the latter instars show a distinct beginning of the development of the wings, which during the fourth instar extend past the second tergite of the abdomen. The first and second instars are more difficult to distinguish from each other. The first instar of the three species is generally smaller than the second instar. In addition, the pronotum is shorter than the head in the first instar and about as long as the head in the second. The second instar shows a broadening of the posterior edges of the mesonotum and metanotum, and this characteristic can be easily observed.

In distinguishing the corresponding instars of the three species, consistent use was made of the general shape of the antennae, the darker lateral borders on the back part of the abdomen (linea lateralis) and the little lines on the edges of the dorsal side of the pronotum (carina lateralis) (CLARK, 1943).

M. maculatus is the easiest to distinguish from the two *Chorthippus* species because from the first instar on, this species has easily recognizable antennal clubs. In addition, the linea lateralis does not form an unbroken line but per segment forms an angle with respect to the dorsal abdominal line.

Chorthippus species do not have clubbed antennae. In the first instar of *C. biguttulus,* the linea lateralis is broken by a per segment shift. This also appears in the first instar of *C. brunneus,* but in the same nymphs of *C. albomarginatus* these stripes run almost continuously from front to back. The second, third, and fourth instars of *C. biguttulus* are distinguished from the same instars of *C. albomarginatus* by the fact that the carina lateralis of the pronotum of the former is not straight, but bent inward.

THE NUMBER OF INSTARS

For *M. maculatus, C. biguttulus,* and *C. albomarginatus* four instars and the adult are distinguished in the field. UVAROV (1928) reports that the most of the species of Acrididae have five instars, while BEI-BIENKO (quoted by UVAROV, 1928) has observed four instars in various grasshoppers occurring in Siberia.

RICHARDS & WALOFF (1954) distinguish four instars in the field. BEIER (1956) states that the nymphs go through five or six moults; here the moulting of the "vermiform" larvae is probably included. When higher mean temperatures occur during development, one moulting can be omitted, and female nymphs often have one more moult than the males (BEIER, 1956).

During rearing of the nymphs from the egg to the adult stage in the laboratory, more than four instars were found in a few *C. biguttulus.* Two of these insects moulted, after passing through the first instar, to small grasshoppers whose characteristics, as used in field-identification, were not distinguishable from the first stage. Another nymph passed through the first instar twice and through the second instar twice during its development. The subsequent development of these insects agreed with that of the other nymphs of the same species. In establishing the number of instars, the vermiform larval stage preceding the first instar was not included.

THE SAMPLING TECHNIQUE

In preparing the distribution study of the three species of grasshoppers, it was my intention to become familiar with the distribution of the individual immature stages and the adults in the various types of vegetation. The technique had to be adapted to the collection of the required insect material and be related to the behaviour of the insects. The older nymph instars and the adults move with great rapidity, particularly in sunny, dry weather, while the younger nymph instars show a tendency to remain concealed in the vegetation.

Other attempts have been made, in various ways, to determine the size of a grasshopper population as representatively as possible, e.g., by the male song; by catching, marking and releasing the insects (LINCOLN Index); by beating strips of vegetation and attempting to count and identify the escaping insects; and by repeating a fixed number of passages with a net through the vegetation. All these techniques, however, provide a more or less inadequate picture. Often the nymphs are excluded from consideration. The technique of catching, marking and releasing is only suitable for adults because during moulting the nymphs lose their external markings. The beating of strips of vegetation is only applicable in identical types of vegetation and strips of appreciable size (BALOGH, 1958). The yield is also highly dependent on weather conditions and the moistness of the vegetation.

Taking into account the nature of the insects and the vulnerability of the nymphs, a technique was developed for this investigation that served quite satisfactorily under the given conditions, although it was somewhat laborious. The requirements set for this sampling technique are summarized in the following six points:

(1) All adult insects and nymphs must be caught without injury and later released;

(2) During sampling no immigration or emigration may take place in the quadrat;

(3) The vegetation must be disturbed as little as possible during the sampling;

(4) The apparatus used for sampling must be easy to manipulate;

(5) The sampling must not require too much time;

(6) Sampling must be feasible over long periods without loss of accuracy.

These considerations led to the construction of the "box", an apparatus consisting of four wooden frames, each 75 cm high and 175 cm long, on which gauze is stretched. The surface to be covered in this way is about three sq.m.

The grasshoppers were caught in a glass tube, identified, and held away from sunlight. After all animals were caught, the insects were released within the sampled area. This technique consumed the most time during the spring, when the vegetation is populated with large numbers of nymphs. Under such conditions the sampling of the 50 quadrats sometimes took as much as three days. Later in the season they were worked in a day and a half.

The box is difficult for one person to operate alone. Collection of data was consistently done by two persons, one of whom found the insects while the other checked the sides of the box and recorded the data. Working together, the two could move the box to a new site quickly and easily. Since the terrain chosen for the investigation lies around the Biological Station, no difficulties were encountered with the transportation of the box.

The box was placed over permanent quadrats. Inside it a small crate from which the grasshoppers could be hunted, was placed over the vegetation. By moving the crate the vegetation could be searched from various spots. Only the edges of the crate pressed against the vegetation, keeping damage at a minimum. The vegetation was searched thoroughly, which, especially in the thick grass cover, took a great deal of time.

During the early summer when the field population was mainly nymphs, sampling was done every week when possible, the period later being lengthened to 14 days. The times of day and weather conditions suitable for sampling are important. This work cannot be done at all times and under all conditions. When the vegetation is wet (e.g., in the early hours of the morning in the dense grass vegetations and after rain) and the small nymphs are disturbed, they come into contact with the droplets of water; observations have shown that many of them do not survive this contact. All sampling was therefore done in quiet, dry weather in dry vegetation, usually between 11:00 p.m. and 5:00 a.m. When the wind increased in velocity during sampling, the box was anchored with guy-ropes.

During the three years in which the study was carried out, 50 permanent quadrats each measuring three square metres were sampled with the box, 17 times in 1953 and 1954, and four times in 1955. In addition, in 1955 another 23 quadrats were chosen and sampled 17 times in order to increase the number of observations at specific places.

In 1954, a small box measuring one sq.m and 20 cm in height was used to sample 55 quadrats in the period during which the first instar occurred in the field, in order to provide more information concerning their hatching sites.

The systematic sampling of the quadrats was accompanied by a daily visit to the field for observations concerning the occurrence of the three species outside the quadrats. The collection of grasshoppers for laboratory examination was not done on the terrain of investigation, but elsewhere in the dry grasslands of the landward dunes.

PERIODICITY AND PHENOLOGICAL DATA

This chapter treats the periodicity associated with the grasshopper and, where possible, its relationship with a number of climatic factors.

In winter, no active stages of the three species are seen in the field. Only the eggs survive the winter. During April and May, large numbers of the first instar appear. Within a month and a half the nymphs develop into adults, and the latter populate the field during the summer and part of the autumn. In this period, the eggs are laid.

Although it was not always possible to determine the time of the appearance and disappearance of each instar with equal exactness, the field observations give an adequate picture of the occurrence of these stages in the course of the year. The adults were recorded according to sex.

A daily search for the first nymphs was made from 1 April on, in order to determine the commencement of the activities in the field. The date on which the first instar of *M. maculatus* appeared could be determined exactly because this was the first species to be observed in the field. The first nymphs of the three species appeared in 1953—1955 in the last ten days of April and the first ten days of May (Table 3).

Table 3. Occurrence of the first nymphs of *M. maculatus, C. biguttulus,* and *C. albomarginatus* in the field in 1953—1955.

	1953	1954	1955
M. maculatus	23 April	21 April	23 April
C. biguttulus	5 May	6 May	29 April
C. albomarginatus	8 May	6 May	8 May

Wide variations in the appearance of the nymphs do not occur in the successive years in spite of the differences in weather conditions in the periods preceding hatching. The monthly reports on general weather conditions issued by the K.N.M.I. (Royal Netherlands Meteorological Institute) at De Bilt give the following data: in 1953, January and February were rather cold and clouded winter months; March and April followed with dry weather and a more or less normal temperature curve. In 1954, the first two months of the year were again cold, but March was warmer than normal and April sunny, dry but rather cold. In 1955, January, February, and March were cold, April was dry with normal temperatures; March and April were rather sunny. Two factors predominate in these reports: temperature and sunshine.

According to RICHARDS & WALOFF (1954), the hatching of the eggs in the field depends upon the air temperature in the spring months. The average temperature of the month in which the first eggs hatch is ordinarily 10° C or higher (8.3° C in 1950). In the cold spring of 1951 the average temperature in April and May was 6.7° C and 9.4° C respectively. In that year in Silwood Park, Berkshire (England) the first nymphs of five species (including *M. maculatus*) under study did not appear until the first weeks of June, six weeks later than in 1948 and 1949.

No air temperatures are known for Voorne in 1953—1955. The nearest meteorological station is in Hoek van Holland, which did not publish continuous observations. Although the station in Vlissingen is far away from Voorne, the average temperatures recorded there do not vary greatly from those on Voorne (STOUTJESDIJK, oral communication). In addition, the island lies in a climatological area with mild summers and very mild winters, to which Vlissingen also belongs (MÖRZER BRUIJNS & WESTHOFF, 1951).

If a comparison is made with the values measured in 1954 at the Vlissingen station, then the eggs of *M. maculatus* and *C. biguttulus* hatch in the field at an

Table 4. The average air temperature in March and April, and the first ten days of May and the time at which the nymphs appeared.

	March	April	1—10 May
1953	4,8° C	8,6° C *M. maculatus*	9,7° C *C. biguttulus* *C. albomarginatus*
1954	6,1° C	6,7° C *M. maculatus*	11,1° C *C. biguttulus* *C. albomarginatus*
1955	2,5° C	7,7° C *M. maculatus* *C. biguttulus*	11,5° C *C. albomarginatus*

average air temperature of 6.5° C and those of *C. albomarginatus* at ± 10° C or higher (Table 4).

After a very cold March in 1955, the average month's temperature of April reached a normal value and the grasshoppers appeared on dates which do not differ greatly from those of the preceding years. Low air temperature apparently has no influence, in the direct sense, on the rate of the eggs' development. The amount of sunshine and the amount of radiation heat dependent on it are more important because they determine the course of the temperatures in the surface layer of the soil. The radiation heat was not locally measured, but it may be assumed from the above-normal amount of sunshine in March, 1955 (46%, as against 33% and 24% in 1953 and 1954, respectively) that the eggs received so much heat that their development was not retarded in this cold month.

The first instar nymphs are seen in the field during a period which is longer than the time required by the instar for its development. In 1955 this period was 79 days for *M. maculatus,* 73 days for *C. biguttulus,* and 51 days for *C. albomarginatus.* If the minimum developmental time of the first instar is considered to be ten days, then nymphs must have hatched from the eggs during periods of 69, 63, and 41 days for the respective species.

Table 5. The numbers of the first instar of *M. maculatus* observed in various types of vegetation on 8, 8, and 4 sq.m in 1954 (see also Table 11).

Type	I	II and III	IV
21.IV	2	0	0
23.IV	10	1	0
25.IV	46	0	0
27.IV	109	20	0
29.IV	148	32	0
1.V	326	83	6
3.V	102	108	15
5.V	150	85	9
	8x1 sq.m	8x1 sq.m	4x1 sq.m

In this connection the place where the egg is laid is unquestionably of importance. For its development, the egg requires a given amount of heat which can be expressed in "day degrees" (e.g., ALLEE et al., 1950). One "day degree" is realized if the average temperature during 1 day rises 1 degree above the developmental zero point. This quantity will be realized more slowly in places where the soil is covered than where the soil can profit maximally from solar radiation. For the investigation into the hatching sites (1954), the hatching of larvae of *M. maculatus* was observed from 21 April on (Table 5) in the very thin vegetations in which part of the soil was not covered with moss or herbs. In vegetation of types II and III, in which the moss cover extended over the entire surface, the hatching began between 25 and 27 April, while in type IV, a vegetation with a carpetting layer above the moss cover, the first newly-hatched larvae were seen about 1 May.

RICHARDS & WALOFF (1954) report similar findings. They indicate still another factor influencing hatching time, namely the date on which the egg was laid. Observations in *C. parallelus* and *C. brunneus* point in this direction.

Unfortunately, the results of the winter survival of egg pods collected by me on various dates are so unfavourable that no conclusions can be drawn from them.

When large numbers of nymphs of all instars populate the field later in the early summer, a newly-hatched larva is rarely found. On 4 June, 1954, for instance, on 150 sq.m 27 first instar nymphs were found, and on 23 June only one; on 22 June, 1955, on 69 sq.m 25 nymphs and on 11 July only three. This indicates that during the last twenty days on which first instar nymphs occur in the field, the numbers are very small, and thus that most of the nymphs have hatched in a period of a month after the appearance of the first.

In 1953 and 1954, first instar nymphs of *M. maculatus* and *C. biguttulus* were again seen in the field later in the season, appearing about a month after the first group had disappeared. In 1955 a third instar nymph of *M. maculatus* was found on 6 September after the first group had disappeared by the end of July. For *C. albomarginatus* a newly-hatched larva was seen only once, on 4 August, 1953, half a month after the disappearance of this stage. Certainly these animals are of a second generation of that year.

We were not succesful in raising a second generation within one season in the laboratory. Egg pods collected in the summer months and held at room temperature in damp sand did not hatch in the autumn or later. If they were collected from the field after the winter, for instance in February, they hatched in large numbers. RICHARDS & WALOFF (1954) report the same experience. Eggs of three species of grasshoppers studied by them continued to develop for a while after laying and then entered the diapause. Towards the end of November, if the eggs were brought into damp filter paper at a temperature of 25° C larvae hatched after some time. Eggs of *C. brunneus* laid at the end of August and transferred immediately to a temperature of 25° C failed to hatch. These authors were able, however, to raise generations of grasshoppers throughout the year by giving eggs a cold treatment in which temperature and duration of treatment were important.

Many insects in diapause die without development or grow in an irregular manner when they are brought into temperatures which might be expected to promote

Table 6. The duration of development of the nymphal stages and the date on which the adults disappeared from the field, determined for *M. maculatus, C. biguttulus,* and *C. albomarginatus.*

	Year	Period	Duration	Last observed
M. maculatus	1953	23.IV—30.V	38 days	27.X
	1954	21.IV— 3.VI	44 ,,	27.X
	1955	23.IV—20.VI	75 ,,	1.XI
C. biguttulus	1953	5.V — 1.VII	58 ,,	1.XI
	1954	6.V —29.VI	55 ,,	1.XI
	1955	29.IV—11.VII	74 ,,	1.XI
C. albomarginatus	1953	8.V —20.VI	42 ,,	16.X
	1954	6.V —14.VI	40 ,,	15.X
	1955	8.V — 5.VII	59 ,,	20.X

development (LEES, 1955). The diapause is apparently interrupted when the grasshoppers are exposed to a low temperature for some time. In this connection it is not clear, in the absence of further investigation, how the occurrence of a second generation in the field in the summer is to be explained.

The succession of the nymph stages occurs rapidly. The dates on which the first and the last nymphs of each stage are found in the field were not definitely determined, but since the date on which the first adults appear could be determined exactly, the total duration of the development of the nymphs can be calculated (Table 6).

Table 7. The numbers of males and females found on various dates in 1954 on 150 sq.m.

	M. maculatus		*C. biguttulus*		*C. albomarginatus*	
	♂	♀	♂	♀	♂	♀
25.V	0	0	0	0	0	0
4.VI	28	5	0	0	0	0
14.VI	66	25	0	0	4	0
23.VI	98	47	0	0	7	0
29.VI	107	49	1	0	18	2
9.VII	111	61	0	0	54	11
20.VII	116	107	1	0	97	38
29.VII	93	89	3	3	48	39
6.VIII	51	75	11	4	35	31
14.VIII	30	53	10	7	26	30
28.VIII	23	41	16	16	18	24
7.IX	21	34	11	23	7	15
28.IX	4	5	9	9	1	3
12.X	3	4	2	6	1	2

The duration of development of the nymph stages of these three species was appreciably longer in 1955 than in the two preceding years. The month of May, 1955, was cold and wet, June was on the cold side with a normal amount of sunshine. Apparently in May, 1955, the insects had too little opportuntiy to sun themselves.

As soon as the adults appeared in the field a distinction was made between the sexes. Table 7 gives the numbers of males and females found in the series sampling on 150 sq.m.

The males of all three species were found in the field earlier than the females. Initially, the numbers of males were higher, but in the month of July for *M. maculatus,* and in August for the other two species, they were overtaken by the females.

Thereafter, towards the end of the season, more females than males were found. The numerical variations and the moment at which the largest numbers were found show distinct differences. The males and the females appear in the field at somewhat different periods, the nymph stage of the females apparently having a longer period of development than the males. It is unlikely that the eggs with male insects hatch earlier than the eggs with females.

RICHARDS & WALOFF (1954) found for *C. brunneus* nymphs a sex ratio of 1 : 1, and a surplus of males among the adults. For *C. parallelus* and *Stenobothrus lineatus,* however, they found more females among the nymphs and more males among the adults. Although their figures for *M. maculatus* are rather small compared with those for the other species, there appear to be more males in the first stage, equal numbers in the second, and a surplus of females in the other stages.

Although I collected no data on the sex-ratio of the nymphs, it appears that if the sex is determined per sample for the adults, the ratio during the season is first in favour of the males, and later in favour of the females. *C. biguttulus* shows the most irregular fluctuations, probably as a result of the high activity of this species in the terrain under study and its preference for the borders and the low shrub which could not be included in the sampling. It is for this reason that the numbers on the sampled surface are consistently small.

The adults remain in the field until late in the autumn. After September the numbers decrease rapidly and the insects disappear entirely towards the end of October and beginning of November when the effect of the night frost becomes noticeable throughout the field (Table 6). In 1953 and 1954, *C. albomarginatus* disappeared half a month earlier than the other two species. In 1955, this species was not observed in the dense vegetation after 10 October and in the other vegetations after 20 October. Especially in vegetation of type IV, the microclimate in the autumn is appreciably less favourable for the grasshopper, which requires warmth, than in the less dense growth because in the former on clear nights the night temperatures fall below zero very early in the season.

THE NUMBERS OF GRASSHOPPERS

The sampling of a large number of quadrats at various times during the season provided information concerning the numbers of insects present in the quadrats. It was not intended to use these figures for population studies and for drawing conclusions about such factors as the birth-rate and mortality of the total population in the area under study. Inventories made at regular intervals were intended to provide information about the composition and the numbers of the grasshopper population in a given type of vegetation.

The collected data formed a picture of the following points:

(a) the numbers of insects observed in this terrain in the three years of the investigation;

(b) the way in which the numbers of the nymphs and adults vary in the course of the season; this point is of particular importance for evaluating whether or not the field sampling was adequate;

(c) the composition of the population at various times in the season.

In 1953, 1954, and 1955, from the beginning of the hatching of the nymphs in the field until the disappearance of the insects at the end of October, samples were taken 17 times on suitable days. In the respective years, 150, 150, and 69 sq.m of the field were inventoried. Tables 8, 9, and 10 give, for each date of sampling, the numbers of nymphs of the various stages and of the adults for these three years.

The highest density of the three species was observed early in the season, namely at the end of May or beginning of June, the period in which nymphs are mainly seen. *M. maculatus* was the most numerous species. At the time of peak density, on quadrats of types I—V in which this species was found predominantly, we found 12.3 insects per sq.m sampled in 1954 and 13.8 insects in 1955. The next most frequent species was *C. albomarginatus,* on type III—VI quadrats giving 5.0 insects per sq.m in 1954 and 3.8 in 1955. The least frequent species was *C. biguttulus* in types I—VI, with 1.4 in 1954 and 0.8 in 1955.

Table 8. Numbers of nymphs and adults (a) on the 50 quadrats sampled in 1953.*

	M. maculatus					*C. biguttulus*					*C. albomarginatus*				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
22.VI	1	85	109	123	42	18	38	12	6	—	48	62	102	30	3
4.VII	—	15	117	98	91	23	43	17	5	1	11	27	72	89	19
11.VII	—	2	32	73	72	7	23	26	12	2	—	12	39	68	59
16.VII	—	2	18	65	95	1	19	21	18	2	1	5	16	40	75
28.VII	—	—	2	13	113	1	4	10	20	11	—	—	6	13	87
4.VIII	3	1	—	3	108	—	—	2	13	21	1	—	1	6	98
11.VIII	6	2	4	—	102	—	—	—	6	29	—	—	—	1	66
18.VIII	—	3	7	4	84	—	—	—	—	39	—	—	—	—	73
26.VIII	—	—	3	3	79	—	—	—	—	46	—	—	—	—	50
1.IX	—	1	1	4	60	—	—	—	—	29	—	—	—	—	34
8.IX	—	—	—	1	58	—	—	—	—	33	—	—	—	—	32
15.IX	—	1	—	1	45	—	—	—	—	18	—	—	—	—	22
24.IX	—	—	—	—	39	—	—	—	—	23	—	—	—	—	18
2.X	—	—	—	—	32	—	—	—	—	23	—	—	—	—	6
7.X	—	—	—	—	16	—	—	—	—	1	—	—	—	—	1
16.X	—	—	—	—	6	—	—	—	—	—	—	—	—	—	—
27.X	—	—	—	—	2	—	—	—	—	3	—	—	—	—	—

* In this and the following tables containing data pertaining to the sampling of the quadrats, the date indicates the time at which sampling was begun (see p. 378).

Table 9. Numbers of nymphs and adults (a) on the 50 quadrats sampled in 1954.

	M. maculatus					*C. biguttulus*					*C. albomarginatus*				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
24.IV	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.V	501	16	—	—	—	1	—	—	—	—	4	—	—	—	—
25.V	311	646	281	57	—	88	11	—	—	—	360	183	6	—	—
4.VI	27	398	476	253	33	159	54	4	—	—	121	382	41	1	—
14.VI	2	162	240	305	91	107	87	11	2	—	23	153	150	57	4
23.VI	1	53	166	229	145	36	120	25	4	—	3	72	155	90	7
29.VI	—	14	111	138	156	14	60	32	1	1	—	37	109	119	20
9.VII	—	3	31	93	172	12	40	51	13	—	—	14	58	112	65
20.VII	—	—	7	66	223	7	13	33	35	1	—	—	11	95	135
29.VII	5	2	3	22	182	1	6	15	15	6	—	—	2	32	87
6.VIII	8	3	1	3	126	—	1	9	20	15	—	—	2	5	66
14.VIII	9	3	—	—	83	—	—	5	9	17	—	—	—	3	56
28.VIII	3	11	—	—	64	—	2	—	5	32	—	—	—	1	42
7.IX	—	4	9	2	55	—	2	—	—	34	—	—	—	—	22
28.IX	—	—	—	1	9	—	—	—	1	18	—	—	—	—	4
12.X	—	—	—	1	7	—	—	1	—	8	—	—	—	—	3

In the period in which the adults populate the field, numbers have become small and density shows strong local variation. The largest number of adults of *M. maculatus* found on one sq.m is 8.0, of *C. albomarginatus* 28.6, both in 1954. The latter number was found on 20 July, 1954 in Quadrat 6 in a high, dense vegetation of *Calamagrostis epigejos.*

RICHARDS & WALOFF (1954) noted, concerning *C. albomarginatus,* that the largest number of adults found by them in England was only 2.0 to 2.2 insects

Table 10. Numbers of nymphs and adults (a) on the 23 quadrats sampled in 1955.

	M. maculatus					*C. biguttulus*					*C. albomarginatus*				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
25.IV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
29.IV	69	3	—	—	—	1	—	—	—	—	—	—	—	—	—
8.V	402	26	1	—	—	5	—	—	—	—	4	—	—	—	—
20.V	566	122	10	—	—	17	—	—	—	—	45	1	—	—	—
30.V	533	187	32	3	—	22	—	—	—	—	115	16	—	—	—
6.VI	152	232	106	17	—	38	9	—	—	—	55	111	5	—	—
16.VI	86	187	129	58	—	42	12	—	—	—	28	113	13	—	—
23.VI	26	169	143	101	9	22	23	3	1	—	4	77	30	—	—
27.VI	3	75	110	108	26	12	20	7	1	—	1	38	33	14	—
5.VII	2	50	83	81	57	13	38	9	3	—	—	7	26	33	1
11.VII	3	18	61	69	74	5	27	12	3	2	—	—	24	61	16
25.VII	—	—	8	28	70	—	8	6	18	2	—	—	2	16	50
11.VIII	—	—	—	1	58	—	—	1	9	14	—	—	—	—	44
23.VIII	—	—	—	2	34	—	—	—	3	16	—	—	—	—	28
6.IX	—	—	1	—	50	—	—	—	—	25	—	—	—	—	17
3.X	—	—	—	—	28	—	—	—	—	20	—	—	—	—	9
20.X	—	—	—	—	9	—	—	—	—	14	—	—	—	—	1

per sq.m in the favourable year of 1949. In West Siberia, where this species sometimes occurs in such large numbers that the term plague is used, RUBTZOV (as cited by RICHARDS & WALOFF, 1954) reports numbers in the range of 100 to 150 per sq.m.

In the course of the season the numbers of insects gradually decrease. Characteristically, the curves representing the increase and decrease in the numbers of the various stages of the insects are smooth. There are thus no deviating observations suggesting great unreliability in the counts. As the season progresses we also see a series of gradually-occurring peaks, each time lying lower, reflecting the numbers of insects of the successive instars. This is in agreement with expectation, since as a result of mortality each stage would be present in lesser numbers than the preceding one.

The composition of the population on the total surface sampled can be followed easily and offers good comparative material for the study of the data derived from the separate types of vegetation.

THE HATCHING SITES

Introduction

The investigation of the places at which the larvae emerge from the eggs is important because it is from these places that the active stages of the grasshoppers make a choice among the possibilities offered by the vegetation. Information was already available concerning the requirements governing the choice of oviposition substrates by the females of the three species (LENSINK, 1962). This information provides a useful indication of the places in which the initial appearance of the insects can be expected.

The hatching sites were studied in 1954 by means of the quantitative sampling of a large number of quadrats (55 in all) in various types of vegetation which were visited every two or three days, including quadrats on horizontal ground as well at the north and south sides of slopes.

The investigation had to be suspended a month after the appearance of the first instar: by that time there were so many nymphs in the field that sampling became unreliable. As a result of their increased activity, many of the larger nymphs jumped over the edge of the box. The greatest quantity of data was obtained for *M. maculatus,* because *C. biguttulus* and *C. albomarginatus* hatched later. However, numerous observations done apart from the sampling, as well as the data on the distribution of the first instar, were sufficient to provide a good idea of the hatching sites of *C. biguttulus* and *C. albomarginatus.*

The hatching sites of *M. maculatus*

Table 11 gives the numbers of first instar of *M. maculatus* found on various dates on the quadrats sampled, as well as the type to which the vegetation belonged and also exposure, total vegetation coverage in per cents, the proportion of mosses and herbs in these percentages and the height of the vegetation in centimetres.

Table 11. The numbers of the first instar of *M. maculatus* on 55 quadrats measuring

Quadrat	Total coverage in %	Herb layer in %	Moss layer in %	Bare surface in %	Height of vegetation in cm	21.IV	23.IV	25.IV
"NW-NE-slopes" types I, II, and IV								
1	100	80	30	0	10	—	—	—
F	100	60	50	0	5	—	—	—
18	95	40	95	5	5	—	—	—
T	100	25	95	0	10	—	—	—
U	60	40	30	40	5	—	—	—
Y	100	70	50	0	10	—	—	—
BB	100	90	30	0	15	—	—	—
NN	85	40	70	20	5	—	—	—
"SE-SW-slopes" a) type I								
B	50	40	50	40	10	—	1	3
C	60	55	10	40	10	—	2	6
E	90	20	90	10	5	—	—	—
H	40	40	50	40	10	1	—	—
9	50	40	40	60	10	1	2	7
J	70	25	70	30	10	—	1	—
K	60	40	50	40	10	6	16	29
HH	75	30	70	30	10	—	—	—
LL	70	30	50	35	10	1	2	2
b) types II, III, and IV								
A	100	80	30	0	15	—	—	1
G	95	55	60	5	10	—	—	—
L	100	60	50	0	10	—	—	1
P	95	25	95	5	15	1	—	—
V	90	70	30	10	10	—	—	1
GG	100	50	95	0	15	—	—	—
"Flat field" a) type I								
M	95	60	60	10	15	—	—	1
N	25	15	25	75	10	—	—	3
O	30	25	10	75	10	—	—	6
Q	30	25	30	70	5	2	10	32
W	80	60	40	20	20	—	—	2
KK	60	40	20	40	5	—	—	—
JJ	80	70	30	30	5	—	—	1
S	95	50	70	5	5	—	—	1
b) types II, III, and IV								
2	90	75	30	15	20	—	—	—
R	100	85	50	0	10	—	1	—
31	90	80	70	10	10	—	—	—
Z	95	75	60	10	10	—	—	—
CC	90	75	50	10	5	—	—	—
MM	95	70	70	5	5	—	—	—
7	95	50	90	5	10	—	—	—
8	95	50	90	5	10	—	—	—
11	100	50	80	0	10	—	—	1
EE	95	50	50	10	5	—	—	1
FF	100	90	20	10	5	—	—	1

one sq.m, in various types of vegetation, between 21 April and 18 May, 1954.

27.IV	29.IV	1.V	3/4.V	5.V	7.V	10.V	13.V	17/18.V
—	—	—	1	3	1	4	11	1
—	—	—	—	—	—	4	11	5
—	—	2	2	—	5	16	28	5
—	1	—	—	—	2	4	2	2
—	—	1	3	—	1	9	11	1
—	—	—	—	—	2	1	3	1
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	1	14	5
—	14	13	3	8	9	26	8	19
5	6	14	12	11	18	16	14	8
—	—	—	2	4	3	5	25	4
1	4	10	3	6	13	36	33	8
7	11	12	8	10	35	15	19	3
6	4	9	4	9	17	9	10	15
49	49	22	3	7	21	16	8	11
—	3	7	3	1	18	4	17	9
16	6	15	1	2	20	6	11	5
—	—	2	3	3	1	7	9	8
—	—	—	—	2	12	18	16	6
6	4	11	1	8	8	14	13	8
16	20	15	7	12	22	18	12	15
1	3	1	2	5	10	7	11	1
—	—	1	—	5	1	3	12	7
17	21	18	24	24	36	44	32	21
3	32	5	28	28	23	38	17	14
24	34	13	19	19	46	60	59	11
66	80	17	22	22	55	52	37	6
27	117	22	27	27	72	72	65	20
2	24	7	7	7	23	23	12	9
7	13	10	8	8	37	23	15	15
2	5	10	15	15	38	49	28	6
—	1	1	1	3	8	21	9	8
9	13	23	29	26	35	23	5	5
7	9	30	25	19	13	57	38	13
2	3	7	25	11	49	79	129	26
—	1	3	13	8	14	37	49	9
2	3	15	11	16	42	12	22	10
—	2	2	3	—	—	7	12	10
—	—	2	1	2	1	2	31	18
—	3	1	—	—	7	19	20	5
4	5	11	11	2	5	18	13	5
3	1	1	3	2	7	25	65	11

Table 11, continued. The numbers of the first instar of *M. maculatus* on 55 quadrats measuring

Quadrat	Total coverage in %	Herb layer in %	Moss layer in %	Bare surface in %	Height of vegetation in cm	21.IV	23.IV	25.IV
	c) type V							
D	90	75	25	10	15	—	—	—
5	100	100	10	0	15	—	—	—
10	100	85	60	0	15	—	—	—
DD	95	90	20	5	5	—	—	—
38	100	95	40	0	10	—	—	—
	d) type VI							
3	100	100	5	0	15	—	—	—
4	80	80	10	10	40	—	—	—
6	100	100	0	0	30	—	—	—
30	100	100	0	0	15	—	—	—
16	100	100	15	15	10	—	—	—
X	100	100	0	0	15	—	—	—
14	100	100	0	0	15	—	—	—
AA	100	100	5	5	10	—	—	—

The following may be derived from the data in this table.

The first nymphs of *M. maculatus* are found most densely in the areas indicated by "SE-SW-slopes" and "Flat field". In these areas, the quadrats with type I vegetation yielded large numbers. Those with vegetations of types II—IV gave lower hatching figures. In the "Flat field" types I—VII are also found. The numbers of nymphs in type V are small. In type VI the figure was zero or very nearly so. Type VII could not be systematically sampled with the box.

The first nymphs appear much later on the quadrats on the "NW-NE-slopes", in 1954 as much as ten days after the first nymphs had hatched.

In terms of the rate at which the number increased, it can be seen that for the twelve samplings made between 21 April and 17—18 May in 1954 there was a rapid increase in the population of the "SE-SW-slopes" type I quadrats. Except for lower initial rates, the "Flat field" type I quadrats show almost the same picture. For types II—IV, the rate of increase is slower. The slowest rate is found in the "Flat field" types II—IV.

The amount of heat originating from sunlight is of course an obvious factor to consider in relation to these phenomena. In this connection the figures for the "NW-NE-slopes" become meaningful: the first nymphs appear on such slopes after all the other quadrats are populated. The importance of solar radiation for the rate of development of the eggs has already been discussed. In places with a well-developed surface cover, the eggs receive less heat than in uncovered sandy spots. In addition, in the spring appreciably less solar radiation reaches the north slopes than the south slopes (STOUTJESDIJK, 1959), which explains the retardation in the development of the eggs laid on the former. Although the field on the north slopes lends itself well for oviposition, I have never been able to find newly-hatched larvae on them, and this also holds for the skins of the moulting vermiform larvae which precede the first instar. This raises the question of whether we one sq.m, in various types of vegetation, between 21 April and 18 May, 1954.

27.IV	29.IV	1.V	3/4.V	5.V	7.V	10.V	13.V	17/18.V
—	—	2	12	5	11	20	1	4
—	—	—	—	—	—	1	—	2
—	—	4	3	4	1	15	11	4
—	—	—	—	—	—	1	5	3
—	—	—	—	—	2	1	1	1
—	—	—	—	1	—	1	1	4
—	—	—	—	—	—	—	—	—
—	—	—	1	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	1	—	—	—	—	—	—

have to do here with migration from other localities. Several factors may be involved. The insects may have left their hatching sites of their own volition, some of them settling on the north slopes. Such migration would initially be small, because the young are small and not very active. Migration could be promoted by the passage of large animals and of people through the hatching areas; this can be seen to cause the insects to jump away in all directions. The wind may give direction to these movements, as can be observed when walking through vegetation when the wind is blowing hard: the jumping grasshoppers are swept in one direction by the wind. Before the first instar was found on the north slopes, a moderate to strong west to south wind blew from 1 May, 1954 on, so that the nymphs which hatched on the south slopes could have been blown into the north slopes.

If we now return to the absolute figures given in the table for the various sectors, we note large differences. In some places large numbers of nymphs are found, in others very few. In a part of the field with sites suitable for oviposition, few or no young nymphs were found, and in the summer months few adults were seen in the same places. The oviposition substrate is evidently only one of the factors to play a role in distribution.

In most places, the observations made in 1953 and 1955 agreed with those made in 1954. In 1955, however, there were local modifications in the vegetation. In the cold, damp spring of 1955, such grasses as *Helictotrichon pubescens* reached their full growth very early and the structure of the vegetation in which they occurred, showed marked changes earlier in the season than would normally be expected. In the autumn of 1954, many eggs were found in the soil of a part of the terrain with a thin vegetation (type IV), but in 1955 the same locality showed a much denser vegetation at hatching time because of the rapid growth of these grasses. Nevertheless, large numbers of nymphs hatched in this moderately dense growth (type V). In agreement with expectation, almost no eggs were laid in this part of the vegetation in the summer of 1955. It follows from this observation that such deviations from the normal can only be explained when the situation in the vegetation during the period of oviposition is known.

Lastly, it can be seen from the table that on 3—4 May the numbers of nymphs, particularly on the very thinly covered plots, were markedly reduced. On 3 May there was a severe hail storm, just after sampling was begun, the entire field being strewn with hailstones. Sampling was resumed after the vegetation had dried, and was continued on 4 May. The numbers of insects found on the very thinly-covered quadrats were appreciably smaller than those on 1 May (Table 5). The hail took a great toll of the first instar nymphs. In the denser vegetation little or no effect was seen, the nymphs having been much better protected. On 5 May, many newly-hatched larvae were again found on the very thinly-covered spots. Other investigators, including UVAROV (1928), CHOPARD (1938) and RICHARDS & WALOFF (1957) have observed the phenomenon of a sudden increase in hatching after rain. I have observed this phenomenon, apart from this case of a hail storm, once after rainfall.

The hatching sites of *C. biguttulus*

Because sampling of the hatching sites had to be limited, for practical reasons, to a period of a month, few data could be collected for *C. biguttulus,* the species which hatches the latest. The nymphs of this species did not appear until 6 May in 1954, 15 days after the sampling had begun.

Simultaneously with the investigation of the hatching sites, the large-scale series sampling of the three sq.m quadrats was begun. Although the series sampling was done at long intervals in the hatching period, it nevertheless provided sufficient data to create an impression of the places where the first instar appears in the field. Table 12 gives the numbers of first instar nymphs of *C. biguttulus* found on 46 quadrats measuring three sq.m, classified according to the six types of vegetation, from 24 April to 4 June, 1954. Table 13 gives the results of the 1955 sampling of 23 quadrats measuring three sq.m, from 25 April to 16 June. Where possible, the table for 1954 is supplemented with data from the sampling of the hatching sites.

In no case do the numbers reach the high values found for *M. maculatus.* Just as for *M. maculatus,* the date of first appearance in vegetations with incomplete soil coverage (type I) falls earlier than in vegetation with a complete moss cover and a well-developed herb layer (types II—V). This can be seen very clearly in the table for 1955. In the absence of part of the sampling on 14 May, 1954, Table 12 gives only a slight indication in this direction.

The places where the most first instar nymphs of *C. biguttulus* were found, according to Tables 12 and 13, have vegetations belonging to types I—V, especially in the very thin grass cover, but also in dense, herb-rich grass vegetation. The numbers of nymphs found in the dense, high grass cover (type VI) are very small. If we assume that the nymphs of this species could migrate only very short distances during the periods indicated in the tables, these samples of the first instar give a good picture of the hatching sites. To make this picture as complete as possible,

Table 12. The numbers of the first instar of *C. biguttulus* on various quadrats measuring three sq.m in six types of vegetation from 24 April to 4 June, 1954.

	Quadrat	24.IV	6.V	14.V	25.V	4.VI
Type I	2	—	1	11	9	7
	9	—	—	1	3	1
	11	—	—	16	5	16
	19	—	—	—	1	1
	20	—	—	—	—	1
	29	—	—	•	5	12
	31	—	—	15	8	22
Type II	7	—	—	10	2	1
	8	—	—	—	—	1
	18	—	—	—	1	3
Type III	34	—	—	•	11	5
	39	—	—	•	—	2
	47	—	—	•	—	5
	48	—	—	•	—	2
	50	—	—	•	—	12
	44	—	—	•	7	7
	46	—	—	•	1	—
	13	—	—	—	3	—
Type IV	5	—	—	—	—	1
	10	—	—	5	3	21
	21	—	—	—	8	4
	22	—	—	—	1	7
	23	—	—	•	1	—
	25	—	—	•	—	1
	26	—	—	•	—	—
	27	—	—	•	—	1
	38	—	1	•	2	4
Type V	3	—	—	—	5	2
	4	—	—	1	3	6
	16	—	—	—	1	3
	17	—	—	—	—	—
	24	—	—	•	—	—
	32	—	—	•	—	—
	33	—	—	•	—	1
	30	—	—	•	5	12
Type VI	6	—	—	—	—	—
	14	—	—	—	—	—
	15	—	—	—	1	—
	28	—	—	•	—	—
	35	—	—	•	—	—
	37	—	—	•	1	1
	40	—	—	•	—	—
	42	—	—	•	—	1
	43	—	—	•	—	—
	45	—	—	•	—	—
	49	—	—	•	4	—

• not sampled
— no larvae

Table 13. The numbers of the first instar of *C. biguttulus* on various quadrats measuring three sq.m in five types of vegetation from 25 April to 16 June, 1955.

	Quadrat	25.IV	29.IV	8.V	20.V	30.V	6.VI	16.VI
Type I	2	—	—	—	1	—	1	4
	B	—	1	4	7	1	—	—
	9	—	—	1	—	—	1	—
	11	—	—	—	—	1	1	—
	L	—	—	—	7	6	2	8
	31	—	—	—	—	1	6	6
	C	—	—	—	1	1	4	6
Type II	7	—	—	—	—	—	—	2
Type IV	5	—	—	—	—	—	—	—
	H	—	—	—	—	5	1	—
	J	—	—	—	—	1	—	—
	10	—	—	—	—	2	5	1
	8	—	—	—	1	—	—	1
	A	—	—	—	—	2	1	1
Type V	D	—	—	—	—	—	11	13
	4	—	—	—	—	—	3	—
	N	—	—	—	—	—	3	—
Type VI	3	—	—	—	—	—	2	—
	6	—	—	—	—	—	—	—
	F	—	—	—	—	—	—	—
	G	—	—	—	—	—	—	—
	K	—	—	—	—	2	—	—
	M	—	—	—	—	—	—	—

a study of the oviposition sites was made during the winter. The greatest numbers of eggs were found in bare, sandy soil and in sandy soil with a moss cover. A few egg pods were also found in soils with many roots in small, bare spots in the dense, herb-rich vegetation.

Laboratory experiments concerning the choice of the oviposition substrate are in good agreement with these findings (LENSINK, 1962). The insects were provided with a number of substrates, collected from the field and kept as much intact as possible, representing bare sandy soil, sandy soil with a moss cover, dead grass, and a grass tussock. The eggs were laid in the bare sandy soil and in the sandy soil covered with moss, using the places in the latter exposed by splitting of the moss. Oviposition also appeared possible beside the grass tussock where the soil was well-supplied with roots. No eggs were found in the grass tussock proper. *C. biguttulus* therefore appears to have very ample opportunity for oviposition: its substrate is present throughout the field, only the very dense grass cover being unsuitable.

The absolute numbers of nymphs found on various plots of each type of vegetation show wide variation, however. The position of the quadrat in relation to its surroundings appears to be important. In this sense we find in type I, which shows strikingly few adults during the summer, the largest numbers on Quadrats 2, 11, 29, and 31. With the exception of Quadrat 29, these quadrats lie in the immediate

Table 14. The numbers of the first instar of *C. albomarginatus* on various quadrats measuring three sq.m in six types of vegetation between 24 April and 4 June, 1954.

	Quadrat	24.IV	6.V	14.V	25.V	4.VI
Type I	2	—	—	—	2	—
	9	—	—	—	—	—
	11	—	—	1	1	—
	19	—	—	—	—	—
	20	—	—	1	—	—
	29	—	—	•	2	1
	31	—	—	•	3	1
Type II	7	—	—	—	3	—
	8	—	—	—	—	—
	18	—	—	—	—	—
Type III	34	—	—	•	3	3
	39	—	—	•	15	1
	47	—	—	•	4	1
	48	—	—	•	1	—
	50	—	—	•	1	1
	44	—	—	•	31	—
	46	—	—	•	—	7
	13	—	—	—	—	—
Type IV	5	—	—	15	82	33
	10	—	—	—	3	3
	21	—	—	1	3	—
	22	—	—	—	—	—
	23	—	—	•	1	—
	25	—	—	•	1	—
	26	—	—	•	2	—
	27	—	—	•	—	—
	38	—	—	•	27	7
Type V	3	—	—	15	10	1
	4	—	—	5	—	—
	16	—	—	2	—	—
	17	—	—	—	—	—
	24	—	—	•	5	1
	32	—	—	•	10	7
	33	—	—	•	11	2
	30	—	—	•	2	—
Type VI	6	—	—	29	47	21
	14	—	—	1	1	5
	15	—	—	1	—	—
	28	—	—	—	4	—
	35	—	—	—	2	2
	37	—	—	•	5	4
	40	—	—	•	9	3
	42	—	—	•	8	2
	43	—	—	•	8	4
	45	—	—	•	14	4
	49	—	—	•	18	—

• not sampled
— no larvae

vicinity of type V (dense, herb-rich vegetation) and type VII (*Salix repens* shrub), vegetations in which many adults were seen. The other quadrats of type I are distributed in the field among type II vegetation. This indicates that the combination of environments suitable to the adult insect and a suitable oviposition substrate plays an important role in the distribution of these insects.

The hatching sites of *C. albomarginatus*

For *C. albomarginatus,* too, the hatching site samplings provided little data concerning the places where the first nymphs appear in the field. The nymphs of this species appeared in 1954 on 6 May in the field, i.e., halfway through the period of sampling. As for *C. biguttulus,* the data from the sampling of the three sq.m quadrats in 1954 and 1955 give a rather good impression of the hatching sites. Supplementary data is provided by the otherwise scarce data obtained from the study of the oviposition substrate.

Table 14 gives the numbers of the first instar of *C. albomarginatus* found on 46 quadrats measuring three sq.m, classified according to the six types of vegetation, between 24 April and 4 June, 1954. Table 15 shows the results of the large-scale series sampling in 1955 on 23 quadrats measuring three sq.m, between 25 April and 16 June. The numbers of the first instar found in the field are, with a few exceptions, not very large. With respect to population numbers, *C. albomarginatus* falls between *M. maculatus* and *C. biguttulus.* On only one spot in the field did this species take the leading position, especially in 1953 and 1954. The relevant quadrats were, in 1954 Quadrats 5 and 6, and in 1955 Quadrats 5, H, and J.

The first instar nymphs of *C. albomarginatus* were found, according to both tables, in all the types of vegetation, but the highest numbers were found in the more dense vegetation, in 1954 in types III, IV, V, and especially VI, and in 1955 only in type IV.

The absence of the hatching of nymphs in type VI in 1955 is even more remarkable in relation to the data from the summer of 1954, when large numbers of adults of this species were found in this type of vegetation. In Quadrat 6, for instance, situated in a part of the terrain in which large numbers of *C. albomarginatus* were consistently found, gave on 20 July, 1954 the maximum number of 86 adults insects on three sq.m.

We can be certain that eggs were laid in the summer of 1954 in the dense, high grass vegetations because they were found in a number of places between dead grass blades. It is probable that there was a high mortality among the egg pods in this dense vegetation, possibly caused by a deviation in the normal spring temperatures. In the spring of 1955, the minimum values for the air temperatures were often very low. Especially in the high, dense grass vegetation, temperatures in the latter part of the night may reach very low values, with local frost. Further investigation will be required to determine whether eggs can be damaged by low temperatures in the last stage of their development.

The search for egg pods in the winter months showed that they had been deposited not only in type VI vegetation, but also in the moss layer of types III

Table 15. The numbers of the first instar of *C. albomarginatus* on various quadrats measuring three sq.m in five types of vegetation between 25 April and 16 June, 1955.

	Quadrat	25.IV	29.IV	8.V	20.V	30.V	6.VI	16.VI
Type I	2	—	—	—	5	2	3	1
	B	—	—	—	2	3	—	—
	9	—	—	—	—	5	—	—
	11	—	—	—	3	5	2	—
	L	—	—	—	—	—	—	2
	31	—	—	—	1	1	—	—
	C	—	—	—	—	2	—	—
Type II	7	—	—	—	—	6	3	1
Type IV	5	—	—	—	5	13	13	7
	H	—	—	3	10	37	10	8
	J	—	—	1	17	24	17	7
	10	—	—	—	—	2	2	—
	8	—	—	—	—	2	—	1
	A	—	—	—	—	3	2	—
Type V	D	—	—	—	1	2	—	1
	4	—	—	—	—	—	—	—
	N	—	—	—	—	4	—	—
Type VI	3	—	—	—	—	—	1	—
	6	—	—	—	—	—	—	—
	F	—	—	—	—	—	—	—
	G	—	—	—	—	1	2	—
	K	—	—	—	1	2	—	—
	M	—	—	—	—	1	—	—

and IV in the immediate vicinity of high, dense grass growths in which the adults occur during the summer months.

Experiments concerning the choice of oviposition substrate (LENSINK, 1962) support these data. *C. albomarginatus* was provided with a number of substrates collected as nearly intact as possible from the field. From the substrates provided (bare sandy soil, moss-covered sandy soil, dead grass, and a grass tussock) the females chose not only the tussock and the dead grass but also the moss-covered sandy soil. The eggs were laid against the stalks of the grasses and dead grass leaves and between the moss plants. No eggs were found in or on the bare sandy soil.

C. albomarginatus thus has a great many possibilities for the deposition of eggs in the terrain in which the study was made, since its preferred substrates occur widely. The wide variations in the numbers of nymphs on the various quadrats within the types of vegetation on which the largest numbers occurred indicate, however, that for this species, too, the oviposition substrate is only one of the factors which determine distribution in the field. In 1954 in type III, the largest numbers were recorded for Quadrats 39 and 44, in type IV on 5 and 38, and in 1955 in type IV on 5, H, and J. The largest numbers of the first instar were found on those plots lying closest to the type VI vegetations where the most adults of this species were found during the summer months. These plots lie at a maximum distance of five metres of the edge of the high, dense grass cover. The remaining quadrats in types III and IV lie at a great distance, in various parts of the terrain.

Within type I, too, Quadrats 11 and 31 lie within five metres of the dense, high grass vegetations. The small numbers of nymphs occurring on these very thinly-covered spots indicate the unsuitability of these vegetations for oviposition.

THE DISTRIBUTION OF THE GRASSHOPPERS DURING THE SEASON

The distribution of *M. maculatus*

The investigation into the hatching sites of *M. maculatus* shows that most of the nymphs hatch in particular types of vegetation. During their development the insects spread out over a large part of the terrain. This dispersion was followed by means of a series of 17 samplings taken during the season in 1953, 1954, and 1955 in six types of vegetation. In 1953, after a preparatory period, sampling was not begun until 26 June, when adults were already present in the field. The data from these samplings are therefore not suitable for systematic analysis, but have been used, where relevant, in the discussion of the results of the 1954 and 1955 sampling.

Comparison of the total number of nymphs of each of the four stages with each other and with the adult stage occurring on the quadrats of each type of vegetation, is sufficient to give a general picture of what takes place in the field. Tables 16 and 17 give these figures for the nymphs and the adults in 1954 and 1955.

In Table 16 the columns for the first and second instars have been corrected because a change in weather conditions interrupted the sampling on 14 May. Only 22 of the 46 quadrats could be sampled. The loss of part of the sample, just in a period when the nymphs of the first instar are numerous in the field, meant the loss of a number of data. In order to provide comparable values for the table, an estimate was made of the numbers of nymphs of the first and second instar which could be expected on 14 May on the 46 quadrats. For this use was made of the data collected from the 22 quadrats over the entire season. We then compared the numbers of nymphs of the first and second instar found on 14 May and the numbers of nymphs of the first and second instar found on those 22 quadrats during all samplings. This gave the part taken by the 14 May sampling in the total series. Table 18 gives these figures.

It appears that the numbers of nymphs of the first instar found on 14 May on 22 quadrats in vegetation types I—IV (there were still almost no nymphs present in types V and VI) represent almost half in type I and appreciably more than half in the other types of the numbers observed with the entire sampling. Table 16 gives the estimated data for 14 May, arrived at by taking the total numbers of nymphs of the first and second instar found during the other samplings and multiplying by 2 and 1¼ respectively.

Tables 16 and 17 give the data for a number of quadrats in type I vegetation separately, since in connection with their special position these quadrats show marked differences from the others. For the same reason the data from the three quadrats in type VI are given separately in Table 16.

Table 16. The total numbers of nymphs and adults (a) of *M. maculatus* found on the quadrats of each type of vegetation during the entire season in 1954.

Instar	1	2	3	4	a	No. of quadrats sampled
Type I	430	115	41	33	37	5
Type I	121	146	122	84	155	2
Type II	200	101	26	14	16	3
Type III	400	560	353	228	191	8
Type IV	300	387	330	248	238	9
Type V	21	159	281	332	460	8
Type VI	1	15	26	43	45	8
Type VI	0	14	33	90	97	3
No. of samplings	7	8	9	9	13	

Table 17. Same observations as Table 16, but in 1955.

Instar	1	2	3	4	a	No. of quadrats sampled
Type I	900	328	118	55	67	4
Type I	474	248	188	125	150	3
Type II	44	53	16	6	5	1
Type III	—	—	—	—	—	—
Type IV	332	359	266	158	92	6
Type V	96	80	95	104	91	3
Type VI	0	6	8	10	11	6
No. of samplings	11	10	10	10	10	

The data in these tables, taken together, give an idea of events in the field, but three factors must be kept in mind:

(a) the numbers of quadrats within each type of vegetation are not the same, so that the horizontal columns may not be directly compared (for instance, type II is poorly represented in this sense);

(b) during the presence of each stage in the field the quadrats were not sampled the same number of times, so that direct comparison of the vertical columns is not possible (Tables 16 and 17);

(c) the intervals between two successive samplings are not always the same (Tables 19 and 20).

It is clear that the nymphs and adults populate almost all the various types of vegetation in the terrain. Small numbers are found only for type VI, the high, dense grass cover. Within types I and II, it is striking that the number of nymphs decreases strongly from the first to the fourth instar. In 1954 in type I the figures for the first to the fourth instar averaged 12.3, 2.9, 0.9, and 0.6 nymphs respectively per quadrat per sampling. In 1955 the figures were 20.4, 8.2, 2.6, and 1.4.

This sharp decrease is not found for types III and IV. Here the average num-

Table 18. *M. maculatus,* sampling, 14 March, 1954. See text, p. 398.

Type	I		II		III		IV	
Instar	1	2	1	2	1	2	1	2
22 quadrats, 14.V	128	37	132	20	21	9	121	34
22 quadrats all samplings, 1954	282	209	230	91	27	41	234	222

bers of nymphs per quadrat and per sampling for 1954 is 7, 9, 5, and 3 in type III, and 5.3, 6, 4.6, and 3.4 in type IV; for 1955: 5, 6, 4.4, and 2.6 in type IV.

For the quadrats within type V the average values for 1954 are 0.38, 2.5, 4, and 4.5, and for 1955: 3, 2.7, 3.2, and 3.46 nymphs.

A decrease in numbers is to be expected in all cases as a result of mortality among the insects. Unfavourable conditions in a given environment will increase this mortality. But unfavourable conditions in a given environment may also lead to migration. The character of the first two types of vegetation suggests that in the course of the early summer, climatic conditions are unusually unfavourable for the grasshoppers. The vegetation supplies a distinct indication for this. It is an obvious assumption that migration will occur from places where conditions are becoming less favourable toward more protected vegetation. This assumption is supported by the variations in the values for types III through V. In types III and IV the initial decrease is zero, but it is later smaller than that in the first two types. Type V even shows a distinct initial increase in numbers.

The discussion which follows concerns the course of the development in space and time, within each type on the individual quadrats.

Type I. Vegetation of type I is characterized by the very thin structure of the plant growth. Tables 19 and 20 give the numbers of the various nymph stages and adults (a) found on quadrats belonging to type I in the course of the season in 1954 and 1955, respectively. Many nymphs of the first instar were found on these quadrats and during the first month after hatching this quadrats are the most densely populated. On one quadrat on a south slope with a very thin cover and extreme exposure to wind and rain, however, very few grasshoppers were seen during the entire season.

During the early summer, the numbers of nymphs of the older instars decreased rapidly on the type I quadrats in 1954 (Table 19) and 1955 (Table 20). Starting with the third and fourth instars, the numbers are small compared to those for the first and second instars. Adults are scarce during the summer, but in late summer and autumn the numbers show a relative increase in comparison to the other types. In the latter period the density of the adults has already fallen far below the highest values.

On Quadrats 2 and 11 in 1954 and 1955 the situation took a different course. The numbers of first to fourth instar nymphs did decrease, but to a much smaller extent than in the other quadrats of this type. Nymphs and especially adults were found on Quadrats 2 and 11 throughout the season. If the vegetation of these

Table 19. Numbers of nymphs and adults (a) of *M. maculatus* on quadrats belonging to type I in 1954.

Quadrat	9					31					2					11				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
24.IV	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.V	36	2	—	—	—	68	—	—	—	—	35	2	—	—	—	8	2	—	—	—
14.V	38	5	—	—	—						33	18	3	—	—	26	3	—	—	—
25.V	4	4	—	1	—	11	7	3	1	—	5	40	16	4	—	8	19	4	1	—
4.VI	—	3	3	—	—	6	12	2	2	—	1	20	9	3	—	—	24	19	—	1
14.VI	—	—	—	—	—	—	2	5	1	2	—	10	14	6	2	—	4	14	13	1
23.VI	—	1	—	—	—	—	1	3	4	1	—	—	16	7	9	1	1	7	1	—
29.VI	—	—	1	1	—	—	—	1	1	—	—	—	9	10	6	—	2	1	5	1
9.VII	—	—	—	—	—	—	—	—	—	1	—	—	5	12	5	—	—	3	3	3
20.VII	—	—	—	—	—	—	—	—	1	2	—	—	1	11	25	—	—	1	5	15
29.VII	—	—	1	—	—	1	1	1	—	1	2	—	—	2	11	—	—	—	2	9
6.VIII	2	—	—	1	—	—	—	—	—	—	—	—	—	1	7	1	—	—	—	2
14.VIII	—	—	—	—	—	8	2	—	—	—	—	—	—	—	23	—	—	—	—	1
28.VIII	—	—	—	—	—	1	6	—	—	3	1	1	—	—	13	—	—	—	—	3
7.IX	—	—	—	—	5	—	1	2	—	1	—	—	—	—	13	—	—	—	—	2
28.IX	—	—	—	—	1	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—
12.X	—	—	—	—	3	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—

Table 20. Numbers of nymphs and adults (a) of *M. maculatus* on quadrats belonging to type I in 1955.

Quadrat	B					31					2					11				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
25.IV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
29.IV	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.V	132	4	—	—	—	15	—	—	—	—	30	2	—	—	—	23	3	—	—	—
20.V	108	15	1	—	—	45	1	—	—	—	72	20	2	—	—	46	12	2	—	—
30.V	74	27	5	1	—	34	2	—	—	—	27	21	7	—	—	28	15	1	1	—
6.VI	22	17	4	1	—	24	17	5	1	—	5	26	29	3	—	10	9	5	—	—
16.VI	9	19	7	1	—	11	15	3	1	—	—	6	19	8	—	6	9	7	4	—
23.VI	—	14	9	5	1	5	20	6	—	—	—	11	18	22	3	3	7	7	3	1
27.VI	—	8	10	9	—	2	7	5	3	—	—	5	12	22	7	—	4	5	2	2
5.VII	—	2	7	5	2	1	5	4	2	1	—	6	16	13	15	—	2	1	3	—
11.VII	—	3	2	4	1	—	4	3	1	1	—	—	4	4	15	—	—	3	4	2
25.VII	—	—	4	3	3	—	—	—	1	1	—	—	—	—	14	—	—	—	—	3
11.VIII	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	—	—	—	—	5
23.VIII	—	—	—	—	2	—	—	—	1	2	—	—	—	—	8	—	—	—	—	2
6.IX	—	—	—	—	7	—	—	—	—	3	—	—	—	—	7	—	—	—	—	2
3.X	—	—	—	—	13	—	—	—	—	1	—	—	—	—	1	—	—	—	—	2
20.X	—	—	—	—	3	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—

two quadrats is compared with that of the others, little difference is found, but there is a difference in their location in the field. Quadrats 2 and 11 are located to the south of a four metre high hawthorn hedge (2) and along a shrub of creeping willow (11). The remaining quadrats lie distributed over the terrain, among vegetations of types II, III, and IV. Along the edges of the hedge and the shrub there is a rather well-developed strip of grass in which older nymphs and adults were observed throughout the summer, the vegetation apparently being extremely suitable for habitation.

Regarding the situation in the vegetations of type I, we may state that *M. maculatus* hatches in it in large numbers; that the numbers of nymphs of the later immature stages are low when this vegetation is surrounded by types II, III, and IV but that nymphs and adults can maintain themselves if there is a protective vegetation in the immediate vicinity; and that while the adults are initially scarce they nevertheless occur in larger numbers later in the season.

Type II. The vegetations grouped under type II are distinguished from those of type I by the development of the moss layer. The high herb layer gives slightly more coverage than that of type I. The results of the counts on Quadrat 7 are given in Table 21.

Here, too, as in the type I quadrats, many nymphs are hatched. However, the numbers of specimens of later instars found later in the season are appreciably smaller. Adults were scarce until late in September. On north slopes, on which there are about 150 sq.m of uniform vegetation, very few grasshoppers were observed during the three years of the investigation.

Type III. The vegetations belonging to type III are characterized by a dense moss and lichen layer and grass tussocks in the high herb layer. This type was not sampled in 1955. The results of the counts are given in Table 21.

Nymphs hatched on all quadrats. Hatching was observed on small, bare spots under blades of *Festuca* grass and in places where ants regularly brought sand to the surface. Because a large number of quadrats in this type could not be sampled on 14 May, 1954, little can be said concerning the numbers of the first instar hatched and later present on them. On 13 May, 1954, however, in connection with the study of the hatching sites of *M. maculatus*, three quadrats measuring one sq.m in type III vegetation were sampled (EE, FF, and CC, Table 11). On these quadrats, 13, 65, and 49 first instar nymphs were found, respectively. The quadrats measuring one sq.m were located in the same part of the terrain as Quadrats 46, 47, 48, and 50. These data, taken together with the large numbers of second instar nymphs found on the quadrats, justify the assumption that the numbers of nymphs hatched on the unsampled plots were large.

Nymphs of the third and fourth instar remain in type III vegetation in larger numbers than in types I and II. Adults are found primarily in the summer months. During the sampling of these quadrats in July and August on warm, sunny days, most of the older nymphs and adults were seen in or close to the grass tussocks.

Summarizing, we may state that many nymphs hatch in type III vegetation but also that the sharp decrease in numbers that occurs in types I and II is not seen

Table 21. Numbers of nymphs and adults (a) of *M. maculatus* on quadrats belonging to type II in 1954 and 1955, and to type III in 1954.

Type	III					III					II						II				
Quadrat	39 (1954)					47 (1954)					7 (1954)						7 (1955)				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a		1	2	3	4	a
24.IV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25.IV	—	—	—	—	—
6.V	18	—	—	—	—	3	—	—	—	—	3	—	—	—	—	29.IV	—	—	—	—	—
14.V											57	15	—	—	—	8.V	—	—	—	—	—
25.V	14	51	3	—	—	12	50	11	—	—	38	18	3	—	—	20.V	6	4	1	—	—
4.VI	1	23	27	13	1	—	12	17	3	—	6	11	5	—	—	30.V	25	9	—	—	—
14.VI	—	13	10	13	3	—	5	8	8	1	—	11	5	1	—	6.VI	8	12	3	1	—
23.VI	—	—	6	3	3	—	4	7	9	10	—	1	1	1	—	16.VI	2	11	2	—	—
29.VI	—	—	5	2	4	—	1	3	8	3	—	1	1	—	—	23.VI	3	9	3	2	—
9.VII	—	1	1	3	4	—	1	—	5	5	—	—	1	1	—	27.VI	—	3	5	1	—
20.VII	—	—	—	—	3	—	—	—	1	4	—	—	—	—	—	5.VII	—	—	3	—	1
29.VII	—	—	—	—	2	1	—	—	1	2	—	—	—	—	—	11.VII	—	1	1	—	—
6.VIII	—	—	—	—	5	—	—	—	—	7	—	—	—	—	1	25.VII	—	—	—	2	1
14.VIII	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	11.VIII	—	—	—	—	1
28.VIII	—	—	—	—	—	—	—	—	—	3	—	—	—	—	2	23.VIII	—	—	—	—	—
7.IX	—	1	—	—	5	—	—	—	—	—	—	—	—	—	—	6.IX	—	—	1	—	1
28.IX	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.X	—	—	—	—	1
12.X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	20.X	—	—	—	—	—

Table 22. Numbers of nymphs and adults (a) of *M. maculatus* on quadrats belonging to type IV in 1954 and 1955.

Quadrat	10 (1954)					21 (1954)						H (1955)					10 (1955)				
Instar	1	2	3	4	a	1	2	3	4	a		1	2	3	4	a	1	2	3	4	a
24.IV	—	—	—	—	—	—	—	—	—	—	25.IV	—	—	—	—	—	—	—	—	—	—
6.V	6	—	—	—	—	19	1	—	—	—	29.IV	—	—	—	—	—	—	—	—	—	—
14.V	38	6	—	—	—	41	8	2	—	—	8.V	1	—	—	—	—	2	1	—	—	—
25.V	17	29	4	—	—	25	15	2	1	—	20.V	4	—	1	—	—	12	1	1	—	—
4.VI	—	10	10	—	—	—	8	7	4	1	30.V	9	5	2	—	—	25	4	3	—	—
14.VI	—	5	6	4	1	—	4	5	1	1	6.VI	5	2	7	1	—	7	9	4	2	—
23.VI	—	3	5	7	2	—	2	11	3	1	16.VI	3	15	6	5	—	4	8	4	1	—
29.VI	—	—	3	3	—	—	—	4	2	1	23.VI	2	7	19	6	—	—	8	5	5	—
9.VII	—	—	5	1	2	—	—	2	—	4	27.VI	—	1	7	8	2	—	—	6	3	—
20.VII	—	—	1	4	6	—	—	1	1	8	5.VII	—	—	3	9	6	—	4	5	3	3
29.VII	—	—	—	—	2	—	—	—	1	2	11.VII	—	1	4	2	6	—	—	3	5	2
6.VIII	—	1	—	—	5	3	1	—	—	3	25.VII	—	—	—	4	1	—	—	—	2	2
14.VIII	—	—	—	—	7	—	—	—	—	1	11.VIII	—	—	—	—	2	—	—	—	—	1
28.VIII	1	—	—	—	4	—	2	—	—	9	23.VIII	—	—	—	1	4	—	—	—	—	—
7.IX	—	1	1	—	5	—	1	3	—	6	6.IX	—	—	—	—	—	—	—	—	—	1
28.IX	—	—	—	—	1	—	—	—	—	—	3.X	—	—	—	—	—	—	—	—	—	—
12.X	—	—	—	—	—	—	—	—	—	—	20.X	—	—	—	—	—	—	—	—	—	—

to the same extent in type III. Type III vegetation evidently induces a population of more stable size.

Type IV. The vegetations grouped under type IV possess a moss layer covered by a rosette layer and a dense carpetting layer. The results of the counts in this type of vegetation are given in Table 22.

M. maculatus was consistently observed on all the sampled quadrats during a large part of the season. Nymphs were hatched although not in such high numbers as were reached on types I and II, the typical hatching sites. Older stages remain present in relatively large numbers, while the adults populate the quadrats in varying density.

Type V. The vegetations included in type V are characterized by the large proportion of grasses in the high herb layer. The results of the counts are given in Table 23.

The numbers of nymphs hatched in this type of vegetation are very small, and the first instar is later poorly represented as well. Quadrat D formed an exception in this respect in 1955. In 1954 the situation in this locality was quite different from 1955, which is important for the evaluation.

In the months June and July the quadrats were populated by large numbers of second, third, and fourth instar nymphs and adults. Since repeated observation of these vegetations showed that few or no nymphs hatched, the increase in the numbers of older nymphs and adults must be ascribed to migration from less dense vegetations.

The adults, which are initially numerous in this type of vegetation, either occur rarely or are entirely absent from the middle of August on. This phenomenon was particularly distinct in 1954, in a period in which appreciable numbers of nymphs still populated the field.

The type IV quadrats were chosen in the terrain such that they were located not only in the transitional areas between high, dry parts and lower, damp parts but also in the three to four metre wide strips along the hedges surrounding the terrain. In one part of the terrain along a hawthorn hedge in which Quadrats 3, 4, and D were chosen five, three and one metres respectively from the edge of this vegetation, large numbers of nymphs and adults occurred in the summers of 1953 and 1954. In the summer of 1955, due to the early and vigorous growth of the grasses, the vegetation of this part of the terrain was so changed in structure that a large part of the cover outside the one metre wide borders had to be assigned to type VI. The adults were found in this year almost exclusively in these borders. In 1956 both the vegetation and the *M. maculatus* population in this part of the terrain were comparable to those in 1954.

A similar "border population" was observed outside the terrain of investigation in a type V vegetation occurring in a corner of the landward dunes about 15 metres in width. Older nymphs and adults of *M. maculatus* were found in 1954 in the approximately five metre wide border, although few or no other grasshoppers were found in this vegetation.

Table 23. Numbers of nymphs and adults (a) of *M. maculatus* on quadrats belonging to type V in 1954 and 1955.

Quadrat	3 (1954)					4 (1954)						D (1955)					4 (1955)				
Instar	1	2	3	4	a	1	2	3	4	a		1	2	3	4	a	1	2	3	4	a
24.IV	—	—	—	—	—	—	—	—	—	—	25.IV	—	—	—	—	—	—	—	—	—	—
6.V	1	—	—	—	—	1	—	—	—	—	29.IV	1	—	—	—	—	—	—	—	—	—
14.V	2	6	—	—	—	9	11	—	—	—	8.V	11	2	—	—	—	—	—	—	—	—
25.V	9	24	9	—	—	4	11	17	3	—	20.V	41	11	—	—	—	—	—	—	—	—
4.VI	—	22	31	17	3	1	26	35	21	1	30.V	25	24	3	—	—	—	1	1	—	—
14.VI	—	5	14	22	7	—	2	7	13	3	6.VI	12	12	10	2	—	—	1	1	3	—
23.VI	—	—	5	24	13	—	—	5	6	7	16.VI	3	9	26	10	—	—	—	—	1	—
29.VI	—	2	4	12	27	—	—	2	13	18	23.VI	1	8	10	19	1	—	—	—	2	—
9.VII	—	—	—	8	17	—	—	—	1	12	27.VI	—	1	9	18	6	—	—	1	4	2
20.VII	—	—	1	4	32	—	—	—	4	14	5.VII	—	1	9	14	14	—	—	2	7	1
29.VII	—	—	—	2	14	1	—	—	3	24	11.VII	—	3	6	10	17	—	—	1	1	4
6.VIII	—	—	—	1	18	—	—	—	—	7	25.VII	—	—	—	3	8	—	—	—	1	7
14.VIII	—	—	—	—	9	—	—	—	—	—	11.VIII	—	—	—	—	12	—	—	—	—	3
28.VIII	—	—	—	—	—	—	1	—	—	—	23.VIII	—	—	—	—	4	—	—	—	—	2
7.IX	—	—	—	—	1	—	—	—	—	—	6.IX	—	—	—	—	3	—	—	—	—	—
28.IX	—	—	—	—	—	—	—	—	—	—	3.X	—	—	—	—	—	—	—	—	—	—
12.X	—	—	—	—	—	—	—	—	—	—	20.X	—	—	—	—	—	—	—	—	—	—

Type VI. Type VI vegetation includes the high-growing, dense grass and herb-rich dune meadows. Few or no *M. maculatus* were found in the eight quadrats chosen in this type of vegetation. Three quadrats, however, lay in this vegetation, which became type III with almost no transition.

The situation on these quadrats is comparable to that in type V: no hatching; migration of older instars from outside the quadrats. It was noted for one of the quadrats, located in the eastern corner of the terrain, that after a period with strong west wind more adults were observed in the border zone than elsewhere, a case for which the direct influence of macroclimatological conditions may be assumed to the exclusion of microclimatological influences.

Summary. Summarizing the results of the observations during the period in which *M. maculatus* populated the field, we may state the following:

(a) The greatest numbers of nymphs hatch in vegetation types I and II; in places where the moss layer is only partially developed (type I), unusually high numbers hatch;

(b) Nymphs hatch in types III and IV vegetation, but in smaller numbers than in types I and II;

(c) Nymphs hatch in types V and VI only in very small numbers;

(d) In types I and II the numbers of nymphs drop rapidly a month after hatching; few nymphs of the third and fourth instar occur; adults are scarce, although there is reason to assume that they are relatively more numerous later in the season;

(e) In types III and IV the numbers of nymphs decrease during the early summer, but at an appreciably slower rate than in the types I and II;

(f) During the first month after the beginning of hatching, nymphs of the second and older instars enter type V vegetation, and this also occurs in the borders of vegetations of type VI;

(g) Later in the season, in about the middle of August, no adults are observed in vegetation of type V and in the borders of type VI.

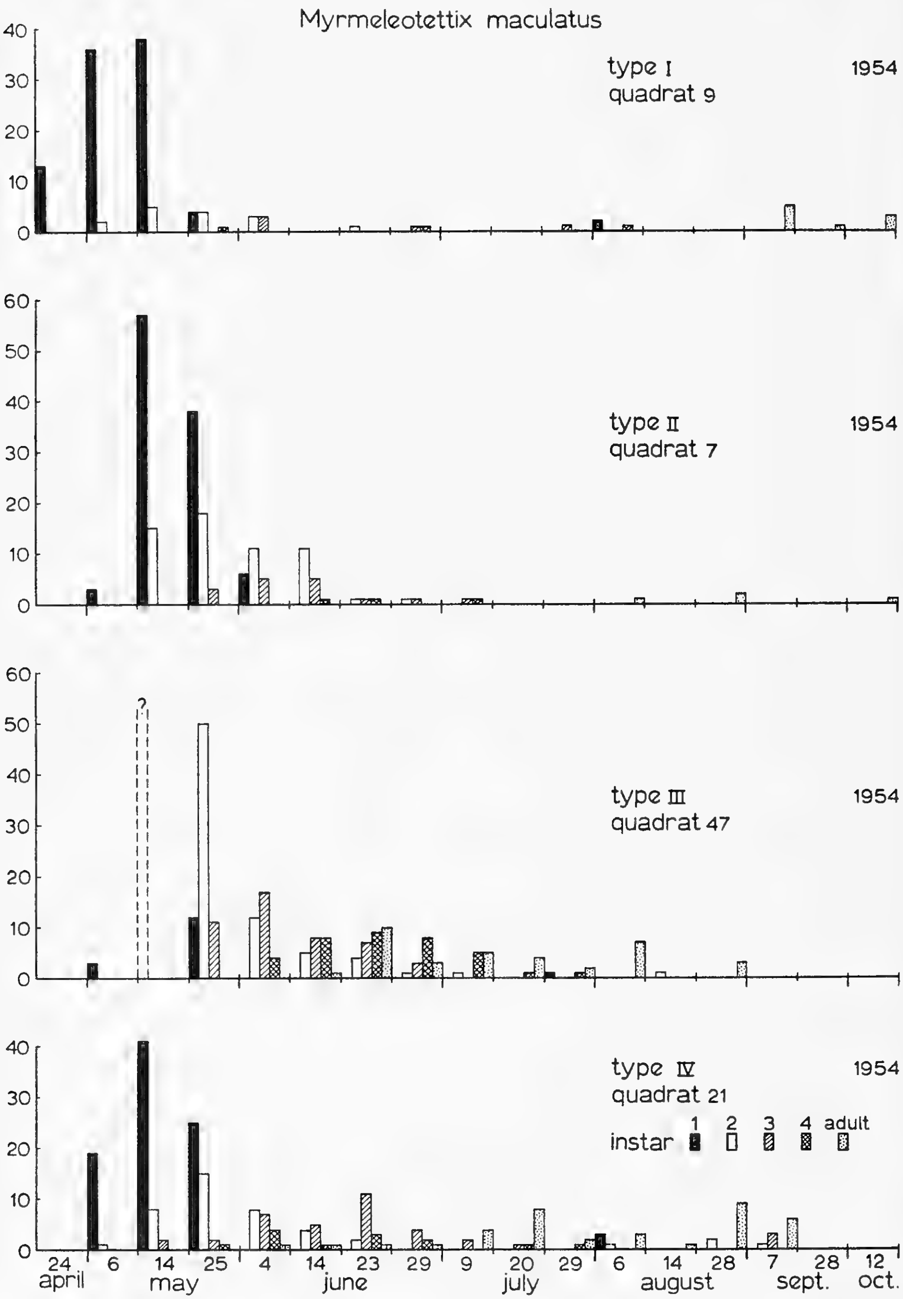
Results. The study of the occurrence of *M. maculatus* has shown that the occurrence of grasshoppers cannot be determined by means of one or more incidental observations. We have seen that in the course of the season in which this species populates the field, the places in which the most nymphs hatch become empty, while older nymphs appear in the dense, herb-rich vegetations. Migration thus occurs in the course of the season from less dense to denser vegetations, evidence of a shift in the choice of the habitat.

The results of this migration from types I and II to types III and IV is hardly or not at all noticeable in large parts of the field because the surface of the terrain covered by type I and II vegetation is very small in comparison to the surface covered with types III and IV, and the spread is consequently very great. Only in places where there are many grasshoppers, i.e., where vegetation types I and II lie close to types IV and V, can this shift be clearly demonstrated, as is the case, for example for Quadrats 2, B, 3, 4, and D.

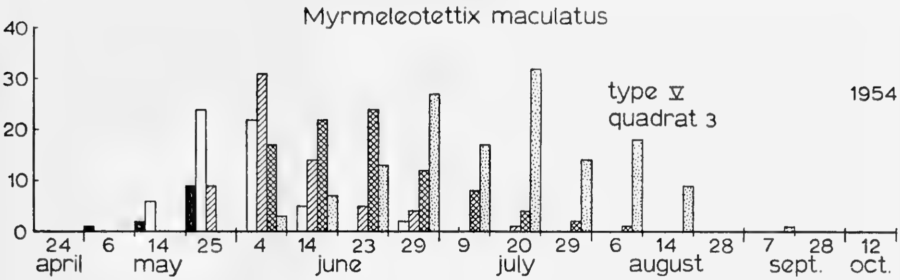
Later in the season, when mostly only adults are present, the insects disappear

Table 24. Numbers of adults of *M. maculatus* on a number of quadrats belonging to types I and V in 1953, 1954, and 1955.

Type	I		V			I		V			I		V	
Quadrat	9	2	3	4		9	2	3	4		9	B	2	4
1953					1954					1955				
23.VI	—	1	2	13	4.VI	—	—	3	1	23.VI	—	1	3	—
1.VII	—	—	12	17	14.VI	—	2	7	3	27.VI	—	—	7	2
9.VII	—	2	6	4	23.VI	—	9	13	7	5.VII	—	2	15	1
15.VII	—	6	10	6	29.VI	—	6	27	18	11.VII	3	1	15	4
23.VII	1	3	10	7	9.VII	—	5	17	12	25.VII	1	3	14	7
3.VIII	—	7	4	3	20.VII	—	25	32	14	11.VIII	2	—	12	3
10.VIII	3	4	3	5	29.VII	—	11	14	24	23.VIII	—	2	8	2
17.VIII	2	3	2	3	6.VIII	—	7	18	7	6.IX	8	7	7	—
26.VIII	3	8	—	1	14.VIII	—	23	9	—	3.X	6	13	1	—
31.VIII	4	5	1	—	28.VIII	—	13	—	—	20.X	—	3	1	—
7.IX	3	3	—	—	7.IX	5	13	1	—					
14.IX	—	1	—	—	28.IX	3	2	—	—					
24.IX	6	1	—	—	12.X	1	1	—	—					
2.X	1	2	—	—										
17.X	1	—	—	—										
16.X	2	—	—	—										
27.X	—	—	—	—										



Graph 1. *Myrmeleotettix maculatus.* Abundance of the various stages on the sampling dates. Absciss: dates on which the samples were taken; ordinate: number of specimens. Further explanation in text. Continued on next page



Graph. 1. Continued from p. 410

from the dense, herb-rich vegetations. An increase in the numbers of adults in the less dense vegetations is difficult to demonstrate, because in this period the density of the insects has already passed its maximum and the spread is again very great. It was nevertheless striking that, for instance, in Quadrat 9, there was a distinct increase in the number of adults. This Quadrat was located at a distance of about 30 metres of type V vegetation. For purposes of illustration, Table 24 gives the numbers of adults found on type I and type V quadrats in 1953, 1954, and 1955. Graph 1 shows the variations in population in 1954 in a number of quadrats belonging to types I—V, also for illustrative purposes.

The distribution of *C. biguttulus*

As has already been said nymphs of *C. biguttulus* were found to hatch in vegetation types I—V. The majority, however, hatched in the very thin vegetations of type I, particularly where this type lay in the vicinity of types V and VII.

The numbers of insects of this species observed in the terrain were consistently small. In 1955 the numbers were so small that conclusions can barely be drawn. The largest numbers (63 nymphs) were found on 5 July, 1955 (on 23 quadrats measuring three sq.m each).

If, as for *M. maculatus,* we compare the total numbers of nymphs of each of the four instars and the adults found on the quadrats of each type of vegetation during the season in 1954, a general picture of the variation in numbers is again apparent. The figures are given in Table 25.

Table 25. The total numbers of nymphs and adults (a) of *C. biguttulus* found on the quadrats of each type of vegetation during the entire season in 1954.

Instar	1	2	3	4	a	No. of quadrats sampled
Type I	48	28	3	2	4	5
Type I	79	38	8	2	11	2
Type II	17	5	2	1	1	3
Type III	119	91	16	6	11	8
Type IV	105	97	35	20	35	9
Type V	34	48	59	40	39	8
Type VI	18	43	57	29	31	11
No. of samplings	10	10	9	9	10	

Table 26. Numbers of nymphs and adults (a) of *C. biguttulus* on seven quadrats of type I and three quadrats of type II and on Quadrats 2 and 11 of type I in 1954.

No. of quadrats	7					3					2					11				
Type	I					II					I					I				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
24.IV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.V	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
14.V											11	2	—	—	—	16	—	—	—	—
25.V	31	3	—	—	—	3	1	—	—	—	9	2	—	—	—	5	—	—	—	—
4.VI	60	14	2	—	—	5	1	—	—	—	7	2	1	—	—	16	3	—	—	—
14.VI	16	17	3	—	—	6	1	—	—	—	1	4	1	—	—	3	5	—	—	—
23.VI	4	14	1	—	—	—	2	—	—	—	2	8	1	—	—	—	2	—	—	—
29.VI	4	9	1	—	—	2	—	—	—	—	2	4	1	—	—	2	1	—	—	—
9.VII	—	4	1	—	—	1	—	—	—	—	—	1	1	—	—	—	1	—	—	—
20.VII	3	2	2	—	—	—	—	1	—	—	3	1	2	—	—	—	1	—	—	—
29.VII	1	1	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—
6.VIII	—	—	1	2	1	—	—	—	1	—	—	—	—	1	—	—	—	1	—	1
14.VIII	—	—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
28.VIII	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7.IX	—	2	—	—	5	—	—	—	—	1	—	—	—	—	2	—	—	—	—	1
28.IX	—	—	—	1	5	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—
12.X	—	—	—	—	4	—	—	1	—	—	—	—	—	—	2	—	—	—	—	—

In this table a correction has been applied for the first instar on the five type I quadrats, because of the partial loss of 14 May, 1954 sampling (p. 398). The numbers of the first instar missed on type I vegetation are estimated to be $^1/_3$ of the numbers observed during the other samplings.

Quadrats 2 and 11 were sampled on 14 May and the data from these quadrats are given separately in the table because by far the largest numbers were found on these two quadrats. The numbers of the first to fourth instar decrease strongly in vegetation types I and II, the average figures per quadrat in type I being 1.81, 0.94, 0.17, 0.06, and in type II 0.56, 0.17, 0.08, and 0.04. These figures clearly reflect the limited density.

In the type III tussock vegetation and the type IV herb-rich vegetation, the numbers also drop during development, but not with the initial rapidity found for the two other types. For type III the average figures are 1.50, 1.14, 0.22, and 0.08 and for type IV 1.16, 1.08, 0.43, and 0.25 nymphs per quadrat respectively. In the dense, low herb-rich vegetation of type V and the dense, high grass cover of type VI, very few nymphs of the first instar were found initially, but the numbers increased with the more advanced instars. Per quadrat the average figures for type V are 0.42, 0.60, 0.82, and 0.58 and for type VI 0.16, 0.40, 0.58, and 0.29 nymphs respectively.

Comparison of these values indicates that in the types I and II vegetations the numbers of nymphs drop more rapidly during development than in types III and IV and that there is an initial rise in types V and VI, followed by a drop.

As for *M. maculatus,* we may state that in addition to mortality there will be an effect due to migration from the microclimate of vegetation types I and II (where conditions tend to become extreme in the course of the early summer) to vegetations that offer more protection, i.e., types III through VI. The fact that migration is not noticeable in types III and VI may be explained on the basis of the fact that both the latter types of vegetation constitute an appreciably larger proportion of the terrain than the former. The spread is consequently very great.

The data for the individual quadrats will not be discussed because the numbers are so low, especially those for the older stages, but the general tendencies in the individual types will be evaluated.

Types I and II. Table 26 gives the total numbers of nymphs of all instars and the adults found on the 1954 sampling dates on seven quadrats of type I and three quadrats of type II. Table 29 gives the same data for seven type I quadrats in 1955. These tables show that the quadrats with a very thin cover are populated principally by nymphs of the first and second instar, the older instars being found only in small numbers. Beginning in July, this species has almost disappeared from these quadrats. Adults are not seen on them until the end of August, although in 1954 they were seen on 29 June and in 1955 on 11 July, during field sampling.

Quadrats 2 and 11 showed the largest numbers in 1954 in comparison with the other quadrats of the same type. The location of these quadrats is exceptional, next to a hawthorn hedge and creeping willow shrub (see for *M. maculatus* p. 403) in which and beside which adults of *C. biguttulus* were seen throughout the sum-

Tables 27 and 28. Number of nymphs and adults (a) of *C. biguttulus* on quadrats belonging to different types in 1954.

Table 27.

No. of quadrats	8					9				
Type	III					IV				
Instar	1	2	3	4	a	1	2	3	4	a
24.IV	—	—	—	—	—	—	—	—	—	—
6.V	—	—	—	—	—	1	—	—	—	—
25.V	22	—	—	—	—	14	3	—	—	—
4.VI	33	14	1	—	—	40	5	1	—	—
14.VI	45	24	—	—	—	32	17	1	—	—
23.VI	15	34	1	—	—	14	35	2	—	—
29.VI	2	10	—	—	—	2	20	5	—	—
9.VII	2	8	5	1	—	2	7	13	3	—
20.VII	—	2	2	2	—	2	5	7	6	—
29.VII	—	1	4	1	—	—	3	3	6	1
6.VIII	—	—	1	1	3	—	1	3	2	2
14.VIII	—	—	2	—	1	—	—	2	2	4
28.VIII	—	—	—	1	5	—	2	—	2	11
7.IX	—	—	—	—	1	—	—	—	—	13
28.IX	—	—	—	—	1	—	—	—	—	3
12.X	—	—	—	—	2	—	—	—	—	1

Table 28.

No. of quadrats	8					11				
Type	V					VI				
Instar	1	2	3	4	a	1	2	3	4	a
24.IV	—	—	—	—	—	—	—	—	—	—
6.V	—	—	—	—	—	—	—	—	—	—
25.V	10	3	—	—	—	6	1	—	—	—
4.VI	12	15	—	—	—	2	3	—	—	—
14.VI	7	18	4	2	—	—	6	3	—	—
23.VI	1	17	7	2	—	7	10	10	2	—
29.VI	2	12	12	2	1	1	6	12	—	1
9.VII	4	5	16	4	3	2	17	14	4	—
20.VII	1	3	10	15	5	—	1	10	1	—
29.VII	—	1	3	4	6	—	—	5	5	—
6.VIII	—	—	—	7	2	—	—	2	6	2
14.VIII	—	—	1	5	9	—	—	—	1	3
28.VIII	—	—	—	1	6	—	—	—	—	11
7.IX	—	—	—	—	5	—	—	—	—	7
28.IX	—	—	—	—	4	—	—	—	—	6
12.X	—	—	—	—	1	—	—	—	—	1

mer. This species also showed the highest numbers on Quadrat 2 in 1955. The vegetation along the edge of low shrubs apparently provides a very favourable habitat for this species.

Types III and IV. Tables 27 and 30 give the results of the counts in 1954 and 1955 in the same way as the tables for types I and II. Type III was not studied in 1955. First and second instar nymphs predominated on the quadrats of both types. Here again the numbers of the third and fourth instar nymphs are distinctly lower. Adults appeared first at the beginning of August in 1954 and the end of August in 1955.

Types V and VI. Tables 28 and 31 give the results of the counts in 1954 and 1955. First instar nymphs were observed on these quadrats too. In comparison with the figures for the other types of vegetation, the numbers in type VI are appreciably lower.

Experiments concerning the choice of oviposition substrate have shown that the uninterrupted vegetation and the insulating layer of dead grass are not suitable for oviposition (Lensink, 1962). In the high, dense grass vegetation an egg pod of *C. biguttulus* was occasionally found in old molehills (which occur here and there in low-lying spots), and this explains the observation of newly-hatched larvae of this species in this type of vegetation.

In 1954 nymphs or adults were found throughout the whole season in both the low dense (V) and the high dense (VI) grass vegetations. The numbers of the second, third and fourth instar are higher than that of the first instar, indicating migration from the less dense vegetation in which the larger numbers of the first instar are found. This is also apparent from the totals of all the quadrats per type.

This migration is hardly noticeable for 1955 in the tables. It should be remarked here that in that year the grass cover of types V and VI showed a rapid growth early in the summer in comparison with 1953 and 1954, so that the structure was unusually dense, particularly in type VI. Migration reached only the edges of these vegetations. The same phenomenon was observed in Quadrats D and 4, located in the same area along the hawthorn hedge as Quadrat 2.

No reduction in the numbers of insects in these dense types of vegetation, such as that found for *M. maculatus* in type V, was seen for this species. Fewer specimens were seen and heard towards the end of August in the edges of low creeping willow shrubs. This could not be demonstrated by sampling because the densities had already become very low. These observations point to a shift to more open vegetation, which is also expressed in the data for the quadrats of the first four types of vegetation at the end of the season and the large numbers of newly-hatched larvae in this types in spring.

A comparison of the numbers of adults found on the various dates of sampling in the quadrats of the various vegetation types fail to explain this shift conclusively.

Summary. In the period during which *C. biguttulus* occurs in the terrain in which the investigation was carried out, we see the following:

Tables 29, 30, and 31. Numbers of nymphs and adults (a) of *C. biguttulus* on quadrats belonging to different types in 1955.

Table 29						Table 30					Table 31									
No. of quadrats	7					6					3					6				
Type	I					IV					V					VI				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
25.IV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
29.IV	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.V	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20.V	16	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
30.V	10	—	—	—	—	10	—	—	—	—	—	—	—	—	—	2	—	—	—	—
6.VI	15	6	—	—	—	7	2	—	—	—	14	—	—	—	—	2	—	—	—	—
16.VI	24	7	2	—	—	3	4	—	—	—	13	1	1	—	—	—	—	—	—	—
23.VI	12	10	3	—	—	6	8	—	—	—	2	4	—	—	—	—	—	—	—	—
27.VI	4	8	3	1	—	6	5	1	—	—	2	5	3	—	—	—	2	—	—	—
5.VII	5	17	10	2	—	5	8	3	—	—	4	8	—	2	—	—	1	1	—	—
11.VII	—	7	—	—	—	1	14	4	1	—	2	2	4	—	2	2	2	1	1	—
25.VII	—	1	1	5	—	—	6	1	2	—	—	—	3	6	—	—	1	1	5	2
11.VIII	—	—	1	1	—	—	—	—	4	—	—	—	—	3	3	—	—	—	5	11
23.VIII	—	—	—	—	1	—	—	—	2	4	—	—	—	1	3	—	—	—	—	8
6.IX	—	—	—	—	3	—	—	—	—	6		—	—	—	9	—	—	—	—	7
3.X	—	—	—	—	9	—	—	—	—	6	—	—	—	.	5	—	—	—	—	—
20.X	—	—	—	—	9	—	—	—	—	1	—	—	—	—	3	—	—	—	—	1

(a) The insects hatch in all types of vegetation, but the largest numbers hatch in type I where it borders on type V or type VI or along the hedges locally bordering the terrain and beside growths of creeping willow (VII);

(b) During development the numbers of nymphs in types I and II decrease and few or no specimens of older instars occur in these types during the summer; a decrease is obvious in types III and IV, although during the summer older instars do occur, albeit in limited numbers; in types V and VI in 1954 an increase in the numbers of the second and third instar was observed in relation to the numbers of nymphs hatched in this type of vegetation; in 1955 this increase was not observed in type VI (probably as a result of the very rapid growth of the vegetation which became dense very early in the season);

(c) Adults were not found in the quadrats of types I, II, III, and IV until late in the season (at the end of August) in 1954 and 1955; in the remaining quadrats in both dense vegetation structures they were found from their first appearance in the field until the period of the night frosts in October.

Results. The investigation into the distribution of *C. biguttulus* again showed that incidental observations are insufficient to establish the occurrence of the species from egg to adult. And shifts occur for this species also. The oviposition sites are located in entirely different parts of the field than are the places in which the adults live.

There is distinct migration towards the dense, herb-rich growths and grass vegetations. The numbers of adults are limited and they are found primarily in the denser vegetations. Only later in the season do they occur elsewhere, in the types I—IV vegetations. These latter insects could not have developed from a locally present population, so they must have shifted from the more dense to the less dense vegetation.

The distribution of *C. albomarginatus*

The investigation into the hatching sites of *C. albomarginatus* showed that the first instar was present in all the vegetations of the terrain. Since the nymphs are not very mobile during the days immediately following hatching, it may be assumed that they had hatched where they were found and that they later spread out from these hatching sites. The largest numbers of older nymphs were found in the denser grass vegetations, in 1953 and 1954 especially in types V and VI and in 1955 especially in type IV.

Tables 32 and 33 give the figures for the nymphs and adults in 1954 and 1955. The "14 May, 1954" correction (p. 398) was applied to Table 32. The numbers of nymphs of the first instar in types V and VI were augmented by 50 on the basis of the data obtained from the 22 quadrats which could be sampled on 14 May.

In both 1954 and 1955 there were few nymphs and adults of this species on the very thinly-covered places (types I and II). In 1954 the numbers were much larger in type III, although they rapidly decreased. The figures for the first to the fourth instar were 1.52, 1.23, 0.08, and 0.02 nymphs per quadrat respectively.

Table 32. The total numbers of nymphs and adults (a) of *C. albomarginatus* found on the quadrats of each type of vegetation during the entire season in 1954.

Instar	1	2	3	4	a	No. of quadrats sampled
Type I	11	2	2	0	0	7
Type II	3	3	0	0	0	3
Type III	73	69	6	2	4	8
Type IV	183	81	21	10	51	8
Type V	100	86	33	26	25	9
Type VI	233	509	489	475	436	11
No. of samplings	6	7	9	10	12	

Table 33. Same observations as Table 32, but in 1955.

Instar	1	2	3	4	a	No. of quadrats sampled
Type I	37	35	13	5	3	7
Type II	10	3	0	0	1	1
Type III	—	—	—	—	—	—
Type IV	280	210	46	17	61	6
Type V	8	24	12	14	11	3
Type VI	7	45	52	84	118	6
No. of samplings	7	7	7	4	8	

Larger numbers were initially found for the first instar in type IV. In 1954 the numbers of the older nymphs decreased rapidly, i.e., from the first to the fourth instar the averages were 3.81, 1.45, 0.29, and 0.13 nymphs per quadrat respectively. In 1955 the decrease took place only after the second instar. This undoubtedly related to the prolonged cold spring. The average figures were 6.67, 5.00, 1.09, and 0.71, respectively. More adults occur in this type of vegetation than in the three previously mentioned types.

No large numbers of this species were found in type V in 1953, 1954, and 1955. The figures for the first to fourth instar in 1954 were 1.85, 1.36, 0.48, and 0.29 and in 1955: 0.38, 1.14, 0.57, and 1.16. In the terrain this vegetation type is found beside hedges and low shrub, surrounded by a thin grass cover and constitutes only a small proportion of the terrain.

The numbers of nymphs found in type VI show the most interesting variations: the average figures in 1954 were 3.54, 6.60, 4.94, and 4.74 nymphs per quadrat respectively, and in 1955: 0.17, 1.07, 1.24, and 3.50. In both years a distinct increase in the numbers of the second instar was observed, caused by migration from less dense vegetation. The numbers of the older instars are much larger than in types I—V.

Types I and II. Very few nymphs and adults of this grasshopper species occur in the vegetations with a broken or unbroken moss cover and a very thin grass and herb cover. The numbers of insects on the quadrats with these growths are given

Tables 34, 35, and 36. Numbers of nymphs and adults (a) of *C. albomarginatus* on quadrats belonging to different types in 1954.

Table 34						Table 35					Table 36									
No. of quadrats	10					8					4					Quadrat 6				
Type	I and II					V					VI					VI				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
24.IV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.V	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
14.V	2	—	—	—	—											29	1	—	—	—
25.V	11	4	—	—	—	38	27	—	—	—	20	41	7	2	—	47	21	—	—	—
4.VI	2	1	—	—	—	11	40	8	—	—	9	49	11	1	—	21	83	8	—	—
14.VI	1	—	1	—	—	2	16	14	3	—	1	42	29	13	—	1	5	53	30	4
23.VI	—	—	—	—	—	—	1	5	8	—	—	1	35	22	1	—	35	79	34	4
29.VI	—	—	—	—	—	—	1	1	6	1	—	3	24	31	11	—	22	52	52	7
9.VII	—	—	—	—	—	—	1	4	2	4	—	1	1	26	10	—	7	37	68	37
20.VII	—	—	—	—	—	—	—	—	5	6	—	—	—	9	26	—	—	7	58	86
29.VII	—	—	—	—	—	—	—	—	—	5	—	—	—	7	19	—	—	2	20	43
6.VIII	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	—	—	1	2	20
14.VIII	—	—	—	—	—	—	—	—	—	2	—	—	—	1	4	—	—	—	2	18
28.VIII	—	—	—	—	1	—	—	—	—	1	—	—	—	—	4	—	—	—	—	11
7.IX	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	8
28.IX	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Tables 37 and 38. Numbers of nymphs and adults (a) of C. *albomarginatus* on quadrats beloging to different types in 1954.

Table 37										Table 38										
No. of quadrats	6					Quadrats 39 and 44					7					Quadrat 5				
Type	III					III					IV					IV				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
24.IV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.V	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
14.V																15	—	—	—	—
25.V	9	5	1	—	—	46	13	—	—	—	10	5	—	—	—	82	6	—	—	—
4.VI	12	15	1	—	—	1	24	3	—	—	3	8	—	—	—	33	10	1	—	—
14.VI	1	3	2	—	—	4	7	—	1	—	1	4	1	1	—	8	14	3	—	—
23.VI	—	1	—	—	—	—	—	1	—	—	—	1	—	—	—	—	2	3	1	—
29.VI	—	—	—	—	—	—	—	1	1	—	—	—	1	—	—	—	—	5	—	—
9.VII	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	4	2	—
20.VII	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	1	3	—
29.VII	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
6.VIII	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	3
14.VIII	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19
28.VIII	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	13
7.IX	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	6
28.IX	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
12.X	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2

in Tables 34 and 39, from which it can be seen that neither type provides a suitable habitat. Only a small number of nymphs hatch there and the numbers of older instars and adults are small to very small.

More of the second and third instar occurred in 1955 than in 1954. If it may be assumed that the developing nymphs in these vegetations migrate in response to extreme microclimatological conditions occurring in the early summer and the absence of adequate shelter, the prolongation of this migration over a longer period in 1955 may be attributed to the relatively low temperatures in the early spring and early summer of that year, as a result of which extremely high temperatures did not occur until later in the year.

In 1955 adults first were found after the middle of August. In 1953 and 1954 the adults found on all of these quadrats were also first seen only after the middle of August. If migration occurred from the denser to the less dense vegetation, it would explain these small numbers. For the total number of adult insects in the field is in the process of decreasing strongly in the middle of August, while almost all the quadrats of both types are located at a distance of 50 metres from the growths in which the most adults live during the summer.

Type III. In the quadrats covered with vegetations in which tussocks of *Festuca ovina* dominate heavily, the distance separating them from a high, dense grass cover (type VI) plays an important part in determining how many of this species are present. Table 37 gives the results of the 1954 counts (no inventory was made of this type of vegetation in 1955). Quadrats 39 and 44 lie at a distance of five to ten metres from the edge of the dense vegetations, and the other quadrats are separated from them by more than twenty metres. The numbers are not very large, but the difference is obvious.

These vegetations are also hatching sites of nymphs which are rarely or never seen in them from the beginning of the third instar. Adults are also almost never seen. In 1953 they were seen in small numbers much later in the season; in 1954 and 1955 the figures were negligible.

Type IV. Nymphs of *C. albomarginatus* occur locally in this type of vegetation. Tables 38 and 40 give the data for 1954 and 1955, respectively. The quadrats with the most nymphs, including especially the first, second and third instars, lie in the vicinity of vegetations belonging to type VI in which especially adults are found in the summer (1954, Quadrat 5 and 1955, Quadrats 5, H, and J, in Tables 38 and 40, respectively). The other quadrats of this type are located more than 20 metres away of the edge of a high, dense grass cover. Only very small numbers of nymphs were seen on these quadrats.

In 1953 sampling was not begun before the second half of June, a time at which in all three years few nymphs were still present. The fourth instar was seen in small numbers; in 1953 and 1954 adults were seen during August on the sampled quadrats of this type. This is remarkable because the first adults were seen in the field as early as 20 June in 1953 and on 14 June in 1954. In 1955 the first adults were not seen in the field until 5 July, while they were found in type IV on 25 July during the sampling. Their late appearance in 1955 is attributable to the

Tables 39, 40, 41, and 42. Numbers of nymphs and adults (a) of *C. albomarginatus* on quadrats of different types in 1955.

Table 39						Table 40					Table 41					Table 42				
No. of quadrats	8					3					3					6				
Type	I and II					IV					V					VI				
Instar	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a	1	2	3	4	a
25.IV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
29.IV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.V	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20.V	11	1	—	—	—	32	—	—	—	—	1	—	—	—	—	—	—	—	—	—
30.V	24	1	—	—	—	74	13	—	—	—	6	1	—	—	—	4	1	—	—	—
6.VI	8	14	—	—	—	40	82	3	—	—	—	4	—	—	—	3	4	1	—	—
16.VI	4	10	3	—	—	22	83	7	—	—	1	8	—	—	—	—	11	3	—	—
23.VI	—	6	6	—	—	4	55	15	—	—	—	5	3	—	—	—	10	6	1	—
27.VI	—	4	1	—	—	1	14	12	—	—	—	3	3	2	—	—	14	16	13	—
5.VII	—	2	3	5	—	—	3	15	13	—	—	—	3	6	1	—	2	8	9	—
11.VII	—	—	—	—	—	—	—	4	5	—	—	—	2	6	2	—	—	18	48	15
25.VII	—	—	—	—	—	—	—	1	2	8	—	—	—	1	2	—	—	1	13	40
11.VIII	—	—	—	—	2	—	—	—	—	10	—	—	—	—	3	—	—	—	—	28
23.VIII	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	26
6.IX	—	—	—	—	1	—	—	—	—	5	—	—	—	—	3	—	—	—	—	7
3.X	—	—	—	—	2	—	—	—	—	5	—	—	—	—	—	—	—	—	—	2
20.X	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

retarded development of the nymphs caused by the low temperatures during the spring.

Since it is excluded (certainly in 1953 and 1954) that the adults developed from the first instars present on these quadrats in the spring, this must have been a case of migration from other, in this case denser, vegetation. The low numbers are explained by the fact that here, too, the population throughout the terrain is becoming reduced. In addition, the surface of the terrain covered with type VI vegetation is appreciably smaller than that covered with less dense vegetation types. In other words, the spread is very large here, so that the chances of finding adults later in the season in type IV, on the small numbers of quadrats are very small.

Type V. In this vegetation, very few nymphal stages and adults were seen in 1953 and 1955; in 1954 rather more were observed. This can be clearly seen from Tables 35 and 41, which give the numbers found on the various quadrats belonging to this type, in 1954 and 1955.

The adults were seen primarily in the summer months of July and August. Later, in September, they appear only sporadically. In view of the findings in the less dense vegetations, we may assume that the adults migrate out of type V vegetation during the month of August.

Type VI. During a large part of the season *C. albomarginatus* is found (sometimes in large numbers) in the high, dense grass cover of this type. This vegetation occurs in the lower, damp parts of the terrain, especially along hedges. In the lower parts the height of the grass cover is rather even, and large tussocks of grass alternate with a lower herb-rich cover. On the higher parts *Calamagrostis epigejos* dominates, forming an unbroken cover. At first, in winter and early spring, the grasses that form by far the most important part of this type of vegetation still lie flat on the thick layer of dead grass which covers the soil. During the spring, sparsely scattered blades of grass begin to shoot up. In May and June, however, when the grass is 30 to 40 cm above the dead layer, it forms a complete cover. In the time during which it flowers, and the flower stalks stick out above the cover, the vegetation often does not become higher because the wind tends to flatten it. This creates a thick mat of grass on the ground. In the lower parts of the terrain, herbs flower locally between the grass clumps.

Tables 36 and 42 give the numbers of nymphs and adults, as found from the various data of 1954 and 1955. Differences between 1953 and 1954 on the one hand and 1955 on the other, require separate discussion.

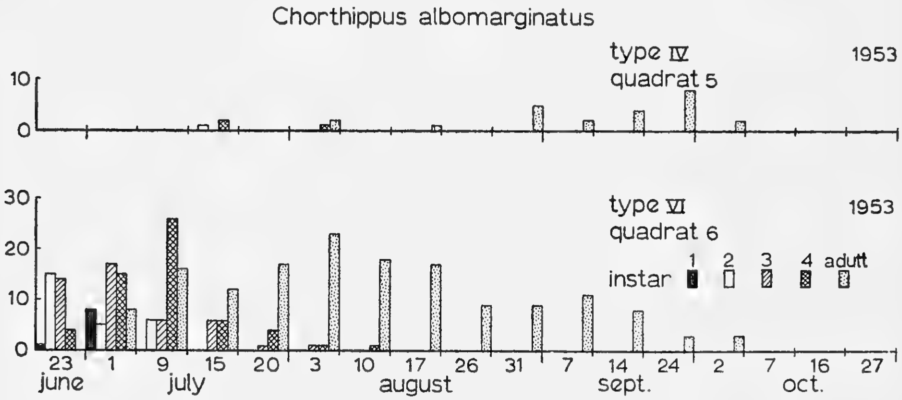
In 1954, newly-hatched larvae were found on all the plots. Except for Quadrat 6, their numbers were consistently very small. The smaller nymphs can still be found in the as yet rather open grass cover in May, although extreme care had to be used in counting a three sq.m quadrat. It seems to me unlikely that the small numbers of the first instar are to be attributed to errors in the sampling technique.

The numbers of the second and third instar are higher for almost all quadrats than the numbers of the first instar. Because mortality during development reduces the numbers of nymphs, this increase must be seen as the result of the arrival of nymphs from less dense vegetations to these high, dense growths of grass. The adults occur in these vegetations from the beginning of July on.

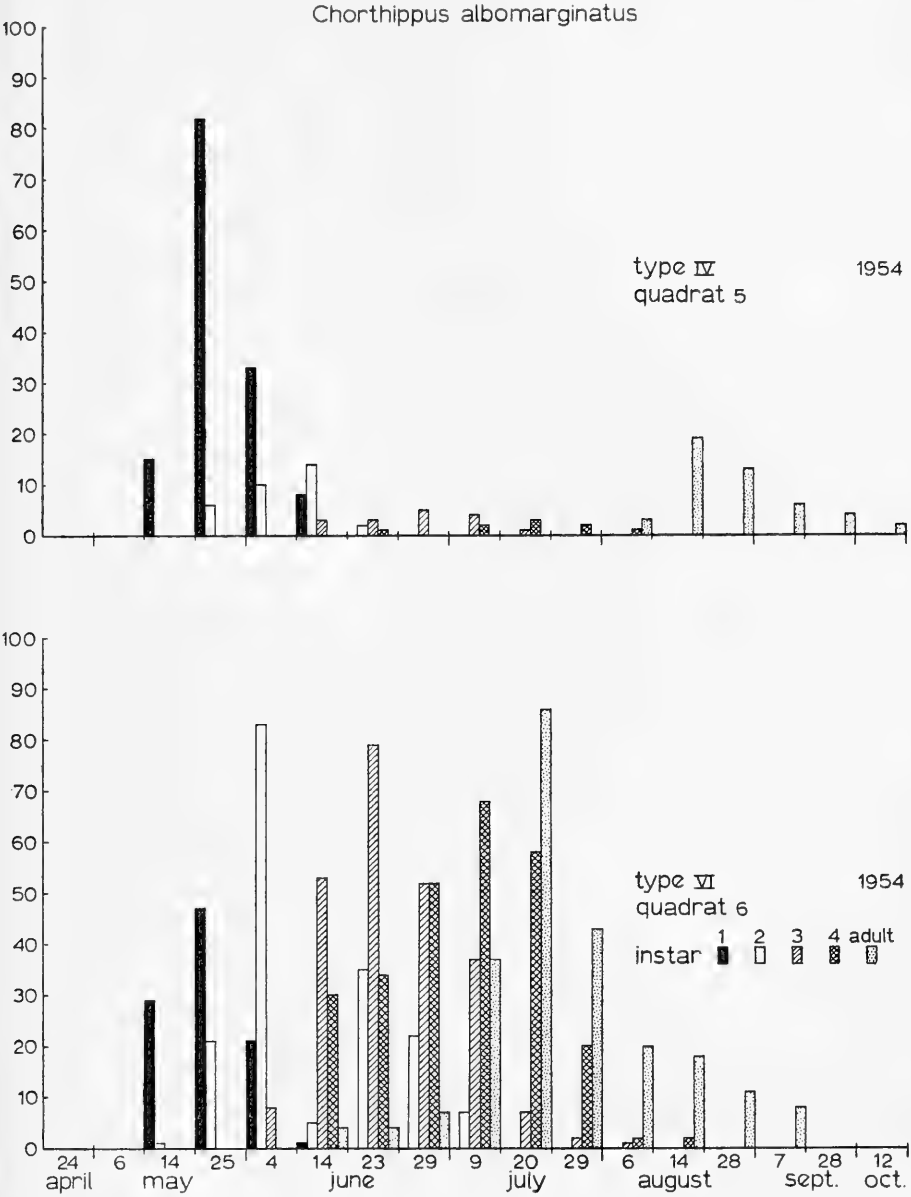
As for the type V quadrats (but here to a greater extent) the numbers drop sharply after the middle of August. Here, too, migration to the surrounding thin vegetations must be considered.

In 1953, before the start of sampling, numerous nymphs of this species were found in the high, dense grass cover. In this year, too, the adults were preponderantly found in this vegetation. After the end of August, however, the numbers of adults dropped sharply while an increase was found in other places. This phenomenon was clearly seen again in the part of the terrain in which Quadrats 6, F, G (type VI), and 5, H, and J (type IV) (Table 40) were located. During the years of the investigation, this area had very large numbers of this species. The high, dense grass cover is dominated by *Calamagrostis epigejos* which grew very high (70 cm). Quadrats 6, F, and G lay about one metre within the border of this vegetation. Quadrats 5, H, and J were sampled over two to three metres from the outer border of the above-mentioned vegetation, being themselves covered with a type IV vegetation. Graph 2 gives an illustration of the situation on these quadrats.

As early as 1953 it was evident that relatively large numbers of adults of *C. albomarginatus* occurred in Quadrat 6. The numbers dropped in the second half of August, while there was a distinct increase on Quadrat 5 in this period. In 1954, nymphs hatched in Quadrats 5 and 6. In 6, the numbers of older instars increased, but in 5 it dropped markedly. The numbers of nymphs were sharply reduced in 6 during August, but in 5 they increased sharply. In 1955 the numbers of quadrats were increased in order to collect more data on this phenomenon. In that year few or no nymphs of the first instar were observed in Quadrats 6, F, and G, although eggs had been observed during the winter. In all probability, this phenomenon may be attributed to the effect of the very low night temperatures in the spring of 1955. In comparison with 1954, the numbers of older nymphs

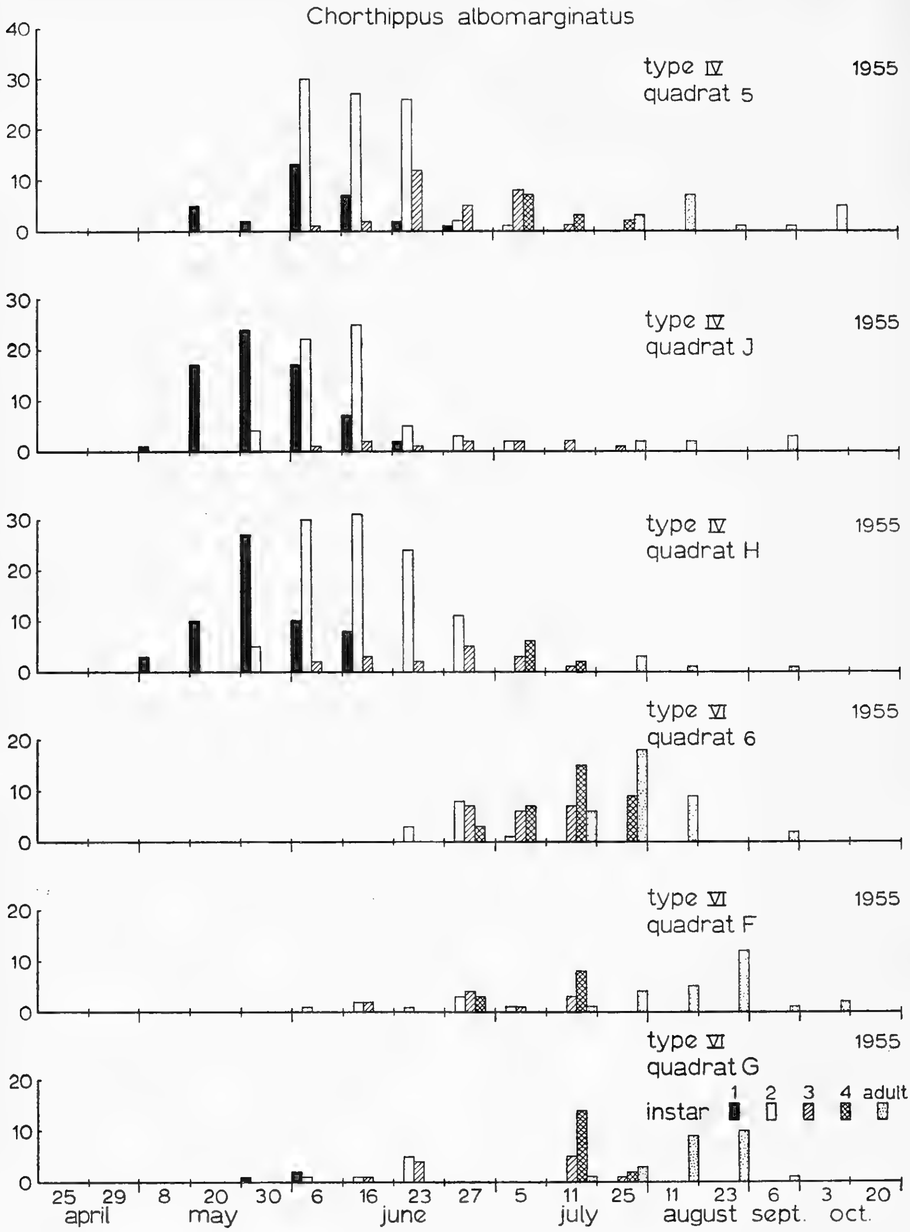


Graph 2. *Chorthippus albomarginatus*. Abundance of the various stages on the sampling dates. Absciss: dates on which the samples were taken; ordinate: number of specimens. Further explanation in text. Continued on next pages



Graph 2. Continued from p. 424

remained small, and development was greatly retarded. The numbers of adults were not large, and they disappeared almost entirely from the sampled quadrats during the course of August. In Quadrats 5, H, and J of type IV, nymphs hatched. Adults were found there rather late in the season, although they were first observed on 5 July, 1955 in the dense, high grass cover.



Graph 2. Continued from p. 425

We may conclude from these data that eggs of *C. albomarginatus* are laid in both the dense grass cover and in the thinner vegetations. In spring, the second and third instar nymphs migrate to the denser and more protective vegetations, where the largest numbers are concentrated during the summer and the females lay their eggs. Later in the season, in the second half of August and later, the adults migrate because the microclimatological conditions begin to deterioriate in the dense grass cover, shifting to the surrounding vegetations which are less dense and relatively warmer, in which they also oviposit.

The same phenomenon is seen in 1955, but the picture is somewhat blurred because as a result of the lower temperatures in the spring and early summer, migration was apparently less pronounced. The rapid growth of the grass, especially in type VI vegetation, also contracted the transition zone between the types of vegetation. In the summer of 1955, the largest numbers of adults were also found in this border zone.

Summary. If *C. albomarginatus* is followed during the season in this terrain, the following is observed:

(a) As soon as the eggs of this species hatch, the first instar nymphs are found in almost all types of vegetation;

(b) Very small numbers of nymphs hatch in vegetation types I and II; few are found in types III and IV except were they border on a high, dense grass cover in which many of the grasshoppers are seen during the summer; most of the nymphs hatch in types V and VI;

(c) In types I—IV, the numbers of nymphs are rapidly reduced during development, and few or no adults are seen during most of the summer;

(d) In types V and VI the numbers of the second and the third instar increase; in July and August the adults populate these types of vegetation;

(e) Later in the season (in general, starting in the middle of August) very small numbers of adults appear in types I, II and III, and somewhat larger numbers in type IV, while in the same period in types V and VI the numbers of adults drop or they disappear entirely.

Results. Investigation of the occurrence of *C. albomarginatus* in the various types of vegetation distinguished here shows that this species and its stages occur not only in the high, dense, relatively moist grass cover but also in the drier, thinner vegetation. The hatching of the larvae was observed in many types of vegetation.

During its development, this species was concentrated in the denser growths. The denser grass vegetations show an increase of the older instars. Adults are first observed late in the season in types I—IV, although they have long been present in the dense types of vegetation. There is evidently migration from the dense back to the less dense vegetation.

THE ACTIVITIES OF THE GRASSHOPPERS DURING THE DAY

Introduction

The preceding chapter has dealt with the activities of the various nymphal instars and the adults of the three species of grasshoppers during the season. The present chapter is concerned with the activities of the grasshoppers during the day.

Attention was drawn to the daytime activities of these insects because, especially for *M. maculatus,* it was observed that at particular places (Quadrats 2 and 11) there was a diurnal variation in the density of the population. What role is played here by the presence of a hedge or a shrub? Do the insects make use of such cover?

We were unable to examine such factors for *C. albomarginatus* and *C. biguttulus,* but a description of the way in which the insects live in the vegetation will serve to clarify the influence of a number of factors that affect the choice of the area in which to live.

The investigation of the activity of the grasshoppers during the day was carried out primarily in 1955. Observations were carried out in various types of vegetation under different weather conditions, sometimes several hours in duration. Attention was given to such behaviour as: eating, sunning, walking, jumping, courting, mating, egg-laying, and reactions to enemies. Special attention was given to the place and height at which the insects were found in the vegetation. All these activities are strongly dependent on the state of the weather. During rain or cold, cloudy weather the insects hardly move at all. With sunny, warm weather they are often extremely active, and are easily disturbed so that observation must be done unobtrusively. Observation was done from places where a number of grasshoppers could be seen simultaneously. The data collected for the three species will be discussed successively. The observations concern primarily *M. maculatus* and *C. albomarginatus. C. biguttulus* is extremely difficult to follow because especially the older instars and the adults are extremely active and sometimes range over large distances.

The diurnal activities of *M. maculatus*

During the morning this species shows almost no activity, in either the thin or denser vegetations, in the spring (May, June) and fall before 9:00 a.m. The nymphs and adults sit quietly on the ground or between the leaves of the herbs.

As the day becomes warmer and the solar radiation begins to penetrate the vegetation, the grasshoppers begin to show activity; they walk and eat and the males begin to stridulate. As the morning advances, these activities increase. The males pursue the females, and courting becomes intense. The nymphs and adults both seek favourable places from which to profit from the sunshine. Oviposition is observed only in places where favourable substrates (especially type I) border on a more protective vegetation, and these are also the most heavily populated parts of the field. During the afternoon, as the sun reaches a lower position and the angle of its rays reduces their penetration, the activity subsides. In the spring and fall, activity ceases between 4:00 and 5:00 p.m. and during the summer months between 6:00 and 7:00 p.m. Only once have I heard a soft singing in a type IV vegetation around 9:30 p.m., on an occasion of high temperature and little wind.

Thus on warm sunny days there is high activity throughout the day. On days with changeable weather, activity increases rapidly during the sunny periods, to drop as rapidly when a cloud passes over the sun. These changes are accompanied by fluctuations in the intensity of the song. It is of interest to mention here that during the eclipse of the sun in 1955 a distinct decrease in activity was observed. On dark days activity is very low. With a cloudy sky and temperatures around 17° C (measured in the weather shed at an altitude of two metres) only scattered soft song was heard and only a few eating insects observed. In this connection it may be mentioned that the activity of the grasshoppers held in cages in the laboratory showed a distinct increase when a lighted electric bulb was hung in the cage; singing and courting followed directly.

Because a sufficiently large population occurs throughout the season in vegetation types III, IV, and V, the diurnal observations were done systematically in them. With favourable weather conditions, more than 40 hours of observation were done in these types during various times in the season. Incidental observing was done during other weather conditions. The most active insects are the males. The nymphs and the females show little activity. They walk short distances, now in a sunny place and then again in the shadow of a grass tussock or the leaf of one of the many herbs. During the middle of the day, when the solar radiation penetrates deep into the vegetation, however, it is observed that many nymphs and adults are found not on the ground but some distance above it on a blade of grass or a leaf.

A large number of grasshoppers were observed for two minutes per insect. The place in which they were located in the vegetation under various weather conditions was noted. These observations clearly showed that with strong radiation, during the middle of the day, most of the animals were found at a height of one cm or more in the vegetation. With alternating sun and cloudiness and/or much wind, most of the insects were seen on the ground. Before 10:00 a.m. and after 4:00 p.m., the insects predominantly sat on the ground sunning themselves. These data, with the locally-measured temperatures, are given in Table 43.

Table 43.

Type of weather	Temperature 1 cm above ground	No. of insects	
		on ground	1 cm high or higher
strong sunshine	30° C	18	56
sunshine/cloudiness/wind	26—30° C	23	3
before 10 a.m. & after 4 p.m.	25° C	27	8

With bright sunlight, the temperature close to the ground is appreciably higher than a few cm above it. The behaviour observed proves the fact that these animals also show a vertical migration. The assumption that by this migration they attempt to avoid extreme temperature, is very probably correct. In the tussock vegetations (type III), in sunny weather, we found the most grasshoppers during sampling in the tussocks on the grass blades at about five cm above the ground. Here again the insects apparently avoid the high temperatures above the moss layer and choose milder places where the temperature lies only a few degrees higher than the air temperature above the grass. For purposes of illustration an excerpt of the field-notes of 24 June, 1955, may be included here; it serves as an example of the behaviour in type IV vegetation in sunny weather with a weak to

moderate N-NW wind and occasional high-altitude clouds. The observation time was between 11:10 and 11:45 a.m. A male *M. maculatus* was followed:
11:10 a.m. — with flank partially in the sun on the rosette leaf of *Hypochaeris radicata* — shifts with the head towards the sun / 11:15 — entirely in sun on leaf, remains immobile till 11:21 — turns with head towards sun, creeps into shadow of leaf of *Calamagrostis epigejos,* again turns half of flank into sunlight / 11:26 — walks ten cm towards shadow of tussock of *Festuca ovina* / 11:29 — walks, jumps fifteen cm further along the ground, sits half in shadow with head in direction of sun, against a leaf, turns flank towards sun / 11:32 — stridulates in this position, walks further, eats on shady side of *Festuca ovina* (sun clouded over), insect leaves shadow (sun returns, veiled), insect turns with flank in sun / 11:40 — (sun gone) head in sun, (sun back) sun on flank / 11:44 — creeps in shadow of clump of *Festica ovina*...... 11:45.

Similar observations were consistently made for nymphs and adults in vegetation types III, IV, and V. The most striking point is that they alternately sit in the sun and then in the shade of a leaf or stalk. No such opportunity is offered by the more open vegetations (types I and II), in which the environment is extreme and which are therefore almost unpopulated during the summer months.

In places where types I and II vegetations border on type V or VII (the most populated parts of the terrain), the behaviour is even more remarkable. In these very thin vegetations, in contrast to other parts of the field, nymphs and adults are seen regularly. A series of continuous observations were made in this kind of vegetation. One of the observation points chosen was a small terrain with a low *Salix repens* growth along a strip approximately one metre wide, of almost bare sandy soil. On the other shide of this strip there was a vegetation of type IV with transtition to type V. *M. maculatus* and a few *C. biguttulus* were preponderantly observed here, with an occasional specimen of *O. coerulescens.*

The observations were made in a plot two metres long and one metre wide of almost bare sandy soil for a total of six days, representing 58 hours (Tables 44 and 45), by two observers in a position to note all grasshoppers going or coming between types VII and IV, and the stretch of sand. The total observation time was divided into half-hour periods. For each period notation was made of the numbers of insects present on the strip as determined by the numbers which left or entered the strip, as well as their activities such as eating, oviposition, walking, etc. Notes were also made of the behaviour of the grasshoppers present in the *Salix* growth. Table 44 gives the numbers of males and females observed in the strip in the successive half-hour periods, the numbers of females which dug into the soil with their abdomens while searching for oviposition substrates, and the numbers of females which then laid eggs. The cloudiness in the various periods is indicated by the letters A—D.

The weather conditions on the different days were:
25 July — moderate NW wind, sunny, occasional high-altitude clouds, in the afternoon increasing cloudiness, after 6:30 p.m. very cloudy with some rain;
26 July — moderate NE wind, half overcast;
27 July — sunny, warm weather, clear, later in the day some cloudiness;

Table 44. Observations on activity of *M. maculatus.*

		♂	♀	b	o		♂	♀	b	o		♂	♀	b	o		♂	♀	b	o		♂	♀	b	o		♂	♀	b	o
7:30— 8:00	A	—	—	—	—	D	—	—	—	—		—	—	—	—	D	—	—	—	—	A	—	—	—	—					
8:00— 8:30		—	—	—	—	D	—	—	—	—	D	—	—	—	—		1	—	—	—		—	—	—	—					
8:30— 9:00	A	7	—	—	—		—	—	—	—		—	—	—	—	A	3	—	—	—	D	1	—	—	—					
9:00— 9:30		6	3	—	—	D	—	—	—	—	D						11	4	—	—		1	1	—	—	A				
9:30—10:00	A	9	4	1	1		5	2	—	—						A	10	5	2	—	D	12	4	1	—					
10:00—10:30		12	3	—	—	C	9	3	—	—	D	—	—	—	—		6	8	3	1		12	6	2	—	A	7	3	—	—
10:30—11:00	A	9	5	1	1		5	8	4	1		—	—	—	—	B	15	9	1	—	A	10	5	1	—		10	9	2	1
11:00—11:30	B	5	3	1	1	A	6	6	2	—	D	—	—	—	—		9	6	2	1		5	11	4	—	A	9	10	4	2
11:30—12:00		5	3	—	—		6	7	2	1		—	—	—	—	B	8	7	3	—	A	9	10	5	1		14	13	4	2
12:00—12:30	A	3	1	—	—	D	11	5	1	1	D	5	2	—	—		14	6	3	1		11	10	4	—	A	12	7	4	—
12:30—13:00		4	2	—	—		6	3	—	—						A	10	10	2	—	A	8	5	4	1		12	8	2	1
13:00—13:30	B	3	1	—	—	C	9	9	4	2	D						11	9	3	1		8	3	—	—		9	4	1	1
13:30—14:00		5	2	1	—		11	12	4	—		3	4	—	—	B	10	9	5	—	A	7	3	—	—	A	9	7	1	—
14:00—14:30	A	3	3	2	2	D	7	12	3	—	D	3	3	3	1		15	10	6	—		7	2	—	—	A	8	10	3	—
14:30—15:00		5	—	—	—		8	8	2	1		7	3	1	—	B	8	14	7	1	C	12	4	—	—		12	11	5	1
15:00—15:30	A	6	2	1	1	A	10	10	3	1	D	4	3	—	—		12	7	—	—		6	3	—	—	A	12	12	4	3
15:30—16:00		9	5	—	—		10	8	2	—		3	1	—	—	A	14	5	—	—	C	11	8	1	—		10	7	4	1
16:00—16:30	B	14	6	2	—	A	9	4	—	—	D	2	1	—	—		12	4	2	—		12	9	3	1	A	8	9	2	1
16:30—17:00		8	7	1	—		8	3	1	—		—	—	—	—	B	8	5	—	—	A	11	6	4	—		14	10	1	1
17:00—17:30	B	11	4	—	—	A	4	3	1	1	D	—	—	—	—		12	9	3	—		4	5	2	1	A	13	6	—	—
17:30—18:00		9	6	2	—		—	—	—	—		—	—	—	—	A	11	6	2	1	A	3	5	—	—		14	3	—	—
18:00—18:30	A	6	6	3	1		—	—	—	—							3	5	1	—		—	—	—	—	A	2	1	—	—
18:30—19:00		1	4	—	—		—	—	—	—						A	—	—	—	—		—	—	—	—		—	—	—	—
after 19:00		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—		—	—	—	—
	25—VII					28—VII					29—VII					30—VII					1—VIII					5—VIII				

b numbers of females boring with abdomen
o numbers of females laying eggs after abdominal boring

A clear sky
B hazy but sunny

C half overcast
D completely overcast

28 July — rather strong N-NE wind, initially cloudy, later half overcast; during the afternoon distant thunder showers followed by half to full overcast;
29 July — heavily overcast, somewhat less during middle of day, some sunshine later followed by heavy overcast and drops of rain; moderate N-NE wind;
30 July — heavy overcast before 8:00 a.m., light to heavy overcast throughout day, light N wind;
1 Aug. — initially cloudy, completely overcast between 8:30 and 10:00 a.m., followed by some variation in light NE wind;
5 Aug. — sunny, warm weather, some distant clouds.

The general picture of the diurnal activities can be sketched as follows. In the morning before 8:30 in sunny weather few or no insects are seen on the open sandy soil. Initially there is also no activity in the *Salix* growth. As the effect of the sun becomes stronger, the latter places begin to show signs of life, soft stridulating is heard and here and there the insects begin to eat the grasses.

Males soon arrive on the sand; they jump rapidly out of the plant growth, sometimes two or three at once, and then return just as rapidly. Once in a while a female is seen, often pursued by a number of males. In the shrub stridulating and courting increase. After 9:00 a.m. there are more insects on the sand. Most of the females are animals which, in view of the size of their abdomens, will shortly begin to oviposit. These females often are seen digging into the sand with their abdomens. Now and then this digging is followed by oviposition. The laying of eggs is confirmed by the size of the females' abdomens. The females then usually disappear again into the *Salix* or along its edges (oviposition in the shrub was not observed).

As soon as the sun is covered by clouds the male song ceases and the number of arrivals from the *Salix* on the sand also drops sharply.

In the middle of the day when the weather was very warm, the activity was concentrated under the *Salix* overhanging the sand. After 6:00 p.m. most of the insects return to the shrub, where they remain throughout the night.

On days when the sky was completely overcast (e.g., 29 July, 1955), few insects were seen on the sand. When the sun came out briefly during the afternoon or a little radiation penetrated the thin cloud cover, more insects appeared on the sand although activity remained low. Although oviposition was primarily observed on sunny days, egg-laying females were also seen on darker days when a number of days of dark, cold weather were followed by a day with higher temperatures. This is undoubtedly a case of increased drive, as a result of which oviposition is resumed even under less favourable conditions. During the six observation days, boring was seen 161 times, followed in 40 cases by oviposition.

It should be noted that the observations included in Table 44 do not directly reflect the movements from and to the surrounding vegetation; the course of the activities is presented as a static picture. Table 45, however, gives the numbers of adult insects, which in each of the half-hour observation periods on 30 July, 1955, went from the *Salix* and type IV vegetation to the sand and back. This table clearly shows that Table 44 gives an inaccurate picture of the local situation: the actual population is in motion, and it is quite clear that the presence of the denser vegetations in the immediate vicinity is of conclusive significance.

Table 45. Observations on activity of *M. maculatus*.

	From *Salix*-shrub to bare area	From bare area to *Salix*-shrub	From Type IV to bare area	From bare area to Type IV
7:30— 8:00	—	—	—	—
8:00— 8:30	1	—	—	—
8:30— 9:00	3	—	—	—
9:00— 9:30	10	—	2	—
9:30—10:00	4	3	1	—
10:00—10:30	2	—	—	2
10:30—11:00	7	2	4	2
11:00—11:30	3	5	1	—
11:30—12:00	6	2	2	1
12:00—12:30	6	4	4	4
12:30—13:00	7	7	2	1
13:00—13:30	7	11	1	1
13:30—14:00	4	1	3	1
14:00—14:30	5	3	3	4
14:30—15:00	12	4	5	2
15:00—15:30	5	4	1	—
15:30—16:00	2	1	6	3
16:00—16:30	2	3	5	—
16:30—17:00	5	—	2	—
17:00—17:30	4	6	4	1
17:30—18:00	5	3	—	1
18:00—18:30	2	4	—	—

A simular situation is found in the part of the terrain in which Quadrats 2 and C are located, where the behaviour of *M. maculatus* during the day was also studied. During sampling, this species was seen regularly. Closer observation showed that they came from the neighbouring vegetation during the morning and returned there during the evening. The activity was often great: there was a continuous procession from the bordering vegetation to the open vegetation and back again.

Concerning the factor of food, it may be noted that from among the large numbers of species of herbs and grasses, there is a strong preference for the grasses. Observations concerning the use of food plants were made during the study of the diurnal activities in particular, but also during other investigations. A list is given in Table 46 of a number of plant species predominating in the vegetation of the terrain studied, and the numbers of times *M. maculatus* was observed feeding on these plants is indicated.

The preference for grasses and *Carex arenaria* is clear, and *Festuca rubra* subvar. *arenaria* forms the main food of the grasshoppers under observation. It was striking that nymphs and adults preferred blades of grass lying on the ground to erect ones. Although especially the tips of the blades are gnawed off and eaten, grasshoppers were seldom seen in the erect grass. The wide, stiff leaves of *Calamagrostis epigejos* are also seldom used for climbing. The first instar fed at their hatching sites (types I and II), especially on *Phleum arenarium* which is abundant during the hatching period (April and May), and on *Festuca rubra* subvar. *arenaria.* It is striking that almost no herbs are consumed. When the insects have no other choice, for instance in the laboratory, herbs are also used as food. *Galium verum* var. *maritimum* is, however, consistently refused, and when a grasshopper gnaws one of its leaves, death follows rapidly. In this connection it is remarkable that for *O. coerulescens* it was observed several times in the field that these insects consume *Galium verum* var. *maritimum* without adverse effects as shown by the check.

The diurnal activities of *C. biguttulus*

The low population density of *C. biguttulus* in the terrain meant that only a small number of observations of the activities of this species could be collected. The study of the distribution of *C. biguttulus* indicated that in the period in which older nymphs and adults occur, they are to be found primarily in the dense grass cover (types V and VI). Most of the insects were found, however, in the grassy edges of the south side of the hawthorn hedges surrounding the terrain, but for technical reasons these grassy strips could not be quantitatively sampled. The observations of the activities of these insects were done mainly in these border strips, although they were greatly hampered by the thickness of the grasses.

Most of the diurnal activities of *C. biguttulus,* as for *M. maculatus,* were observed on warm, and especially sunny, days. The insects are unusually active under these conditions, particularly the adult males, which walk through the vegetation a great deal. In addition, and more than for the other two species, they are observed to make jumps for which they sometimes use their wings. In a few cases, males could be followed over long distances thanks to an aberration in song. In this way it was observed that on warm and sunny days they covered a distance of about 20 metres through various types of vegetation within a period of three hours, without using the wings in jumping. *C. brunneus* also shows this tendency to cover long distances often without flying. On a few occasions it was observed that an adult flew from a sun-warmed wall to a height of 50—100 cm above the ground and landed 10 to 15 metres away in a hedge, from which a new flight soon followed.

During the morning many of the insects sit sunning themselves. For this they often use wide leaves, particularly horizontal ones like those of blackberry bushes and the lowest branches of the hawthorn trees. With strong solar radiation they become more active and alternate between sitting in the full sunshine and in the shade provided by leaves and stalks.

A special form of migration was observed in part of the terrain shaded on its southern side in the afternoons by a wide, high hawthorn hedge. The vegetation consisted of a dense grass cover (type VI) shifting in the direction away from the hedge to a type V vegetation. In the morning, adults of *C. biguttulus* were seen in type VI vegetation. In the afternoon, when this vegetation was in the shade, the largest numbers of insects were to be found in the type V, which still lay in the sun. Observations at this place showed that as the shade extended over the vegetation, the insects avoided it as much as possible by shifting to sunny spots. This occurred for the most part by walking, but also with small jumps. This species is distinguished in its behaviour by being markedly more active than the other two species, which enables it to find the spots with the most sun.

The diurnal activities of *C. albomarginatus*

The activity of *C. albomarginatus* was studied in the most heavily populated parts of the terrain: the *Calamagrostis epigejos* growths which included Quadrats 6, F, and G. In this vegetation, observation is difficult because the grass is so thick and the grasshoppers can be seen only along the edges of the growth.

The activities were nevertheless studied within the vegetation, making use of a ladder placed over the grass. The series sampling showed clearly that in 1955 in this growth few insects were present, i.e., one to nine insects per square metre (on the sampled quadrats, while along the edges the number was estimated at at least fifteen per square metre).

The broad picture sketched for *M. maculatus* agrees in general with that for *C. albomarginatus.* The activity is highest with favourable weather conditions; in dark or rainy weather little movement is observed. Continuous observations were made in sunny weather in July and August, 1955 and give a picture of the insects activities in this vegetation during the day. Quantitative data are almost impossible to collect, however, because of the relatively few insects seen.

Before 9:00 a.m. little occurs in the grass cover. Most of the insects are found at a level just under the upper grass leaves at a height of 40—60 cm, which particularly in the middle form a dome above the space between the leaves and stems. Between 10:00 and 11:00 a.m. on the sunny side (SE) many insects were seen between the blades at a height of 10—20 cm above the ground. They sit with their heads pointing upwards sunning themselves, a few eating from the leaf. They are also observed on dead grass on the ground, and in the surrounding, less dense vegetation.

On the shady side (NW), however, none are found on the ground; they sit in the tops of the grass, sunning themselves and eating. Later in the morning courting occurs, but on the whole these insects are not very active. There is much less movement than is seen for *M. maculatus.*

The border areas which are shaded in the morning, now begin to receive more sun, and the insects move towards lower levels while in the now shaded parts most of them seek higher places between the grass blades. At about 3:00 p.m. the picture is the opposite of the morning situation. After 4:00 p.m. it is observed that on the side of the vegetation on which the sun shines, the nymphs and adults begin to climb higher in the vegetation. When the sun sinks lower, the leaves and stalks of the surrounding vegetation create a great deal of shade, and this probably explains the vertical migration. The grasshoppers which find themselves shaded by a leaf climb continually higher, consistently seeking the sunniest spots. When there is a lot of wind on the sunny side, most of the insects sit to sun themselves not on the outer side, but between the first rows of blades. Later in the day courting drops in intensity and more eating insects are seen. From this point activity decreases and the largest numbers are found high between the stalks.

The consistent search for the "sun" was successfully observed in an open space with a diameter of about 75 cm in the middle of the vegetation. The largest numbers were at first found high between the leaves, and then as the sun rose in the sky they went lower on the side exposed to the sun, and continued to choose the sunny side until later in the afternoon they were again found high between the tops of the plants.

The reactions to various weather conditions indicate that this species, too, is extremely sensitive to heat, and especially that due to direct radiation. As Stoutjesdijk (1961) demonstrates, in dense grass vegetations like the *Calamagrostis* growths mentioned here, the highest temperatures are measured at the level of the leaf-tips, and this is where during the entire day, in the summer months, the nymphs and adults of *C. albomarginatus* were observed. They migrate to lower levels only when there is a great deal of wind.

In irregular, dense vegetations the highest temperatures are measured in the layer of dead leaves on the ground. A comparable situation is encountered in our case, namely in the opening in the dense vegetation and along its edges where the dense grass cover is very irregular and shows a gradual transition to more open vegetation. Where the rays of the sun can penetrate to the soil, the highest temperatures are found on the ground. When this radiation is interfered with by shade from the surrounding dense grass cover, the highest temperatures are found at higher levels where the direct effect of the radiation is found. The nymphs and adults of *C. albomarginatus* consistently seek the warmest places in the grass cover, producing vertical migration along the edges and in open spaces of the dense grass cover.

For this species a few data were also collected concerning its choice of food in the field. The dense, high grass cover in which most of the observations concerning diurnal activity were made, is composed of a vegetation of *Festuca rubra* subvar. *arenaria* and *Carex arenaria,* dominated by *Calamagrostis epigejos.* Other grasses and herbs are poorly represented, including *Holcus lanatus, Poa pratensis* var. *humilis, Achillea millefolium, Plantago lanceolatum* var. *sphaerostachya, Vicia cracca* and *Rumex acetosa.* The 41 observations of eating habits in this vegetation are shown in Table 47.

The first two grasses, which form the principal mass, are the most frequently eaten.

In 1956 a number of nymphs were put in a cage which was placed over a piece of grass cover of type V vegetation. In this grass cover the predominating species were *Festuca rubra* subvar. *arenaria* and *Agrostis tenuis,* and *Calamagrostis epigejos,* and in lesser amounts *Carex arenaria, Galium verum* var. *maritimum, Achillea millefolium, Poa pratensis* var. *humilis, Cerastium arvense, Thymus pulegioides,* and *Lotus corniculatus* var. *ciliatus.* Twenty nymphs of the second to the fourth instar were observed within two hours; a total of 93 feeding observations were made (Table 48).

In this type of vegetation, too, only grasses were eaten, herbs were not touched.

A similar arrangement was used over a grass cover of type IV vegetation in which the herbs predominated more than in the above-mentioned cover. Forty feeding observations were made in two hours of observing (Table 49).

Here again the grasses are preferred. *Calamagrostis epigejos* was not eaten in

Tables 46—49. Numbers of feeding observations, for explanation see text.

Table 46	*M. maculatus*
Festuca rubra subvar. *arenaria*	261
Festuca ovina	19
Calamagrostis epigejos	7
Phleum arenarium	1
Poa pratensis var. *humilis*	0
Agrostis tenuis	13
Corynephorus canescens	0
Carex arenaria	28
Galium verum var. *maritimum*	0
Lotus corniculatus var. *ciliatus*	0
Thymus pulegioides	0
Leontodon nudicaulis	0
Hieracium pilosella	0
Achillea millefolium	1
Cerastium arvense	3
No. of feeding observations	333

Table 47	*C. albomarginatus*
Festuca rubra subvar. *arenaria*	23
Calamagrostis epigejos	16
Carex arenaria	1
Vicia cracca	1
No. of feeding observations	41

Table 48	*C. albomarginatus*
Festuca rubra subvar. *arenaria*	38
Agrostis tenuis	13
Calamagrostis epigejos	37
Poa pratensis var. *humilis*	5
No. of feeding observations	93

Table 49	*C. albomarginatus*
Festuca rubra subvar. *arenaria*	17
Agrostis tenuis	13
Festuca ovina	3
Carex arenaria	4
Plantago lanceolata var. *sphaerostachya*	3
Calamagrostis epigejos	0
No. of feeding observations	40

the observation period, but is very thinly distributed with few stalks in this cover and was therefore rarely encountered.

When the insects have a free choice, their food is chiefly the grasses and *Carex arenaria.* These grasses occur in almost the entire terrain. Herbs are apparently not considered as food even when they occur frequently in the vegetation. In the laboratory such herbs as *Lotus corniculatus* var. *ciliatus, Achillea millefolium, Hieracium pilosella,* and *Thymus pulegioides* are eaten when little or no grass is present. *Gallium verum* var. *maritimum* was consistently refused by *C. albomarginatus* when offered as food in the laboratory. When an occasional insect "nibbled" on a leaf of this plant, it died within 24 hours.

SUMMARY

(1) Aspects of the lives of three species of grasshoppers (*M. maculatus, C. biguttulus,* and *C. albomarginatus*) in their environment were investigated. These investigations were intended to provide a better understanding of the distribution of these species in the dunes of Voorne (The Netherlands). This distribution was seen as an aspect of the inter-relation of the animated and the inanimate world. This inter-relation can be considered in terms of the related quantities or in terms of the phenomenon of the relationship itself, in the sense of interaction between the factors.

The investigation described here was based on a number of selected quantities: the development of the vegetation with the change of the microclimate and the

development of the grasshoppers. A study was made of the influences which the inter-relationship of the quantities exercises on the distribution of the grasshoppers. This inter-relationship has a special expression in the occurrence of migration in many phases of the life of the insect, another indication that this inter-relationship is dynamic in nature.

(2) The technique consisted of a series of samplings in various types of vegetation distinguished according to structure. Each sampling reflects the situation at a given time. A series of these samplings throughout the year gives a picture of the modifications occurring in the distribution of the grasshopper population. In addition to the investigation of the distribution of the various immature stages of the insects, attention was also given to their activities during the day under various weather conditions and the influence of the microclimate. The essential points may be recapitulated here.

(3) The vegetation is for the grasshopper one of the most important and predominant factors in its environment. Variations in distribution, however, cannot be explained on the basis of dependence on the vegetation as food source because in the dune region the insects eat many species of plants and certainly the most frequently occurring species of the grasses. What the investigation showed especially clearly was that the structure of the vegetation plays an important part in the distribution observed. It was also seen that the characterization of the structure of the vegetation by means of the French-Swiss method of vegetation description was too limited. Seven structural types had to be distinguished in the present study. These types and the internal changes occurring in the course of the year and from year to year are described.

The various types of vegetation have a strong influence on the microclimate. Since both the vegetational structure and the macroclimate are subject to changes in the course of time, the microclimate will also vary continually.

(4) The distribution of the grasshoppers is determined in the first instance by the site of oviposition. The location of these sites was studied by field sampling during the time in which the nymphs hatch. This study showed that various influences are present, such as the distribution of the adults, and the choice of oviposition substrate in the preceding year. These influences and the influence of the combination of vegetation and microclimate on the egg, were expressed not only in the peculiar distribution of the hatching sites but also in the time at which the nymphs appeared in the various types of vegetation and the numbers of nymphs hatched there.

(5) The further distribution of the insects from the hatching sites over the field is distinctly affected by the development of the vegetation and events in the microclimate, which close interconnection is striking.

In general, it may be said that from spring to summer migration occurs from the less dense to the denser vegetations, a tendency observable in all three species.

Concerning two aspects, the microclimate and the demands made by the insects in the various immature stages on their surroundings, the following may be said. The first instars of *M. maculatus* and *C. biguttulus* are almost unable to find shelter against strong solar radiation, hail storms, etc., in vegetation types I and II. They migrate and we then see an increase in the numbers of the third and fourth instar in type V. In type V the microclimate is more clement and high temperatures do not occur; but the fertilized females require an oviposition substrate, causing a return to types I and II. In types III and IV, in which structural changes are less distinct, the insects find not only shelter in the shade of grass tussocks and between the herbs covering the ground, but also adequate opportunity to sun themselves. They are able to maintain themselves in this type of vegetation.

Nymphs of *C. albomarginatus,* hatched in types III and IV, leave this vegetation. At this time an increase in this species is seen in type VI.

(6) As an example of the influence of the macroclimate, the following may serve: As a result of the cloudy weather in the spring of 1955, the microclimatological conditions on plots with vegetation of types I and II were far less extreme than in the preceding year. We see in consequence that the insects remained much longer on these plots, another indication that these conditions are the primary factor under the influence of which the nymphs leave this type of terrain, and not, for instance, the food factor. The climatological conditions had an inhibitory effect on migration, but an activating effect on the growth of the vegetation. Consequently all types of vegetation were denser at the time of migration than in both preceding years, so that migration was more restricted than in 1953 and 1954. During both these years, only the edges of type V were populated by *M. maculatus* and *C. biguttulus.* This vegetation approached more closely the characteristics of type VI. *C. albomarginatus* was also found only in the border zone of type VI.

It may be concluded from this that the insects inhabit the same types of vegetation as in the preceding year, but their distribution over the inhabited terrain varies, and may do so from year to year.

(7) During the summer months the situation is as follows: *M. maculatus* and *C. biguttulus* are found seldom or never in types I and II, in small numbers in types III and IV, and in the largest quantities in type V. *C. albomarginatus* is found especially in type VI or in the dense grass borders of type VII; elsewhere the numbers are small. In this period the vegetation has reached its maximum growth, and it is thanks to the many horizontal leaves in type V that a "geophilic" insect like *M. maculatus* (and this holds to a certain extent for *C. biguttulus* as well) can live in this dense grass cover. In the dense, high grass cover, indeed, we find these species almost exclusively along the edges, while *C. albomarginatus* is able to move throughout this heavy cover.

Local variations from this situation are found in the distribution of *M. maculatus* and *C. biguttulus.* In a few spots covered with types I and II vegetation, individual specimens of these species were seen throughout the season, first nymphs of the various stages and later adults as well. This was possible because of the heavy grasshopper traffic between these terrains and the surrounding types V and VII vegetations. Observations during the day showed that on warm days many of the females search for a suitable oviposition site, which is rarely or never found in type V, and during this time they are pursued by males. These activities, however, are strongly dependent on the weather conditions. In dark, cold weather or in the early hours of the morning or evening, most of the insects are to be found in the denser grass cover. Only with increasing radiation does the activity increase and a varying number moves in and out of the vegetation. But also within a given type migration can be observed throughout the day. With strong sunshine it is seen that the insects make alternate use of sunny and of shaded, cooler spots.

As a result, we see that in their area the greatest numbers of individuals of *M. maculatus* and *C. biguttulus* are found where not only suitable oviposition sites but also suitable places in which to live occur in the immediate vicinity. In parts of the terrain comprising many square metres of suitable oviposition substrate, the population density is very low if no suitable places for the nymphs and adults are available in the neighbourhood. Where suitable type V places in which to live are found, *M. maculatus* is encountered only in places which border on an oviposition terrain. *C. biguttulus* is found much deeper in these growths; it is also far more active than *M. maculatus.*

(8) Later in the season, from the middle of August on, new changes take place in the distribution. In the open vegetations, increasing numbers of adults are observed, and in the denser types V and VI there is a distinct decrease (for *C. albomarginatus*) or even total disappearance (the other two species). In the first place, it seems self-evident to assume that with increasing age the adults make different demands on the environment (oviposition). In the second place, changes in the microclimate in the late summer period begin to play an important part. The continually lower position of the sun and the cooler nights accompanied by local mist clearly affect the denser vegetation in which the day and night temperatures are both lower than in July. In the more open vegetations the soil still reaches appreciable temperatures during the day and even during the night remains warmer than in the denser vegetation. In this period females are regularly seen almost ready for oviposition. They are then found in places where they have not been seen previously, as for instance in types I and II. The distribution of these females is a contributory factor for the distribution of the young insects in the spring. The late summer migration, however, is not so extensive that adults are found in all parts of the terrain with open vegetation. During October the last of the adults die.

DISCUSSION

(1) The preceding summary was given in order to bring out the peculiar features contributing to the picture of the distribution of the grasshoppers in a given area. This basis requires a still broader interpretation to include all these phenomena as a whole. The problem is to determine in what framework to place the picture which evolved from the investigation.

In discussing the relationship between organism and environment, I would like to take as my starting point the concept "habitat" as one of the frequently used ecological concepts. It is used by many investigators, but always formulated somewhat differently. The difficulty arises from the fact that there is a constant shift in emphasis from animal to environment and from environment to animal, while the interrelation between the two is often left very vague. Some authors use a "physiognomic areal concept" (see CARPENTER, 1956) in which the habitat is defined in terms of the character of the landscape or on the basis of an "environmental factors concept" which includes only selected factors (see CARPENTER,

1956) or, as proposed by CLEMENTS (1905): the habitat is "the exact equivalent of the term environment". PEARSE (1926) includes animal and environment in his definition of habitat: "there is some place where an animal system of activities finds an environmental system of activities". PARK (ALLEE et al., 1949) makes the relationship of the animal with its environment clearer by pointing out that the species of animal in its habitat has reached a "survival level". In its environment it has become "self-sustaining". The various definitions contain elements indicating that there is a tendency to place the inter-relationship between animal and environment more in the foreground. PEARSE, for instance, mentions the possibility of the animal to maintain "a reasonable condition of stability" in its existence. In this phrase, however, the inter-relationship is more assumed than made the keystone of the definition.

PEUS (1954) and BODENHEIMER (1958) see the relationship more sharply. PEUS proposes the concept "Oekologischer Umwelt" and BODENHEIMER more or less in agreement with PEUS, uses the concept "Ecoworld" to emphasize the connection somewhat more strongly. BODENHEIMER understands under this term: "the combination of all exogenous and endogenous factors, processes and organisms which have any relation — whether directly or not directly perceived — to the living species". And to avoid any misunderstanding of his meaning, he again clearly states: "The species itself is of course an integral part of this eco-world". Although not expressed directly, it is implied here that BODENHEIMER makes the integration of the quantities so central that the topographical aspect is neglected in his approach.

(2) The observations indicate that a study such as this cannot be limited to the simple notation of the places in which the animals occur, a technique which results in what is called a pattern or mosaic of the distribution. The actual situation in the field requires a somewhat different basis. The presence of the animal cannot be seen as simple presence, it must be seen as the representation of a situation belonging to a particular moment in a particular place. This approach introduces the character of a transitional situation, i.e., it assumes its significance when considered in the light of what has already occurred and what is to occur.

In addition to changes in distribution from year to year and within each year, from week to week and from day to day, there is also variation within each day which is closely related to the development of the vegetation and the microclimate and the physiological condition of the animal. The situation at the end of one year also determines the situation at the beginning of the next.

The complexity of the inter-relationship becomes clear as soon as the external factors seem to predominate in determining the course of events, as for instance in spring when the quantity of solar radiation is important for the hatching of the eggs, or when the extreme conditions of terrains of type I and type II are primarily responsible for migration to the denser vegetations. Then again it is the internal factors that are of dominant importance, for instance because the fertilized females have specific substrate requirements to lay their eggs or because the distribution within the vegetation is limited because of the nature of the behaviour or structure of the organs or locomotion.

It is clear from the foregoing that the distribution itself has a developmental process, for which a complex inter-relationship between internal and external factors is responsible. In the distribution of the insect, the nature and result of this interaction is expressed, which is to say that it provides the basis for drawing conclusions about the inter-relationship.

The concept "habitat" discussed above is inadequate to cover the inter-relationship, which is both functional and topographical in nature. To express both aspects in the inter-relationship more effectively, I would like to propose the concept "vital space". The "vital space" is the totality of relationships in which animal and environment are involved with each other, and one which is subject to change from moment to moment. We have to do with a complex of relationships between quantities in which the relationships are expressed in "actions". These "actions" can be deduced from aspects of the activities of the animals, and this describes the character of their vital space.

ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to Prof. Dr. D. J. Kuenen for his encouragement and stimulating criticism during the completion of this work. I also wish to extend my thanks to Mr. J. J. Busch for the invaluable stimulation of his sustained interest in my work, and to Mr. E. van der Maarel, Dr. P. Smit, and Dr. Ph. Stoutjesdijk for their productive criticism. I am grateful to Mrs. I. Seeger for the translation of this paper in which its original character is retained, to Mr. J. G. M. Marquenie for the photographs, and Mr. N. Teegelaar for the preparation of the figures.

I am greatly indebted to The Netherlands Organization for Pure Scientific Research (Z.W.O.) for the support which made this field study possible. I wish to express my appreciation to the Board of the Foundation for Scientific Duneland Research for the hospitality extended to my wife and myself at the Weevers' Duin Biological Station at Oostvoorne between 1953 and 1955. I am also obliged to the Uyttenboogaart-Eliasen Stichting for a grant that made it possible to appoint an assistant in this work for six months.

The Nederlandsche Entomologische Vereeniging kindly accepted this paper for publication.

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Pl. 2. Landward dunes, the area of investigation

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Pl. 3. Vegetation types I, II, and V; the light area is type I, surrounded by type II, and at right rear is the border of type V. The hawthorn hedge can be seen in the background

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Pl. 4. Vegetation type III

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Pl. 5 Vegetation type VI

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